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► To cite this version:

Jérémy Cours, Lucas Sire, Sylvie Ladet, Hilaire Martin, Guillem Parmain, et al.. Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales. *Landscape Ecology*, 2022, 37 (8), pp.2025-2043. 10.1007/s10980-022-01453-5 . hal-03700534

HAL Id: hal-03700534

<https://hal.inrae.fr/hal-03700534>

Submitted on 7 Jun 2024








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Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales

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Published in *Landscape ecology*, vol. 37, 2022

Abstract

Context Many forest ecosystems around the world are facing increasing drought-induced dieback, causing mortality patches across the landscape at multiple scales. This increases the supply of biological legacies and differentially affects forest insect communities.

Objectives We analysed the relative effects of local- and landscape-level dieback on local saproxylic beetle assemblages. We assessed how classical concepts in spatial ecology (e.g., habitat-amount and habitat-patch hypotheses) are involved in relationships between multi-scale spatial patterns of available resources and local communities.

Methods We sampled saproxylic beetle assemblages in commercial fir forests in the French highlands. Through automatic aerial mapping, we used percentage of dead tree crown pixels to assess dieback levels at several nested spatial scales. We analysed beetle taxonomic, phylogenetic and functional diversity related to differing levels of multi-scale dieback.

Results We found that taxonomic, functional, and phylogenetic diversity of saproxylic beetle assemblages significantly benefitted from forest dieback, at both local and landscape scales. We detected significant effects in the multiplicative models combining local and landscape variables only for phylogenetic diversity. Increased landscape-scale dieback also caused a functional specialisation of beetle assemblages, favouring those related to large and well-decayed deadwood.

Conclusions Increasing tree mortality under benign neglect provides conservation benefits by heterogenising the forest landscape and enhancing deadwood habitats. Legacy retention practices could take advantage of unharvested, declining forest stands to promote species richness and functional diversity within conventionally managed forest landscapes.

Keywords: Scale of effect; Saproxylic beetles; Climate change; Forest decline; Drought; Disturbance legacy

Résumé

Contexte Beaucoup d'écosystèmes forestiers à travers le monde font de plus en plus face à des dépérissements causés par des sécheresses. Ces derniers augmentent l'apport d'héritage biologiques et affectent différemment les communautés d'insectes forestiers.

Objectifs Nous analysons les effets relatifs des niveaux de dépérissement aux échelles locale et paysagère sur les assemblages locaux de coléoptères saproxyliques. Nous avons évalué de quelle manière les concepts classiques d'écologie spatiale (e.g., les hypothèses de quantité d'habitat et de patch d'habitat) sont impliqués dans les relations entre les configurations spatiales multi-échelles des ressources disponibles et les communautés locales.

Méthode Nous avons échantillonné les assemblages de coléoptères dans les forêts de sapin de montagne sous gestion. À travers une cartographie aérienne automatique, nous avons utilisé le pourcentage de pixels de couronnes d'arbre mortes en tant qu'évaluation du niveau de dépérissement à différentes échelles spatiales emboîtées. Nous avons alors analysé la réponse des diversités taxonomique, fonctionnelle et phylogénétique aux différents niveaux de dépérissement multi-échelles.

Résultats Nous avons mis en avant que les diversités taxonomique, fonctionnelle et phylogénétique des assemblages de coléoptères saproxyliques ont significativement bénéficié du dépérissement forestier, tant à une échelle locale que paysagère. Nous n'avons détecté des effets significatifs dans les modèles multiplicatifs combinant des variables locale et paysagère, que pour la diversité phylogénétique. Une augmentation du dépérissement à l'échelle du paysage a aussi causé une spécialisation fonctionnelle des assemblages de coléoptère, favorisant ceux associés à de gros bois morts fortement décomposés.

Conclusions L'augmentation de la mortalité des arbres associée à une stratégie de rétention des héritages fournit des bénéfices de conservation à travers l'hétérogénéisation du paysage forestier et l'amélioration des habitats bois mort. Les pratiques de conservation des héritages pourraient tirer parti des peuplements forestiers non exploités et dépérissants pour promouvoir la richesse des espèces et la diversité fonctionnelle dans les paysages forestiers gérés de manière conventionnelle.

Mots-clés: Echelle de l'effet; Coléoptères saproxyliques; Changement climatique; Dépérissement forestier; Sécheresse; Héritage de perturbation

1 Introduction

Natural disturbances are major drivers of forest spatial and temporal dynamics (Bowd et al., 2021; Kuuluvainen, 2016; Pickett and White, 1985). Multiple disturbance complexes shape the structural heterogeneity of forests and generate key resources such as tree-related microhabitats, canopy gaps, snags, and logs, generally referred to as disturbance legacies (Franklin et al., 2000; Johnstone et al., 2016), which are colonised by diverse, and often specific communities (Kuuluvainen, 2016; Lachat et al., 2016; Swanson et al., 2011). Among them,

saproxylic beetles are a highly diverse group of insects that depend on dead or decaying wood for at least part of their life cycle and play important ecological roles by participating in carbon and nutrient cycles or by complexifying trophic chains (Stokland et al., 2012). However, current silvicultural practices tend to reduce deadwood-related resources and microhabitats (Courbaud et al., 2022; Grove, 2002; Paletto et al., 2014; Siitonen, 2001). As a consequence, saproxylic beetles are at considerable risk in intensively managed forests (Grove, 2002; Seibold et al., 2015), and 17.9% of saproxylic beetle species are now considered threatened in Europe (Calix et al., 2018).

Climate change alters natural disturbance regimes: warmer and drier conditions facilitate drought, wildfire, and insect outbreaks (Seidl et al., 2017). Lately, several large drought-related dieback events have been reported (Sangüesa-Barreda et al., 2015), and a further increase in drought-induced dieback and decline in terms of frequency, intensity, and spatial extent is expected to arise (Allen et al., 2010; Samaniego et al., 2018). As a consequence, deadwood supply, number of tree-related microhabitats and canopy openness are likely to increase and this may favour saproxylic populations (Cours et al., 2021; Müller et al., 2010; Sallé et al., 2020, 2021; Thorn et al., 2017). Several local-scale (i.e. less than 0.5 ha) studies have highlighted different positive relationships between saproxylic beetle populations and forest dieback: (i) pest-related dieback from large outbreaks of spruce bark beetles (*Ips typographus*, Linnaeus, 1758) resulted in an increase in saproxylic beetle species richness, including many red-listed species (Beudert et al., 2015; Cours et al., 2021) and (ii) drought-related dieback of *Quercus* spp. also increased saproxylic beetle species richness (Sallé et al., 2020). It has therefore been hypothesised that declining stands may improve habitat conditions for threatened forest communities such as saproxylic beetles (e.g., Kašák and Foit, 2018; Müller et al., 2010; Sallé et al., 2021). However, these studies have mainly focused on local conditions, regardless of the severity of forest dieback at broader scales. Yet, many previous studies have highlighted the fact that the diversity and structure of local saproxylic beetle communities may also depend on large scale, i.e. landscape, conditions (e.g., Franc et al., 2007; Gibb et al., 2006; Haeler et al., 2021; Økland et al., 1996). Sampling area size influences the detection of biodiversity responses to environmental conditions, a phenomenon known as "*the scale of effect*" (Jackson and Fahrig, 2015; Levin, 1992; Wiens, 1989). Insects are often highly mobile; they spread across landscapes in search of new resources, habitats, and/or reproductive partners (Janssen et al., 2016; Komonen and Müller, 2018; Ranius, 2006) and this mobility may result in potentially large scales of effect (Bergman et al., 2012; Seibold et al., 2017).

The relationship between spatial patterns of available resources and the number of associated species has been explored through several concepts based on ecological mechanisms. Within a given sampling area, the "*habitat-amount hypothesis*" predicts that the cumulative amount of habitat patches at the landscape scale better explains species richness than does local patch size (Fahrig, 2013; Seibold et al., 2017). In contrast, the "*habitat-patch hypothesis*", based on island-biogeography theory, assumes that local species richness is mainly restricted by local patch size and isolation (Fahrig, 2013; MacArthur and Wilson, 1967; Seibold et al., 2017). The "*resource concentration hypothesis*" predicts that the occurrence of a particular resource patch in the landscape induces a concentration of the species specialising on that resource, while at the same time, over-availability of that particular resource, exceeding the reproductive and colonising capacity of the associated species, could lead to a "*dilution effect*" (i.e. a large amount of substrate could lead to a reduction

in the species load colonising the substrate; [Otway et al., 2005](#)). Hence, assessing the relative contribution of both local and landscape conditions on local biodiversity may well be critical; unfortunately, it is often challenging ([Ammer et al., 2018](#)). In recent decades, remote sensing and aerial photography have been widely used to monitor forest conditions and forest disturbances such as fires, defoliation or deforestation at large and nested spatial scales (e.g., [Lambert et al., 2013](#); [Senf and Seidl, 2021a](#)).

Furthermore, most studies focus on the taxonomical responses of biological communities to forest dieback ([Cai et al., 2021](#), but see [Kozák et al., 2021](#); [Sire et al., 2022](#); [Thorn et al., 2014](#)). Nonetheless, phylogenetic and functional diversity are highly relevant indicators of ecosystem functioning ([Devictor et al., 2010](#)). Phylogenetic diversity reflects the evolutionary history of a community through lineage relatedness while functional diversity reflects the diversity of the phenotypical traits selected by a particular environment, i.e. biotic and abiotic filters ([Devictor et al., 2010](#); [Kozák et al., 2021](#)). Consequently, few studies have monitored taxonomic, functional, and phylogenetic responses of arthropods to forest disturbances at various spatial scales ([Kozák et al., 2021](#)).

In our study, we investigated how multi-scale forest dieback shaped local saproxylic beetle assemblages through several diversity dimensions. We analysed aerial photographs with machine-learning algorithms to map dead tree crowns and monitor dieback in silver fir forests in the French Pyrenees. After assessing dieback level at several nested spatial scales, we focused on the taxonomic (α -diversity), phylogenetic, and functional responses of local saproxylic beetle assemblages to the multi-scale spatial structure of the forest dieback. This analysis would be seen as a progress of results from [Cours et al., \(2021\)](#) in which we only studied consequences of local forest dieback on local saproxylic beetle assemblages. Finally, through multiplicative models (with interaction), we investigated subsequent mechanisms of forest dieback effects on the saproxylic beetle assemblages.

As a consequence of the increase in deadwood amount and light availability, we expected positive responses from the saproxylic beetle assemblages along the gradient of forest dieback at several spatial scales ([Bouget et al., 2014](#); [Müller et al., 2010](#); [Seibold et al., 2016](#)). We also expected positive responses from several substrate guilds: firstly wood-eating species, due to an increase in the amount of deadwood; secondly, fungicolous species, due to an increase in the abundance of saproxylic fungal fruiting bodies; and thirdly, cavicolous species, due to an increase in the number of cavities in dying trees ([Cours et al., 2021](#); [Ojeda et al., 2007](#); [Sallé et al., 2021](#)). In addition, we predicted community preferences for larger and more decayed deadwood along the dieback gradient, resulting from the increased amount of deadwood ([Gossner et al., 2013](#)). Furthermore, we expected an increase in functional and phylogenetic diversity of saproxylic beetles, mainly due to the increase in deadwood diversity (as a proxy of niche diversity; [Cours et al., 2021](#); [Seibold et al., 2016](#)). In parallel, saproxylic beetles having relatively great dispersal capacities ([Komonen and Müller, 2018](#); [Ranius, 2006](#)), we expected greater responses to landscape conditions, than local one ([Seibold et al., 2017](#)). Finally, we tested the interactive effects between the local and landscape scales on local saproxylic beetle assemblages, expecting no significant interactions since both scales should additionally affect assemblages ([Seibold et al., 2017](#)).

2 Materials and methods

2.1 Site description

A total of 56 plots were chosen in montane forests dominated by silver fir (*Abies alba* Mill.). The plots were located in two montane regions in the French Pyrenees: 28 plots in the Aure Valley in the Central Pyrenees (854 to 1570 m a.s.l., 1298 m on average; 42° 51'46.8" N 0° 36'08.9" E) and 28 plots on the limestone Sault Plateau in the Eastern Pyrenees (705 to 1557.3 m a.s.l., 1029 m on average; 42° 50'58.7" N 2° 00'41.3" E) (Fig. 1). The average distance between study plots was 860 m (standard deviation (SD) \pm 469 m), with a minimum value at 296 m and a maximum at 2439 m. Forests occupied 50% of the Aure Valley and 75% of the Sault region (Fig. 1). Silver fir dominated in 70% (95% confidence interval (CI95) \pm 12%) of the forests surrounding our plots in the Aure Valley and in 88% (CI95 \pm 5%) of the forests on the Sault Plateau. The secondary species were mainly Norway spruce (*Picea abies* (L.) H. Karst, 1881) and European beech (*Fagus sylvatica* L.). Most of the forest stands surrounding our study plots were managed for timber production. The plots were set up to reflect a gradient of dieback severity at the local scale; the dieback was measured in 2017 and was mainly induced by drought events over the last 30 years (Figs. S3–S5). In addition, local dieback conditions were cross-referenced with the empirical level of dieback in the landscape surrounding each study plot.

2.2 Beetle sampling, identification and characterisation

Saproxylic beetles were captured in two flight–interception traps per plot, each at least 20 m from the other, for a total of 112 traps in the 56 plots studied. Therefore, the traps were placed around the centre of each study plot. The traps consisted of a crossed pair of transparent plastic shields (40 × 60 cm) above a funnel leading into a container filled with an unbaited preservative (50% propylene glycol and 50% water with detergent). The traps were hung roughly 1.5 m above the ground near the centre of the plot and were sampled every month from mid-May to mid-September 2017. All the saproxylic beetles collected were identified to the highest possible taxonomic level (i.e. 83% at the species level, 2% at the genus level and 15% at the family level only (we retained the genera in which at least 100% of French species are known to be saproxylic, and families in which at least 75% of French species are known to be saproxylic), see Tab. S4; see Acknowledgments for the identifiers). We used the FRISBEE database to characterise species trophic guild at the larval stage (wood-eating, i.e. both xylo- and saproxylophagous species), substrate guild (cavicolous or fungicolous), and species rarity (rare vs. common) (Tab. 1; Bouget et al., 2005, 2019). We used genera and families only for global metrics, i.e. abundance and species richness of all saproxylic beetles.

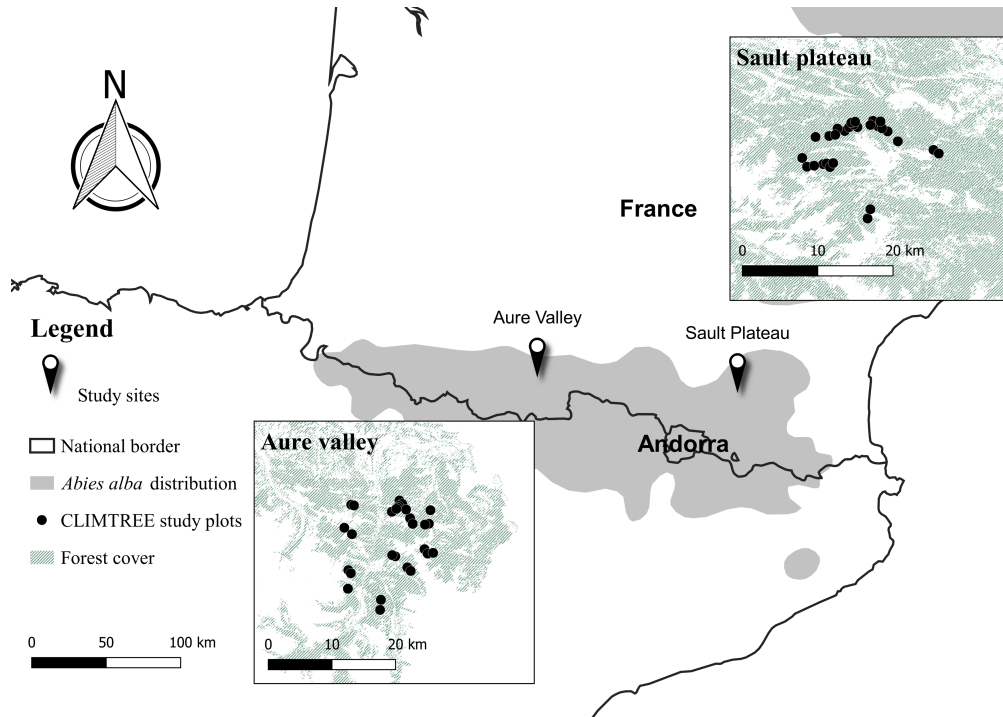


Figure 1: Map of the study sites. Grey areas correspond to *Abies alba* distribution.

2.3 Monitoring forest dieback

2.3.1 Data acquisition

Colour infrared aerial photographs with a 1 m resolution were downloaded from the French National Geographical Institute (NGI) for our two study regions (<https://geoservices.ign.fr>). As NGI aerial photographs are taken approximately every 5 years, we looked for the past photographs closest to our insect sampling year (2017): photographs taken in 2016 for the Aure Valley and in 2015 for the Sault Plateau. We then extracted the forested areas from the colour infrared aerial photographs thanks to a land cover map based on Sentinel-2 images and deleted roads and paths (Inglada et al., 2017).

2.3.2 Machine learning process

We manually constructed vector training data through on-screen interpretation (Fig. 2c), resulting in 4256 polygons for four land cover classes: 1,743 polygons of dead crowns (41%), 1606 of living trees (37.7%), 212 of shady areas (5%), and 695 polygons of bare soil (e.g. meadows; 16.3%). We implemented a machine learning algorithm with the Orfeo Toolbox (OTB) software and we applied both a Pixel-based image analysis (PBIA) and an Object-based image analysis (OBIA) (Grizonnet et al., 2017).

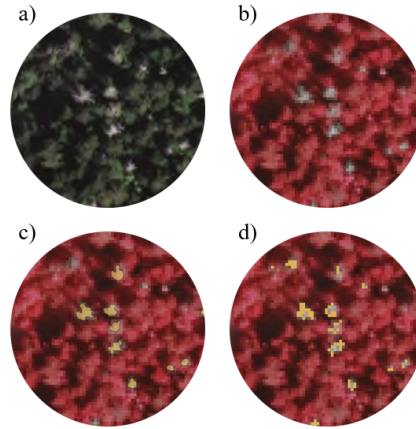


Figure 2: *Machine learning process: a natural colour (RGB) and b infrared colour (IRC) orthophotos of a forest composed of living and dead trees. Dead crowns are easily identifiable by their grey colour due to a lack of photosynthetic activity. We identified four types of polygons in a vector training layer (dead crowns, living trees, shady areas and bare soil—only dead crowns in c, to train a machine learning model with the random forest algorithm. d shows the result of the subsequent dead crown pixel classification in pale orange). All the images were taken from the centre point: lat. 488,182.46, lon. 6,205,612.67 (Lambert-93, EPSG:2154)*

In the PBIA, we ran a Random Forest (RF) classification model (Breiman, 2001). RF is a widely used machine learning classification algorithm relying on a set of decision trees (Breiman, 2001; Immitzer et al., 2016). Fifty percent of the training vectors were used to train the classification model (proposed by default in the OTB) while the other fifty percent were used to validate the classification model.

In the OBIA, we performed segmentation on the colour infrared aerial photographs with the Large Scale Mean Shift method implemented in OTB (De Luca et al., 2019; Immitzer et al., 2016). We used a minimum size of four pixels (4 m^2). As for the PBIA, we ran a RF model to classify the segmented vectors (Breiman, 2001; Immitzer et al., 2016).

In both approaches (PBIA and OBIA), we used the RF default setting values in OTB to train and classify the processes for optimal results (De Luca et al., 2019). Therefore, the maximum depth of the tree was set to 5, the maximum number of trees in the forest to 100 and the out-of-bag error was set to 0.01. The two RF classification models showed very similar accuracy results as measured by the Kappa index (PBIA: 0.72; OBIA: 0.68). Since OBIA does not facilitate dead crown classification compared to PBIA (see Immitzer et al., 2016 with tree species classification), we used only the results from the PBIA method, which requires less computer memory capacity (Grizonnet et al., 2017).

2.3.3 Measuring forest dieback at the landscape scale

We used our RF classification model with the PBIA approach to identify the dead crown pixels over large areas around our study plots. Our approach did not allow us to assess dead-tree density so we estimated the cumulative surface area of the dead and dying tree parts, i.e. the dead crowns (Larrieu et al., 2018). We then mapped and summed the dead crown pixels to assess a level of forest dieback over several spatial scales. We

2.3 *Monitoring forest dieback*

designated several nested buffer zones around our study plots in order to describe forest dieback along the gradient from the local to the landscape scale. The zones had radii of 25, 200, 500, 800, 1100 and 1500 m; we summed dead crown pixels in each of these buffer zones and we divided them by each buffer areas to assess a percentage of dead crown pixels (Tab. 1). Finally, for each buffer zone, we randomly selected non-overlapping buffers for the analysis, resulting for the 25 m buffer in 56 plots, 54 plots in the 200 m buffer, 35 plots in the 500 m buffer, 28 plots in the 800 m buffer, 25 plots in the 1100 m buffer, and 20 plots in the 1500 m buffer. We did not designate larger buffer zones to avoid further data degradation due to overlapping buffers. Hereafter, we designated the 25 m radius as describing local conditions, the 200 m radius as intermediate landscape and the larger radius as landscape-scale conditions (Fig. S.7).

Table 1: Overview of the predictors and response variables used in our study.

Variable	Definition	Mean \pm CI95%	Range (min-max)
Predictors			
<i>Forest dieback severity</i>			
25 m-scale	Percentage of DCP within the 25 m radius	3 \pm 1.2	0–19
200 m-scale	Percentage of DCP within the 200 m radius	2.4 \pm 0.9	0.01–11.1
500 m-scale	Percentage of DCP within the 500 m radius	2.1 \pm 1.01	0.02–10.4
800 m-scale	Percentage of DCP within the 800 m radius	1.98 \pm 1.02	0.02–8.7
1100 m-scale	Percentage of DCP within the 1100 m radius	1.7 \pm 0.96	0.02–7.2
1500 m-scale	Percentage of DCP within the 1500 m radius	1.9 \pm 1.17	0.02–7.4
Responses			
<i>All species</i>			
Abundance	Abundance of all saproxylic beetles	820 \pm 142	179–3052
Richness	Species richness of all saproxylic beetles	83 \pm 4	51–123
<i>Common species</i>			
Abundance	Abundance of common saproxylic beetles	715 \pm 122	120–2716
Richness	Species richness of common saproxylic beetles	70 \pm 4	43–105
<i>Rare species</i>			
Abundance	Abundance of rare saproxylic beetles	22 \pm 9	3–245
Richness	Species richness of rare saproxylic beetles	6 \pm 0.5	2–11
<i>Wood-eating species</i>			
Abundance	Abundance of wood-eating beetles	548 \pm 119	104–2589
Richness	Species richness of wood-eating beetles	31 \pm 2	16–50
<i>Cavicolous species</i>			
Abundance	Abundance of cavicolous beetles	50 \pm 8	8–143
Richness	Species richness of cavicolous beetles	11 \pm 1	3–21
<i>Fungicolous species</i>			
Abundance	Abundance of fungicolous beetles	242 \pm 29	41–622
Richness	Species richness of fungicolous beetles	33 \pm 2	17–47
<i>Phylogenetic diversity</i>			
SES faith's	PD Faith's standardized phylogenetic diversity	-1.35 \pm 0.2	-3.0 to 0.2
Variability	Phylogenetic species variability	0.9 \pm 0.002	0.88–0.91
Evenness	Phylogenetic species evenness	0.78 \pm 0.03	0.35–0.87
<i>Functional diversity (Mouillot et al., 2013; Villéger et al., 2008)</i>			
Richness	Functional richness	44 \pm 2	28–67
Divergence	Functional divergence	0.81 \pm 0.02	0.63–0.94
Evenness	Functional evenness	0.59 \pm 0.01	0.51–0.67
<i>Community weighted mean (CWM)</i>			
DW diameter	Mean trait value of deadwood diameter preference	2.23 \pm 0.03	1.96–2.49
DW decay	Mean trait value of deadwood decay preference	2.48 \pm 0.07	2.1–3.14
Canopy closure	Mean trait value of canopy-closure preference	1.68 \pm 0.02	1.39–1.87
Body size	Mean trait value of body size	4.9 \pm 0.4	2.9–9.9
<i>Functional dispersion (FDis)</i>			
DW diameter	Trait variance of deadwood diameter preference	0.54 \pm 0.04	0.28–0.98
DW decay	Trait variance of deadwood decay preference	0.7 \pm 0.05	0.26–0.95
Canopy closure	Trait variance of canopy-closure preference	0.75 \pm 0.04	0.39–1.2
Body size	Trait variance of body size	0.73 \pm 0.08	0.24–0.32

DCP = dead crown pixels, CWM = community-weighted means, FDis = functional dispersion, DW = deadwood rare species = patrimonial value ≥ 3 in France

2.4 Statistical analysis

Data analysis was conducted with R software 4.0.0 (R Core Team, 2023). Firstly, we pooled the two traps from each plot and calculated abundance and species richness for the substrate and trophic beetle guilds. We also calculated abundance and species richness for both common and rare saproxylic beetle species as well as the total abundance and species richness. Furthermore, to account for missing data, we incorporated the log coefficient based on the number of undisturbed sampling months weighted by monthly arthropod abundance into all models as an offset (trap sometimes destroyed).

Secondly, to assess functional diversity indices for the community, we extracted quantitative values for preferred deadwood diameter and decay level for larval development, canopy openness preference, and mean body size for each of the captured saproxylic beetle species, as in (Gossner et al., 2013; Janssen et al., 2017). For each plot, we calculated two multidimensional indices: community-level weighted means (CWM) and functional dispersion (FDis), defined as the mean and dispersion of the trait values weighted by the relative abundance of each species according to their values of quantitative functional traits (Tab. 1; dbFD function, FD R-package; Laliberté et al., 2014). In addition, we calculated the three functional diversity indices proposed by Villéger et al. (2008) based on four quantitative functional traits (i.e. preferences in deadwood diameter and decay and canopy openness, and mean body size) (Tab. 1): (i) functional richness (FRic), i.e. "the range of functional space filled by the community"; (ii) functional divergence (FDiv), which "relates to how abundance is distributed within the volume of functional trait space occupied by the community"; and (iii) functional evenness (FEve) or "the evenness of abundance distribution in a functional trait space" (Villéger et al., 2008). These three indices should be able to quantify the functional changes occurring in a community after a disturbance (Mouillot et al., 2013).

Thirdly, we calculated Faith's standardized phylogenetic diversity index (SES Faith's PD) to obviate the relationship between Faith's PD and species richness (Pearson's $r = 0.98$, $P < 0.001$). We also calculated two phylogenetic species-diversity metrics: phylogenetic species variability (PSV) and evenness (PSE). PSV "is one when all species are unrelated and approaches zero as species become more related"; PSE "is one when species abundances are equal and species phylogeny is a star" (Tab. 1; Kembel et al., 2020). DNA barcode consensus were mined from the BOLD data system (Ratnasingham and Hebert, 2007) whenever accessible for each saproxylic beetle species morphologically identified. When multiple records and BINs (Ratnasingham and Hebert, 8 juil. 2013) were available for a given species, a choice was made according first to geographic area of sampling, and second to sequence length and quality. Close geographical areas were favoured as were high-quality 658 bp-long sequences ($N < 1\%$) whenever possible. A total of 349 species out of 393 (88.8%) beetle species collected had DNA barcodes available. The dataset of the records we used for phylogenetic diversity is publicly available at the following <https://doi.org/10.5883/DS-PHYLOCOL>. COI consensus were first aligned with BOLD aligner to check for sequence quality and validity. Trimming of longer or misaligned consensus was manually applied whenever necessary. Final sequence alignment was performed in MUSCLE 3.8.425 (Edgar, 2004) with 8 iterations and a maximum-likelihood phylogenetic tree was constructed with a general time-reversible (GTR) model and 500 bootstrap iterations in FastTree ver. 2.1.11 (Price et al., 2010). In order to compare phylogenetic diversity among different dieback levels, an unrooted tree was preferred (Nipperess and Matsen, 2013). With picante package ver. 1.8.2 (Kembel et al.,

2020), we pruned the species present across all our study regions and plotted phylogenetic trees for each study plot. We calculated the respective standardized PD, PSV and PSE values for each plot with the "ses.pd" and "psd" functions (picante R-package).

To deal with the over-dispersion of count variables (Bates et al., 2020), we used the glmmTMB R-package (Magnusson et al., 2020) to run Generalized Linear Mixed Models (GLMMs) with "region" (i.e. Aure Valley or Sault Plateau) as a random variable. In addition, to better include the differences between the two regions in the models, we also added the proportion of fir trees in the surrounding forests, in an area of 700 ha, as a fixed effect (see section 2.1). Response variables were the abundance and species richness for each guild of saproxylic beetles, the functional-trait variables (i.e. CWM and FDis for each quantitative functional trait, and FRic, FDiv and FEve for overall functional diversity), and the phylogenetic diversity indices (i.e. SES Faith's PD, PSV and PSE). We implemented both simple and multiple regressions. The simple regressions, hereafter referred as **univariate models**, were composed of the random variable (i.e. region), proportion of fir trees in the 700 ha area as a fixed co-variable, the offset to account for missing data, and the percentage of dead crown pixels for a particular spatial scale as a predictor. For each response variable, we selected the best-fitting error structure with the fitdist function from the fitdistrplus R-package (Delignette-Muller et al., 2019). Then, we selected the best relationship structure for each response variable and predictor variable (i.e. by comparing the Akaike Information Criterion for small sample sizes (AICc) between linear and logarithmic regressions). Since six different spatial scales were compared (R = 25 m, 200 m, 500 m, 800 m, 1100 m and 1500 m), we applied a Post-Hoc Holm adjustment of p-values ("p.adjust" function). Finally, we extracted estimates (i.e. β -coefficients) and adjusted p-values from each glmmTMB model. We used estimate values to select the best landscape scale for each tested response variable.

We then performed multiple regressions with generalized linear mixed models with "region" (Aure Valley or Sault Plateau) as a random variable and including as fixed variables, the measure of local dieback and the best landscape scale, proportion of fir trees in the 700 ha areas as co-variable, and the offset to account for missing data. We checked for non-collinearity between fixed variables, with the "check_collinearity" function from the performance R-package (Lüdtke et al., 2020) and always observed a variance inflation factor (VIF) below three. As three different terms in the multiplicative models were involved, we performed Post-Hoc Holm adjustments on each of their p-values. Our purpose was to evaluate the potential interactive effect between the local (25 m) and the most appropriate landscape scale (i.e. the landscape scale with the highest β -coefficient and/or highest significance) with a multiplicative interaction model (Eq. 1). Since the 200 m scale was highly correlated with the 25 m-scale (Pearson's $r = 0.78$, $P < 0.001$), we excluded this metric from our analysis (Fig. S.7, Tab. S.1).

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_{12} x_1 x_2 + \varepsilon \quad (1)$$

which is the multiplicative equation assessing whether there is an interactive relationship between X_1 and X_2 . X_1 = severity of local dieback; X_2 = severity of most suitable landscape dieback; β_1 and β_2 = model coefficients for both forest dieback metrics (local and landscape); β_{12} = coefficient for the interaction term

$X_1 X_2$; ε = model residuals.

In multiplicative interaction models, hereafter referred to as "**multiplicative models**", β_1 and β_2 are significantly different from zero when X_1 and X_2 are respectively equal to zero (H_1 : $\beta_1 \neq 0$ when $X_2 = 0$ and vice-versa) (Braumoeller, 2004). We associated the results of the multiplicative models with the ecological mechanisms affecting the spatial pattern of the saproxylic beetles. When H_1 : $\beta_1 \neq 0$ could not be rejected, we hypothesised an effect of local resource concentration since we were assessing the effect of local forest dieback on saproxylic beetles in the case of limited dieback at the landscape scale (Fig. 3a). When H_2 : $\beta_2 \neq 0$ could not be rejected, we hypothesised a spill-over effect since we were assessing the effect of forest dieback at the landscape scale in the case of limited local dieback (Fig. 3b). We hypothesised that a significantly positive interaction term (β_{12}) reflected a synergistic/amplifying effect (Fig. 3c) and that a significantly negative interaction term would support a dilutive/saturated effect and the habitat-patch hypothesis (Fig. 3d; Fahrig, 2013; Seibold et al., 2017). Furthermore, we assumed that a significant response to local forest dieback in the univariate model but not in the multiplicative model and/or a significant response to landscape dieback in the univariate model but not in the multiplicative model would both support the additional importance of both scales to describe local saproxylic beetle assemblages (i.e. the habitat-amount hypothesis; Fig. 3e; Fahrig, 2013; Seibold et al., 2017). Indeed, cancelling univariate significant effects in multiplicative models indicates that the level of forest dieback, i.e. the amount of dieback-induced resources, matters at both local and surrounding landscape scales and not just at one particular scale. In addition, the absence of an interaction effect would also support the habitat-amount hypothesis (Fahrig, 2013; MacArthur and Wilson, 1967; Seibold et al., 2017).

3 Results

Our final dataset comprised 50,067 specimens of 393 saproxylic beetle species belonging to 50 families. The range of species richness was 51–123 species/plot with an average of 83 ± 4 species/plot (CI 95%; Tab. 1).

3.1 Validation of forest dieback metrics

To assess the relevance of the percentage of dead crown pixels as an indicator of forest dieback, we evaluated the accuracy of the relationship between the local sum of dead crown pixels ($R = 25$ m) and field measurements of forest dieback carried out according to the ARCHI protocol. The ARCHI protocol classifies trees in a gradient from healthy to dead, based on their architecture. In our study, we applied the protocol to the 20 fir trees closest to each plot centre. It resulted in a standardised measure of dieback at plot scale according to a hypothetical lower (all 20 trees are healthy) and higher (all 20 trees are dead) values of dieback (i.e. standardised mean dieback of 39% ($\pm 3\%$ CI95%), minimum value at 9% and maximum at 59%). We observed a significant relationship between the two variables (β -Estimate = 0.7; $P < 0.01$; Fig. S.5), which indicates that our classification model of dead crown pixels and the percentage of these pixels provided a consistently accurate description of the local forest dieback assessed on site. In addition, we validated our landscape-scale estimates of forest dieback by cross-checking the relationship between the percentage of dead crown pixels at the landscape scales (i.e. $R = 200$ to 1500 m) with the European disturbance map edited by

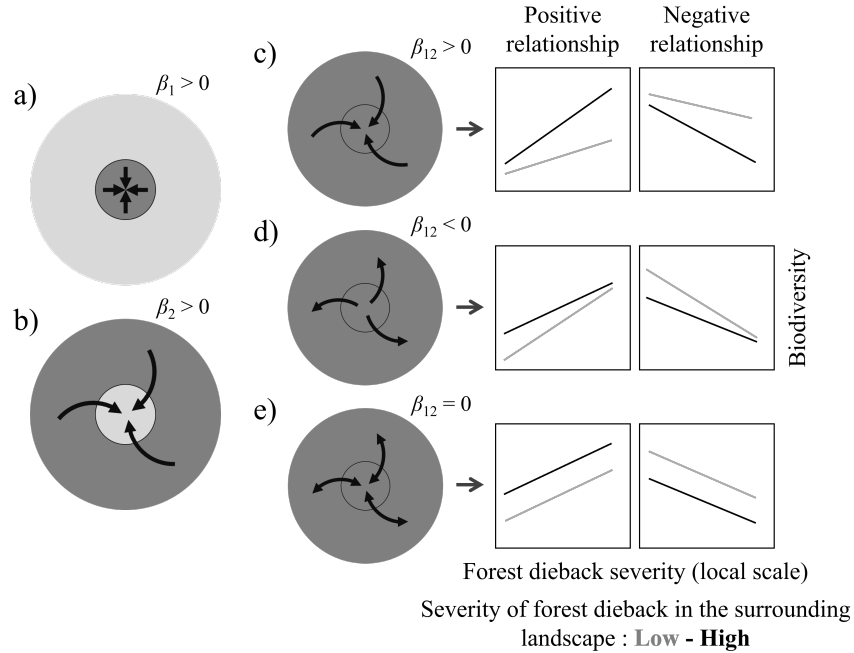


Figure 3: Hypothesised saproxylic beetle responses to the terms of the multiplicative interaction models (inner circle = local conditions (associated estimates = β_1); outer circle = landscape conditions (associated estimates = β_2); light grey = healthy forest area; dark grey = disturbed forests; arrows represent species fluxes) (a and b describe simple terms effects while c–e describe interactive term). a $\beta_1 > 0$ = concentration effect; b $\beta_2 > 0$ = spill-over effect; c $\beta_{12} > 0$ = synergistic effect; d $\beta_{12} < 0$ = dilution or habitat-patch effect; e $\beta_{12} = 0$ = habitat-amount hypothesis. Moreover, if there is a significant local effect in the univariate model but not in the multiplicative model, or a significant landscape effect in the univariate model but not in the multiplicative model, it supports that local and landscape conditions act additionally.

Senf and Seidl (2021a; 2021b), which is based on a time series analysis of the spectral band values of Landsat satellite photographs ($P < 0.001$; Fig. S.6).

3.2 Relationship among taxonomic, phylogenetic and functional diversity

We did not observe a relationship between total saproxylic beetle species richness and the phylogenetic diversity metrics (Fig. S.1). Nevertheless, we found a positive relationship between total species richness and FRic (Fig. S.1), but not with FDiv (Fig. S.1) and FEve (Fig. S.1). We did not observe any relationship between the phylogenetic diversity metrics and FRic, though there was a significantly negative relationship between PSE and FDiv (Fig. S.1) and a positive relationship between PSE and FEve (Fig. S.1).

3.3 Response of taxonomic diversity to dieback

3.3.1 General metrics

In the univariate models, both local and landscape dieback metrics had positive effects on abundance and richness of total and common species, abundance and richness of common species, and on abundance of rare species (Fig. 4a). In contrast, rare species richness did not respond to forest dieback at any scale (Fig. 4a).

For abundances, scales of effect were detected at the local scale, whereas for species richness, scales of effect were detected at 200 m scale (Fig. 4a). No effect was detected in the multiplicative models (Tab. 2).

3.3.2 **Feeding and substrate guilds**

In the univariate models, the abundance of wood-eating species was positively affected by local forest dieback only (i.e. the scale of effect; Fig. 4e). In contrast, the richness of wood-eating species positively responded to both local- and landscape-scale dieback (with higher scale of effect at 200 m scale; Fig. 4e). Still in the univariate models, abundance of cavicolous species positively responded to landscape scales (200 m and 1500 m scales; Fig. 4e), while richness positively responded to both local and intermediate landscape scales (i.e. 25 m and 200 m; Fig. 4e). Nevertheless, they both had scale of effect at 200 m scale (Fig. 4e). In the univariate models, fungicolous species abundance responded positively to forest dieback at the local and landscape scales (with high scales of effect at 200, 800, and 1100 m scales), while richness was only affected by the 200 m scale (Fig. 4e). In the multiplicative models, neither the abundance nor the species richness of wood-eating, cavicolous, and fungicolous beetles significantly responded to forest dieback (Tab. S2).

3.4 **Response of phylogenetic diversity to dieback**

In the univariate models, we only observed negative response of phylogenetic evenness to forest dieback at the 1100 m scale (Fig. 4b). Otherwise, in the multiplicative models, we detected significant responses of standardized Faith's index of phylogenetic diversity: positively to both simple effects (i.e. local and landscape dieback), and negatively to the interactive effect (Tab. 2).

3.5 **Response of functional diversity to dieback**

In the univariate models, we only observed positive effects of both local and landscape forest dieback on FRic (Fig. 4c). Concerning substrate and morphological metrics, we noted positive effects of forest dieback on the mean community preference for deadwood diameter (CWM DW diam.), for deadwood decay (CWM DW decay), and for body size (CWM body size) at the landscape scale (higher scales of effect at 1500 m scale; Fig. 4d). We observed parallel negative effects for forest dieback at the landscape scale on the functional dispersion of deadwood diameter preference (at 200 m scale; FD DW diam.; Fig. 4d) and positive effects, also at the landscape scale, on the functional dispersion of deadwood decay preference (FD DW decay) and body size (FD body size; scale of effect at 1500 m scale; Fig. 4d). In the multiplicative models, we did not observe any significant responses of functional metrics to forest dieback (Tab. 2). Finally, the functional traits canopy opening preference did not respond to forest dieback in either the univariate or multiplicative models (Tab. S2).

4 **Discussion**

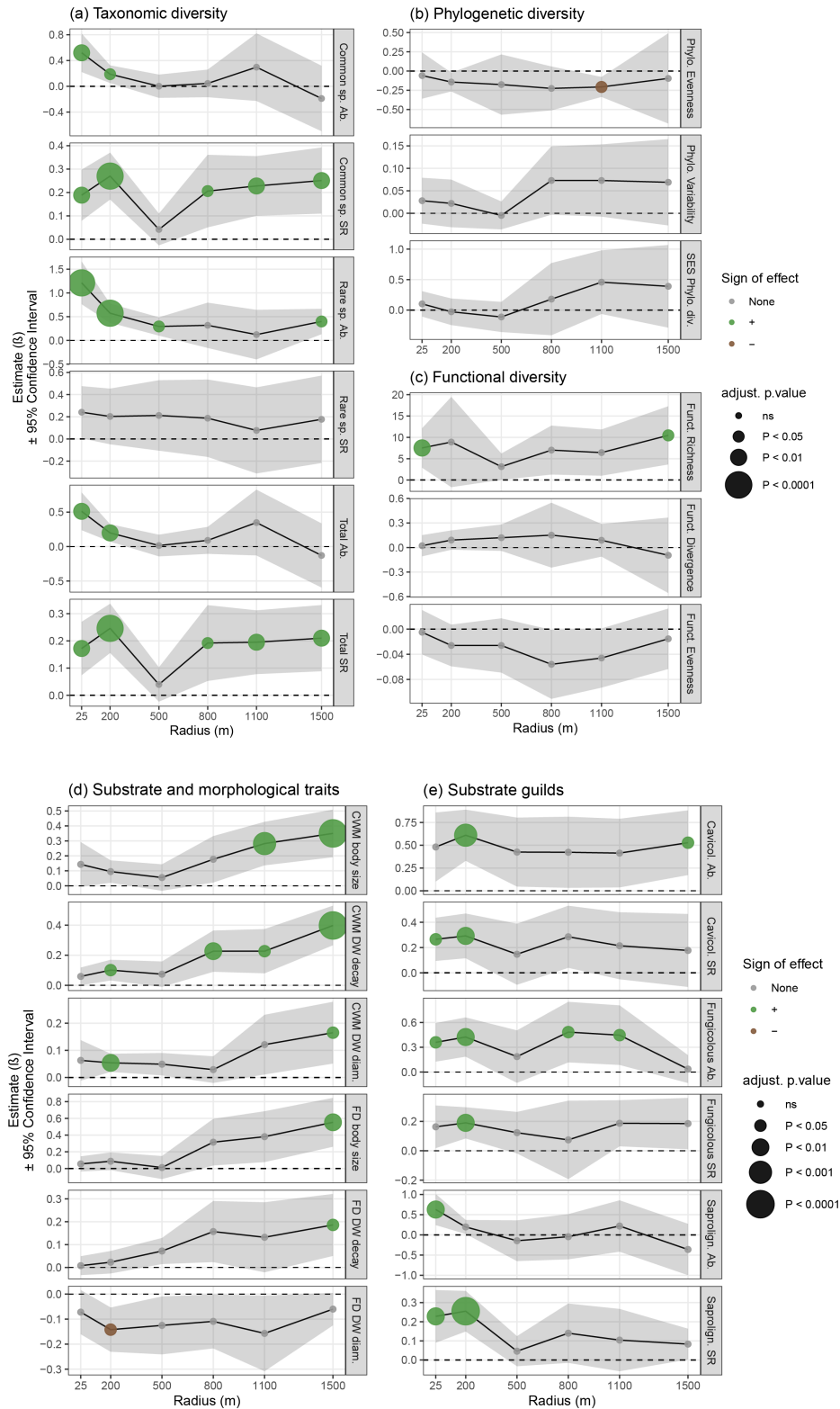


Figure 4: Response of local general saproxylic beetle assemblages to dieback severity measured over different spatial scales (**a** taxonomic diversity; **b** phylogenetic diversity; **c** functional diversity; **d** substrate traits; **e** substrate guilds). Coloured circles indicate β -estimates from the univariate glmmTMB models; their diameter varies with adjusted p value. The shaded grey area indicates the 95% confidence interval of each β -estimate. "DW" = "deadwood"

4.1 Overall forest dieback effect

Given the scale of the expected increase in the frequency and spatial extent of forest dieback and decline in the future, assessing their current and long-term consequences on forest communities is paramount (e.g., [Anderegg et al., 2013](#); [McDowell et al., 2020](#); [Sallé et al., 2021](#)). As expected, we showed that the intensity of forest dieback positively affected the taxonomic diversity of saproxylic beetles, differently at the local and landscape scale (Fig. 4). This probably results from the accumulation of deadwood and tree-related microhabitats associated with increased canopy openness, since both environmental factors generally have positive effects on the species richness and abundance of saproxylic beetles ([Bouget et al., 2014](#); [Godeau et al., 2020](#); [Müller and Bütler, 2010](#); [Sallé et al., 2020, 2021](#)).

4.2 Local- and large-scale effects of forest dieback

Many species of saproxylic beetle are considered highly mobile and therefore only slightly dispersal-limited; they therefore potentially respond to large scales of effect ([Jackson and Fahrig, 2015](#); [Janssen et al., 2016](#); [Thorn et al., 2018](#)). Indeed, they may cover long distances, within a limit of roughly ≤ 10 km ([Komonen and Müller, 2018](#)), to find suitable habitats and/or resources (related to the deadwood size, decay stage, tree species and position; to tree-related microhabitats; or to the presence of open areas; [Grove, 2002](#); [Stokland et al., 2012](#)). Our results highlight the relevance of the landscape scale (i.e. in this study, from 200 to 1500 m) when considering the effect of forest dieback on local saproxylic beetle assemblages. Despite strong correlation with the local scale, we noticed that the 200 m scale could be considered as the scale of effect for species richness of most guilds of saproxylic beetles. In an experimental test of the habitat-amount hypothesis, [Seibold et al. \(2017\)](#) showed that the scales of effect for species richness of saproxylic beetles were about 40 to 120 m depending on the group, which is approximately in line with our results. However, we lack resolution along our buffer gradient and therefore the actual scale of effect is certainly another value close to our result. In contrast, the abundance of all species as well as common, rare, and wood-eating species responded mainly to local forest dieback (Fig. 4). Consequently, species richness and abundance responded differently to forest dieback and should therefore be determined by distinct mechanisms: abundance seems to be mainly driven by patch size while species richness seems to be mainly driven by the local landscape. It has already been shown in previous studies that the accumulation of deadwood, both at local and landscape scales, has positive effects on saproxylic beetles ([Franc et al., 2007](#); [Gibb et al., 2006](#); [Haeler et al., 2021](#); [Økland et al., 1996](#); [Sverdrup-Thygeson et al., 2014](#)). Likewise, local canopy openings as well as an interconnection within the landscape forest matrix of fine patches of open habitats, i.e. gaps, is also beneficial to saproxylic beetle biodiversity ([Bouget and Duelli, 2004](#); [Bouget et al., 2014](#); [Kozel et al., 2021](#); [Seibold et al., 2016](#)). In addition, we observed a significant landscape effect of forest dieback on the abundance of both cavicolous and fungicolous species (Fig. 4e). This result suggest that forest dieback does not just increase deadwood amount and canopy openness but also favours the development of tree-related microhabitats such as the fruiting bodies of saproxylic fungi and cavities (e.g., rot-holes; [Larrieu et al., 2018](#); [Ojeda et al., 2007](#); [Speckens, 2021](#)).

We did not observe any significant interaction between local and landscape forest dieback for metrics of

Table 2: Results from the multiplicative interaction models of the effects of local ($R=25$ m) and surrounding landscape (highest scale of effect) dieback on the taxonomic, phylogenetical, and functional diversity of saproxylic beetles.

Responses of local assemblages metrics	Models Metrics	Description df	R ²	Simple effects β coeff.	Interactive effects β coeff.
<i>Taxonomic diversity</i>					
Abundance (All)	Local	23	0.18	0.5 ^{ns}	-0.03 ^{ns}
	Landscape 1100m			-0.3 ^{ns}	
Richness (All)	Local	18	0.37	0.2 ^{ns}	-0.16 ^{ns}
	Landscape 1500m			0.23 ^{ns}	
<i>Phylogenetical diversity</i>					
SES Faith's PD	Local	18	0.21	0.63*	-0.9*
	Landscape 1500m			1.33*	
Variability	Local	26	0.32	0.11 ^{ns}	-0.06 ^{ns}
	Landscape 800m			0.06 ^{ns}	
Evenness	Local	23	0.31	0.16 ^{ns}	-0.08 ^{ns}
	Landscape 1100m			-0.18 ^{ns}	
<i>Functional diversity</i>					
Richness	Local	18	0.32	4.4 ^{ns}	6.3 ^{ns}
	Landscape 1500m			0.59 ^{ns}	
Divergence	Local	26	0.28	0.3 ^{ns}	-0.76 ^{ns}
	Landscape 800m			0.66 ^{ns}	
Evenness	Local	26	0.32	-0.02 ^{ns}	0.03 ^{ns}
	Landscape 800m			-0.07 ^{ns}	

* Effects were tested with generalized linear mixed models (with "region" as a random variable and proportion of fir trees in landscape as fixed co-variable). Values shown are β -estimates from glmmTMB models. Colours represent the direction of the effect: green for a positive effect of dieback on the considered variable, red for negative effect, and grey when no significant effects were detected. "df" = "degrees of freedom", "R²" = "R-squared" (since there is no method to calculate R² from glmmTMB model, values are derived from glm.nb and glm models). See Tab. S1 and S2 for all response variables. ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

taxonomic diversity (Tab. 2). According to Seibold et al. (2017), the lack of interaction between these two spatial scales could support the habitat-amount hypothesis since the amount of habitat at both scales is merely additive (Fig. 3). This is further supported by the fact that local and landscape effects alone cancelled each other out in our multiplicative models, while most of the univariate-model effects for taxonomic diversity were significant (Fig. 4; Tab. 2). The habitat-amount hypothesis predicts that "species richness in a sample site is independent of the area of the particular patch in which the sample site is located (its local patch)" (Fahrig, 2013). Therefore, in our study, local scale alone (i.e. without any dieback areas in landscape) should not have been sufficient to detect dieback effects on saproxylic beetle biodiversity, even if it appears as the potentially scale of effect. Nevertheless, the opposite is also true: forest dieback surrounding an undisturbed forest patch cannot contribute to local biodiversity, since the habitat or resource of interest is not locally present (Tab. 2). Nevertheless, and despite the non-collinearity in the models ($VIF < 3$), local and landscape conditions of forest dieback were correlated (Tab. S.1) and thus, the cancellation of significant effects in the univariate models could also be the result of statistical artifacts and further research is needed.

Forest dieback at the landscape scale also had effects on the functional diversity metrics, mainly substrate and morphological traits (CWM and FDis) which did not respond to local forest dieback (Fig. 4d). In another study, based on data from the same Pyrenean plots and from plots located in Bavarian montane forests (Cours et al., 2021), we hypothesised that the severity of the local forest dieback in Bavaria was correlated

to forest dieback severity at the landscape scale, as sudden, large-scale tree mortality occurred in the area following a major bark beetle outbreak (mean bark beetle gap size = 6.8 ha; Müller et al., 2008). In contrast, the drought-induced dieback in the Pyrenean forests caused gradual mortality in discrete patches across the landscape; in this case, the local conditions did not necessarily reflect large-scale conditions (Andrew et al., 2016; Cours et al., 2021). These variations in the immediacy and scale-intensity of the dieback may explain (i) why the local forest dieback in the Pyrenean mountains did not affect functional trait metrics in our previous study (Cours et al., 2021), and (ii) why, in this study, the same metrics only responded to landscape-scale conditions. Our results therefore suggest that studying local conditions alone may be insufficient to detect the functional response of saproxylic beetles to forest dieback when tree mortality occurs in discrete patches, and that landscape conditions can act as a strong filter on trait diversity (Fig. 4d; Cours et al., 2021; Gámez-Virués et al., 2015).

4.3 Contrasting responses of different biodiversity dimensions to forest dieback

While taxonomic diversity was affected primarily by local and intermediate-landscape forest dieback (and secondarily by larger landscape scales), it appears from our results that functional diversity, through substrate and morphological traits, responded primarily to forest dieback at the largest landscape scale (i.e. 1500 m; Fig. 4d). In parallel, functional richness responded positively at the local scale and at the 1500 m scale (Fig. 4c). Furthermore, forest dieback only affected phylogenetic diversity through evenness, at the 1100 m scale (Fig. 4b). In contrast, standardized Faith's phylogenetic index (ses.PD) was the only one response variable that significantly responded to local and landscape forest dieback in the multiplicative model (Tab. 2). From this multiplicative model, it seems that the spatial pattern of dieback was important for the ses.PD. Indeed, spatial patterns mixing areas of forest dieback with undisturbed areas seem to lead to higher phylogenetic index values than randomly expected (i.e. phylogenetic overdispersion; Webb and Pitman, 2002).

Consequently, the diversity and quantity of habitats and resources released by forest dieback (i.e. deadwood, tree-related microhabitats and canopy openness) increased abundance and species richness of saproxylic beetles, and lead to more heterogeneous functional assemblages, as suggested by the more-individuals and the habitat-heterogeneity hypotheses (Seibold et al., 2016). Similarly, the increase in spatial heterogeneity due to the mixing of declining and undisturbed forests had a positive effect on phylogenetic diversity. For example, Kozák et al. (2021) showed that phylogenetic diversity of saproxylic beetles was positively affected by canopy openness, which in turn was positively influenced by recent disturbances.

4.4 Functional responses of assemblages to forest dieback: heterogenisation and specialisation

Forest dieback increased beetle functional richness (FRic), at both local and landscape scales (Fig. 4c). In our study, the increase in total species richness seemed to be associated with this increase in FRic. This indicates that the range of functional traits is quite broad in the functional space of disturbed stands and within disturbed landscapes; in other words, functional traits have more extreme values in declining forests (Mouillot et al., 2013). This is congruent with previous observations showing that the functional richness

of saproxylic beetle assemblages is positively influenced by the local amount and diversity of deadwood, as well as by canopy openness (local = 0.1 ha, $R \approx 18$ m; [Thorn et al., 2018](#)), features which are typically favoured during forest decline and dieback ([Cours et al., 2021](#); [Sallé et al., 2021](#); [Thorn et al., 2018](#)). Here, we demonstrate that this probably stands true at larger spatial scales.

In addition, we observed functional specialisation in species preference for deadwood diameter: when forest dieback increased at the landscape scale, local assemblages preferred larger deadwood and functional dispersion was lower (CWM and FDis Diameter; Fig. 4d). A previous study showed that the functional specialisation of saproxylic beetles towards large-diameter and well-decayed deadwood occurs when the overall amount of deadwood increases ([Gossner et al., 2013](#)). This functional specialisation might not account for the needs of species that prefer small-diameter deadwood. Nevertheless, these species still benefit from a relatively high amount of deadwood and are also less sensitive to intense forest management in the surrounding area ([Gossner et al., 2013](#)). Moreover, we observed that forest dieback at the landscape scale led to an increased preference of the saproxylic beetle assemblages for more decayed deadwood, along with a higher functional dispersion than in healthy forests (CWM and FDis Decay; Fig. 4d). Therefore, our results suggest that iterative forest dieback events had released a large amount of large-diameter deadwood in varying stages of decay, which is of great value for biodiversity ([Bouget et al., 2013](#); [Gossner et al., 2013](#); [Kozák et al., 2021](#); [Lachat et al., 2013](#); [Similä et al., 2003](#)). Finally, our results showed that increasing forest dieback at the landscape scale lead to increasing mean body size of local saproxylic beetle assemblages, with higher trait dispersion (Fig. 4d). It means that forest dieback occurring over large areas favoured larger beetle species. Large saproxylic beetle species, preferring larger deadwood pieces are known to be the most threatened across the European forests ([Hagge et al., 2021](#); [Seibold et al., 2015](#)). As a result, forest dieback could benefit threatened species in commercial forests.

Intensive management generally leads to functional homogenisation, which is often driven by the decline of specialist species in favour of generalists ([Clavel et al., 2011](#)). Our study plots were managed, and we found that forest dieback induced functional heterogenisation with an increase in the mean and dispersion of most of the traits tested. We hypothesise that the functional heterogenisation was driven by the high resource availability and habitat diversification subsequent to the forest dieback. At the landscape scale, the dieback logically resulted in a matrix of remaining live trees, acting as disturbance refugia ([Krawchuk et al., 2020](#)), and discrete patches of open woodlands with standing dead trees and snags, logs, large deadwood, tree-related microhabitats, etc. Ultimately, this promoted the coexistence of a wide variety of ecological niches ([Swanson et al., 2011](#)), allowing the co-occurrence of functionally diverse saproxylic beetle assemblages ([Kozák et al., 2021](#); [Thorn et al., 2018](#)).

4.5 Application and conclusions

Our study revealed that the taxonomic, functional and phylogenetic diversity of saproxylic beetle assemblages in Pyrenean montane fir forests significantly benefitted from forest dieback, at both local and landscape scales, mainly thanks to landscape heterogenisation, to a large build-up of deadwood and to more canopy openings ([Bouget et al., 2014](#); [Sallé and Bouget, 2020](#); [Sallé et al., 2020](#); [Thorn et al., 2017, 2018](#)). Our results lead us to consider unharvested declining forest stands as potentially relevant sites for biological conservation

([Hlásny et al., 2021](#); [Müller et al., 2010](#)) because they favour the functional diversity, abundance and richness of saproxylic beetle species otherwise threatened in conventionally managed stands ([Grove, 2002](#); [Hagge et al., 2021](#); [Seibold et al., 2015](#)). Moreover, it seems that local clusters of forest dieback alone may be insufficient to maintain diverse communities of saproxylic beetles. It is also necessary to maintain areas of forest dieback in the landscape, i.e. at scales of at least 1100 m and 1500 m ([Fig. 4](#); [Tab. 2](#)), mainly for functional diversity. Furthermore, the discrepancies we found in the response of various biodiversity dimensions call for a multidisciplinary integrative approach and studies on wide species communities in disturbed forests ([Sallé and Bouget, 2020](#); [Sallé et al., 2021](#); [Sire et al., 2022](#)).

5 Supplementary material

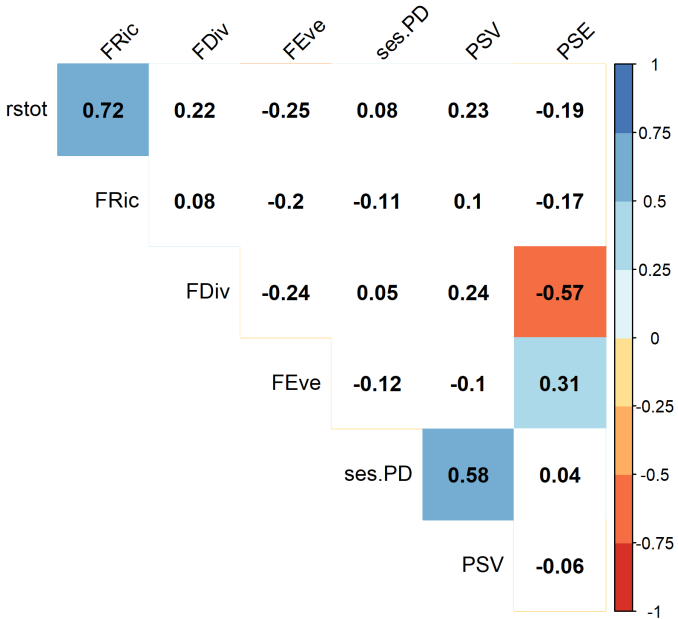


Figure S.1: Correlation table for the diversity indices. Coloured relationships are statistically significant at an α -level of 0.05. Blue represents positive correlations while red represents negative correlations. Numbers are the Pearson's r values. See Sect. 3.

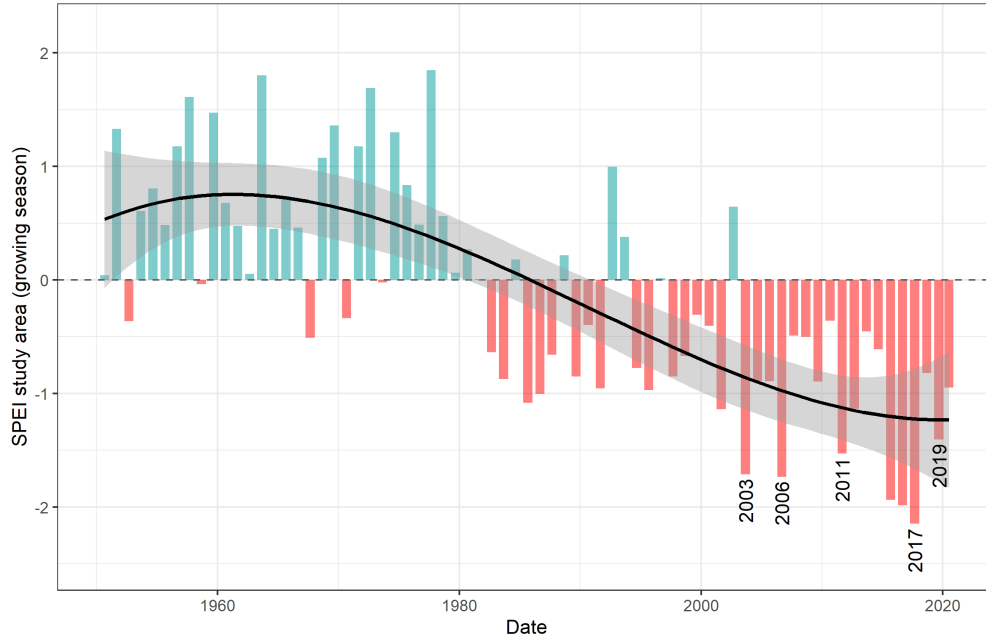


Figure S.2: Changes in the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano *et al.*, 2010) from 1950 to 2020 for the whole study area. Years marked by severe droughts are given under the corresponding bar; red: negative annual water balance (drought); blue: positive annual water balance (water surplus).

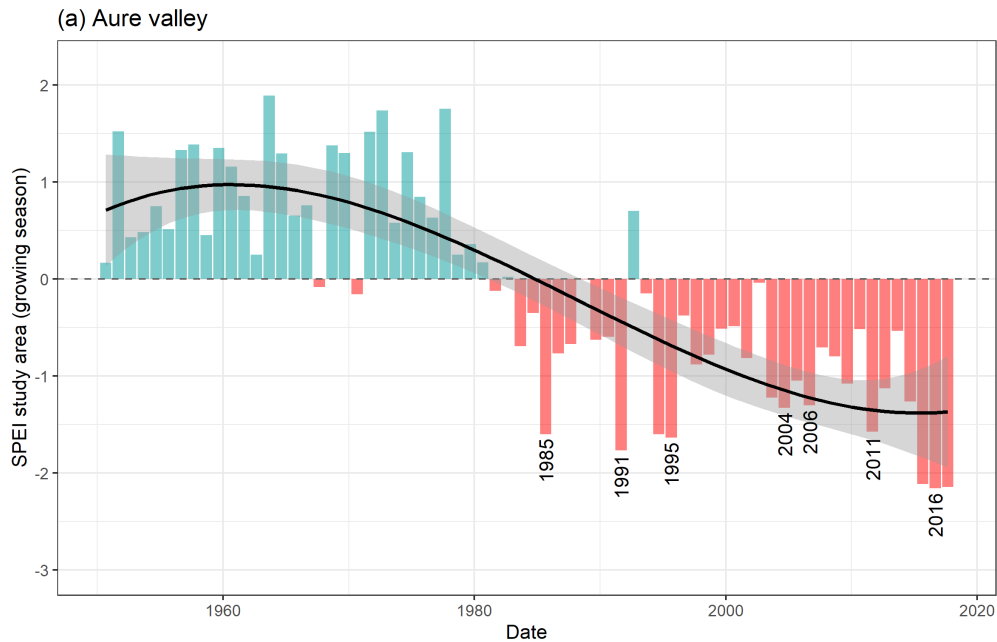


Figure S.3: Changes in the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano *et al.*, 2010) from 1950 to 2020 in Aure Valley area. Years marked by severe droughts are given under the corresponding bar; red: negative annual water balance (drought); blue: positive annual water balance (water surplus).

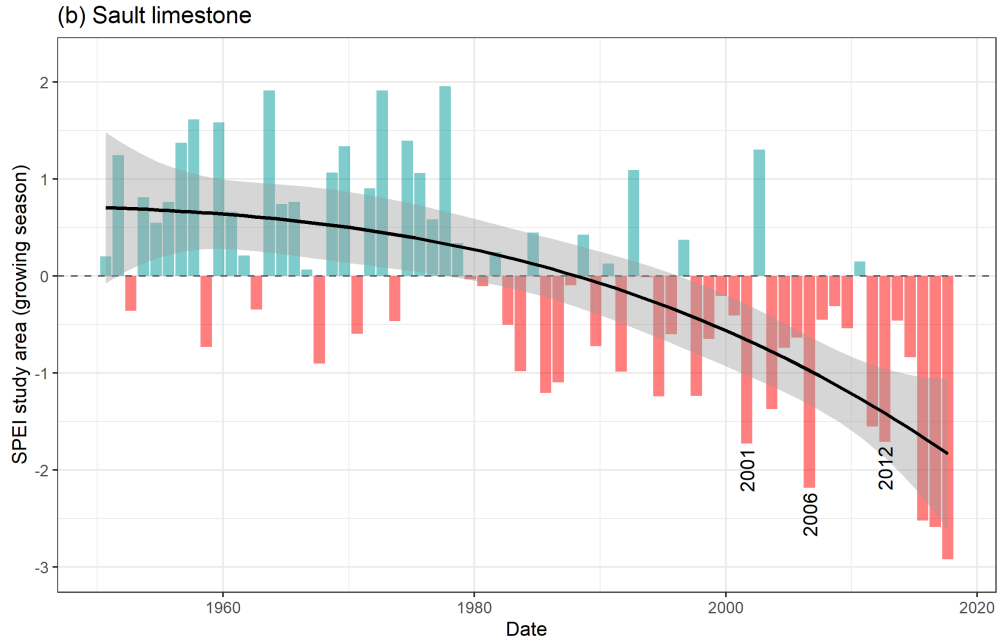


Figure S.4: Changes in the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano *et al.*, 2010) from 1950 to 2020 in the Sault plateau area. Years marked by severe droughts are given under the corresponding bar; red: negative annual water balance (drought); blue: positive annual water balance (water surplus).

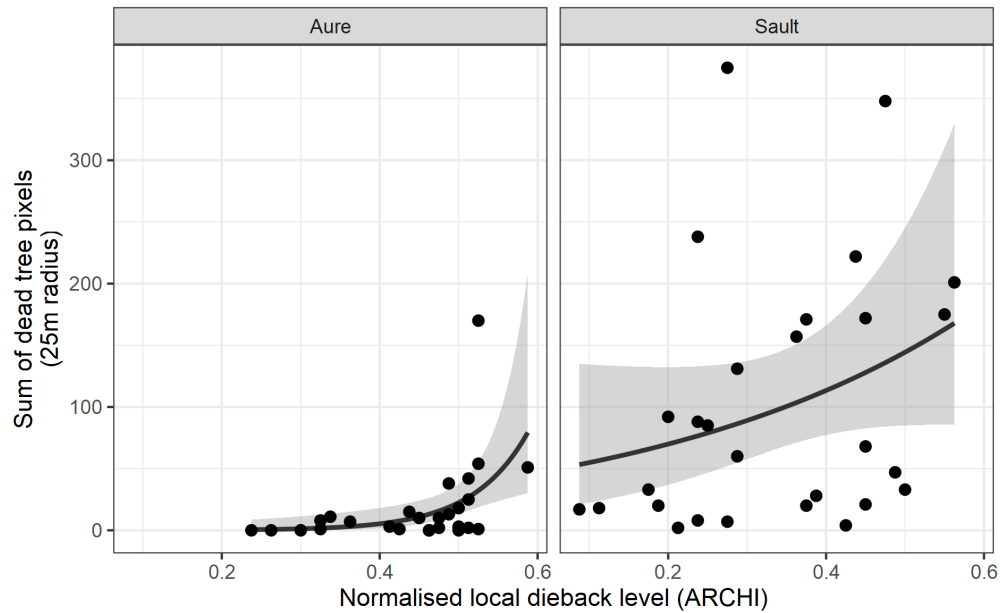


Figure S.5: Relationship between the sum of dead crown pixels in a 25m radius around study plot centres (from machine learning) and the actual forest dieback level quantified in the study plots with the ARCHI method.

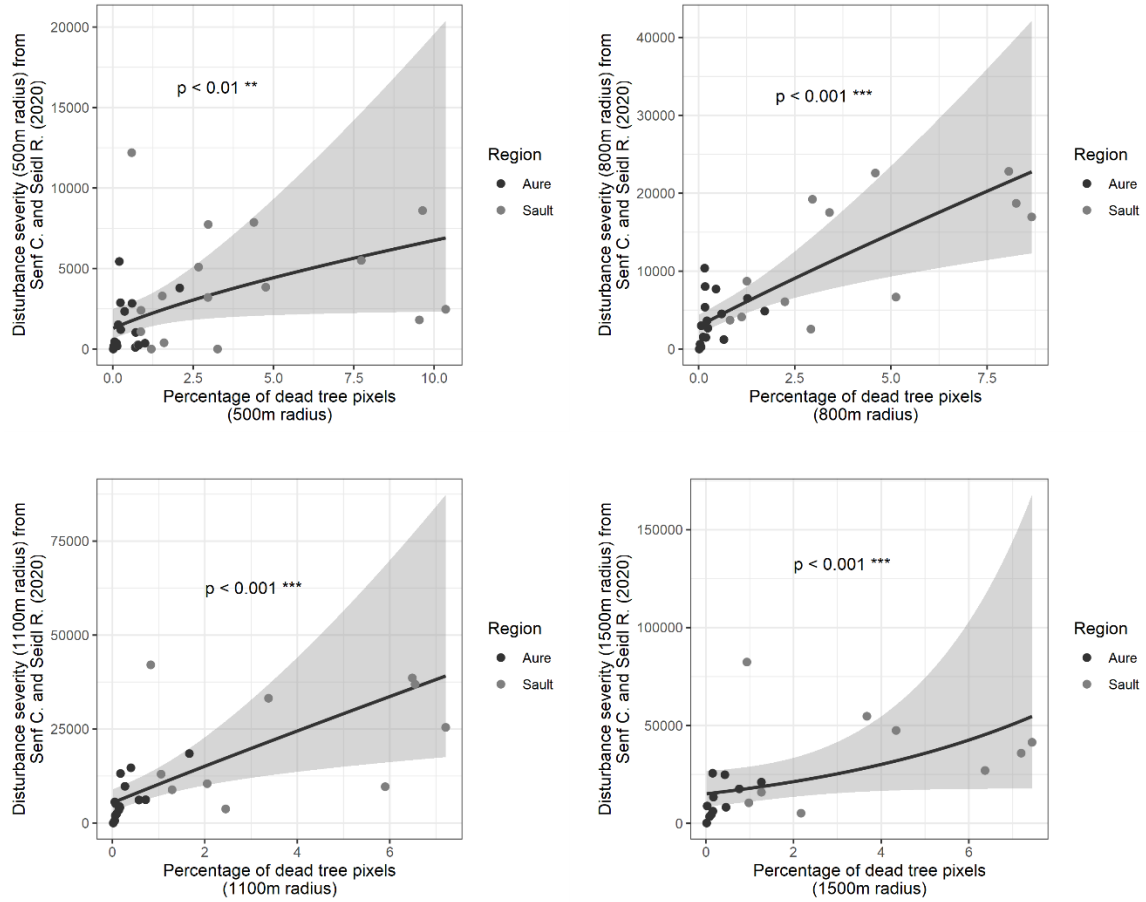


Figure S.6: Relationships between the sum of dead crown pixels at different landscape scales around the study plot centres (from machine learning) and the actual forest dieback level quantified in Senf and Seidl (2021a).

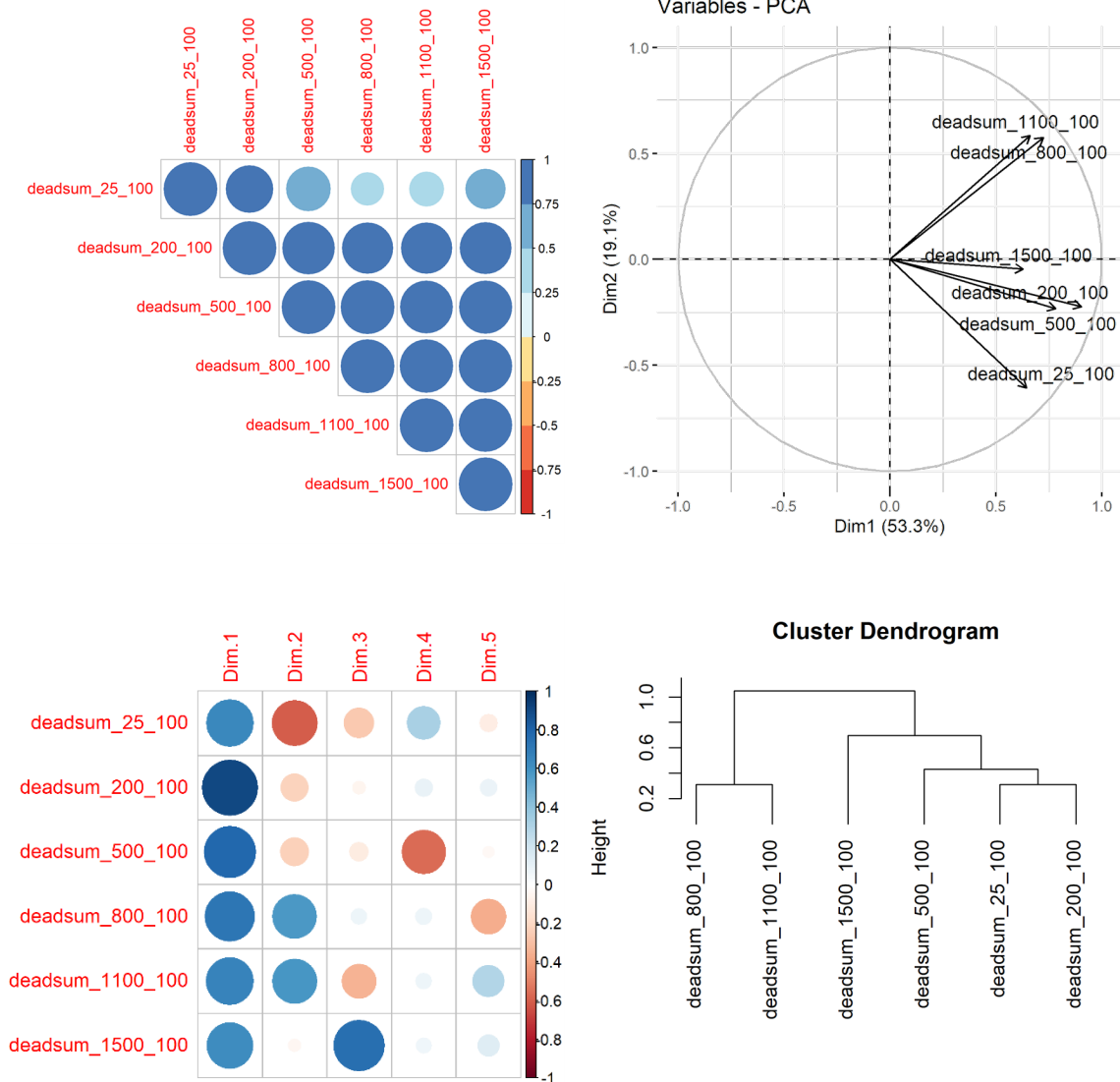


Figure S.7: **Above-left:** correlation table with dead crown sums according to different spatial scales. **Above-right:** results from the Principal component analysis (PCA) of all the spatial scales for forest dieback. **Bottom-left:** correlation between the dead crown sums and PCA dimensions at different spatial scales. **Bottom-right:** cluster dendrogram of the dead crown sums at different spatial scales.

Table S.1: *Pearson's r correlation coefficients between scales of forest dieback in non-overlapping buffers.*

Scales	25m	200m	500m	800m	1,100m	1,500m
25 m	1	0.78	0.68	0.38	0.41	0.55
200 m		1	0.95	0.91	0.91	0.93
500 m			1	0.99	0.97	0.97
800 m				1	0.98	0.99
1100 m					1	0.99
1500 m						1

Bibliography

- C. D. Allen, A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. T. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.-H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4):660–684, Feb. 2010. ISSN 0378-1127. doi:10/c3s4s4. URL <http://www.sciencedirect.com/science/article/pii/S037811270900615X>.
- C. Ammer, A. Fichtner, A. Fischer, M. M. Gossner, P. Meyer, R. Seidl, F. M. Thomas, P. Annighöfer, J. Kreyling, B. Ohse, U. Berger, E. Feldmann, K.-H. Häberle, K. Heer, S. Heinrichs, F. Huth, K. Krämer-Klement, A. Mölder, J. Müller, M. Mund, L. Opgenoorth, P. Schall, M. Scherer-Lorenzen, D. Seidel, J. Vogt, and S. Wagner. Key ecological research questions for Central European forests. *Basic and Applied Ecology*, 32:3–25, Nov. 2018. ISSN 1439-1791. doi:10.1016/j.baae.2018.07.006. URL <http://www.sciencedirect.com/science/article/pii/S1439179118300902>.
- W. R. L. Anderegg, J. M. Kane, and L. D. L. Anderegg. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3(1):30–36, Jan. 2013. ISSN 1758-6798. doi:10.1038/nclimate1635. URL <https://www.nature.com/articles/nclimate1635/>.
- M. E. Andrew, K. X. Ruthrof, G. Matusick, and G. E. S. J. Hardy. Spatial Configuration of Drought Disturbance and Forest Gap Creation across Environmental Gradients. *PLOS ONE*, 11(6):e0157154, June 2016. ISSN 1932-6203. doi:10/gbnqgd. URL <https://dx.plos.org/10.1371/journal.pone.0157154>.
- D. Bates, M. Maechler, B. Bolker [aut, cre, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, and J. Fox. lme4: Linear Mixed-Effects Models using 'Eigen' and S4, Apr. 2020. URL <https://CRAN.R-project.org/package=lme4>.
- K.-O. Bergman, N. Jansson, K. Claesson, M. W. Palmer, and P. Milberg. How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *Forest Ecology and Management*, 265:133–141, Feb. 2012. ISSN 0378-1127. doi:10.1016/j.foreco.2011.10.030. URL <https://www.sciencedirect.com/science/article/pii/S0378112711006530>.
- B. Beudert, C. Bässler, S. Thorn, R. Noss, B. Schröder, H. Dieffenbach-Fries, N. Foullois, and J. Müller. Bark Beetles Increase Biodiversity While Maintaining Drinking Water Quality. *Conservation Letters*, 8(4): 272–281, 2015. ISSN 1755-263X. doi:10.1111/conl.12153. URL <https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/conl.12153>.
- C. Bouget and P. Duelli. The effects of windthrow on forest insect communities: A literature review. *Biological Conservation*, 118(3):281–299, July 2004. ISSN 0006-3207. doi:10.1016/j.biocon.2003.09.009. URL <https://www.sciencedirect.com/science/article/pii/S0006320703003677>.
- C. Bouget, H. Brustel, and L.-M. Nageleisen. Nomenclature of wood-inhabiting groups in forest entomology: Synthesis and semantic adjustments. *Comptes Rendus Biologies*, 328(10-11):936–948, Sept. 2005. ISSN

- 1631-0691, 1768-3238. doi:[10.1016/j.crv.2005.08.003](https://doi.org/10.1016/j.crv.2005.08.003). URL <https://europepmc.org/article/med/16286083>.
- C. Bouget, L. Larrieu, B. Nusillard, and G. Parmain. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation*, 22(9):2111–2130, Aug. 2013. ISSN 1572-9710. doi:[10.1007/s10531-013-0531-3](https://doi.org/10.1007/s10531-013-0531-3). URL <https://doi.org/10.1007/s10531-013-0531-3>.
- C. Bouget, L. Larrieu, and A. Brin. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators*, 36:656–664, Jan. 2014. ISSN 1470-160X. doi:[10/gfdb7s](https://doi.org/10/gfdb7s). URL <http://www.sciencedirect.com/science/article/pii/S1470160X13003634>.
- C. Bouget, H. Brustel, T. Noblecourt, and P. Zagatti. *Les Coléoptères Saproxyliques de France: Catalogue Écologique Illustré*. Number 79 in Patrimoines Naturels. Paris, editions du mnhn edition, 2019.
- E. J. Bowd, S. C. Banks, A. Bissett, T. W. May, and D. B. Lindenmayer. Direct and indirect disturbance impacts in forests. *Ecology Letters*, 24(6):1225–1236, 2021. ISSN 1461-0248. doi:[10.1111/ele.13741](https://doi.org/10.1111/ele.13741). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13741>.
- B. F. Braumoeller. Hypothesis Testing and Multiplicative Interaction Terms. *International Organization*, 58(4):807–820, 2004. ISSN 0020-8183. URL <https://www.jstor.org/stable/3877804>.
- L. Breiman. Random Forests. *Machine Learning*, 45(1):5–32, Oct. 2001. ISSN 1573-0565. doi:[10.1023/A:1010933404324](https://doi.org/10.1023/A:1010933404324). URL <https://doi.org/10.1023/A:1010933404324>.
- W. Cai, C. Yang, X. Wang, C. Wu, L. Larrieu, C. Lopez-Vaamonde, Q. Wen, and D. W. Yu. The ecological impact of pest-induced tree dieback on insect biodiversity in Yunnan pine plantations, China. *Forest Ecology and Management*, 491:119173, July 2021. ISSN 0378-1127. doi:[10/gjk93t](https://doi.org/10/gjk93t). URL <https://www.sciencedirect.com/science/article/pii/S0378112721002619>.
- M. Calix, K. N. A. Alexander, A. Nieto, B. Dodelin, F. Soldati, D. Telnov, X. Vazquez-Albalade, O. Aleksandrowicz, P. Audisio, P. Istrate, N. Jansson, A. Legakis, A. Liberto, C. Makris, O. Merkl, R. M. Pettersson, J. Schlaghamersky, M. A. Bologna, H. Brustel, J. Buse, V. Novák, and L. Purchart. *European Red List of Saproxylic Beetles*. IUCN, Brussels, Belgium, 2018. URL <https://portals.iucn.org/library/node/47296>.
- J. Clavel, R. Julliard, and V. Devictor. Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9(4):222–228, May 2011. ISSN 1540-9295, 1540-9309. doi:[10.1890/080216](https://doi.org/10.1890/080216). URL <https://onlinelibrary.wiley.com/doi/abs/10.1890/080216>.
- B. Courbaud, L. Larrieu, D. Kozak, D. Kraus, T. Lachat, S. Ladet, J. Müller, Y. Paillet, K. Sagheb-Talebi, A. Schuck, J. Stillhard, M. Svoboda, and S. Zudin. 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, 2022. ISSN 1365-2664. doi:10.1111/1365-2664.14068. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.14068>.
- J. Cours, L. Larrieu, C. Lopez-Vaamonde, J. Müller, G. Parmain, S. Thorn, and C. Bouget. Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests. *Forest Ecology and Management*, 482, Feb. 2021. ISSN 0378-1127. doi:10/ghpnxz. URL <http://www.sciencedirect.com/science/article/pii/S0378112720315802>.
- G. De Luca, J. M. N. Silva, S. Cerasoli, J. Araújo, J. Campos, S. Di Fazio, and G. Modica. Object-Based Land Cover Classification of Cork Oak Woodlands using UAV Imagery and Orfeo ToolBox. *Remote Sensing*, 11(10):1238, Jan. 2019. doi:10.3390/rs11101238. URL <https://www.mdpi.com/2072-4292/11/10/1238>.
- M.-L. Delignette-Muller, C. Dutang, R. Pouillot, J.-B. Denis, and A. Siberchicot. Fitdistrplus: Help to Fit of a Parametric Distribution to Non-Censored or Censored Data, Jan. 2019. URL <https://CRAN.R-project.org/package=fitdistrplus>.
- V. Devictor, D. Mouillot, C. Meynard, F. Jiguet, W. Thuiller, and N. Mouquet. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, 13(8):1030–1040, 2010. ISSN 1461-0248. doi:10.1111/j.1461-0248.2010.01493.x. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2010.01493.x>.
- R. C. Edgar. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32(5):1792–1797, 2004. ISSN 1362-4962. doi:10/dz84kz.
- L. Fahrig. Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40(9):1649–1663, 2013. ISSN 1365-2699. doi:10.1111/jbi.12130. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/jbi.12130>.
- N. Franc, F. Götmark, B. Økland, B. Nordén, and H. Paltto. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biological Conservation*, 135(1):86–98, Feb. 2007. ISSN 0006-3207. doi:10.1016/j.biocon.2006.09.021. URL <http://www.sciencedirect.com/science/article/pii/S0006320706004216>.
- J. F. Franklin, D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. Threads of Continuity. *Conservation in Practice*, 1(1):8–17, 2000. ISSN 1552-5228. doi:10.1111/j.1526-4629.2000.tb00155.x. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1526-4629.2000.tb00155.x>.
- S. Gámez-Virués, D. J. Perović, M. M. Gossner, C. Börschig, N. Blüthgen, H. de Jong, N. K. Simons, A.-M. Klein, J. Krauss, G. Maier, C. Scherber, J. Steckel, C. Rothenwöhrer, I. Steffan-Dewenter, C. N. Weiner, W. Weisser, M. Werner, T. Tschardtke, and C. Westphal. Landscape simplification filters species

- traits and drives biotic homogenization. *Nature Communications*, 6(1):8568, Oct. 2015. ISSN 2041-1723. doi:[10.1038/ncomms9568](https://doi.org/10.1038/ncomms9568). URL <https://www.nature.com/articles/ncomms9568>.
- H. Gibb, J. Hjältén, J. P. Ball, O. Atlegrim, R. B. Pettersson, J. Hilszczański, T. Johansson, and K. Danell. Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: A study using experimental logs for monitoring assemblages. *Ecography*, 29(2):191–204, 2006. ISSN 1600-0587. doi:[10.1111/j.2006.0906-7590.04372.x](https://doi.org/10.1111/j.2006.0906-7590.04372.x). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.2006.0906-7590.04372.x>.
- U. Godeau, C. Bouget, J. Piffady, T. Pozzi, and F. Gosselin. The importance of being random! Taking full account of random effects in nonlinear sigmoid hierarchical Bayesian models reveals the relationship between deadwood and the species richness of saproxylic beetles. *Forest Ecology and Management*, 465:118064, June 2020. ISSN 0378-1127. doi:[10.1016/j.foreco.2020.118064](https://doi.org/10.1016/j.foreco.2020.118064). URL <http://www.sciencedirect.com/science/article/pii/S0378112719325940>.
- M. M. Gossner, T. Lachat, J. Brunet, G. Isacson, C. Bouget, H. Brustel, R. Brandl, W. W. Weisser, and J. Müller. Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests. *Conservation Biology*, 27(3):605–614, 2013. ISSN 1523-1739. doi:[10.1111/cobi.12023](https://doi.org/10.1111/cobi.12023). URL <https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/cobi.12023>.
- M. Grizonnet, J. Michel, V. Poughon, J. Inglada, M. Savinaud, and R. Cresson. Orfeo ToolBox: Open source processing of remote sensing images. *Open Geospatial Data, Software and Standards*, 2(1):15, June 2017. ISSN 2363-7501. doi:[10.1186/s40965-017-0031-6](https://doi.org/10.1186/s40965-017-0031-6). URL <https://doi.org/10.1186/s40965-017-0031-6>.
- S. J. Grove. Saproxylic Insect Ecology and the Sustainable Management of Forests. *Annual Review of Ecology and Systematics*, 33(1):1–23, 2002. doi:[10.1146/annurev.ecolsys.33.010802.150507](https://doi.org/10.1146/annurev.ecolsys.33.010802.150507). URL <https://doi.org/10.1146/annurev.ecolsys.33.010802.150507>.
- E. Haeler, A. Bergamini, S. Blaser, C. Ginzler, K. Hindenlang, C. Keller, T. Kiebacher, U. G. Kormann, C. Scheidegger, R. Schmidt, J. Stillhard, A. Szallies, L. Pellissier, and T. Lachat. Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. *Landscape Ecology*, 36(1):89–104, Jan. 2021. ISSN 0921-2973, 1572-9761. doi:[10.1007/s10980-020-01115-4](https://doi.org/10.1007/s10980-020-01115-4). URL <http://link.springer.com/10.1007/s10980-020-01115-4>.
- J. Hagge, J. Müller, T. Birkemoe, J. Buse, R. H. B. Christensen, M. M. Gossner, A. Gruppe, C. Heibl, A. Jarzabek-Müller, S. Seibold, J. Siitonen, J. G. Soutinho, A. Sverdrup-Thygeson, S. Thorn, and L. Drag. What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. *Journal of Animal Ecology*, 90(8):1934–1947, 2021. ISSN 1365-2656. doi:[10.1111/1365-2656.13512](https://doi.org/10.1111/1365-2656.13512). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2656.13512>.
- T. Hlásny, L. König, P. Krokene, M. Lindner, C. Montagné-Huck, J. Müller, H. Qin, K. F. Raffa, M.-J. Schelhaas, M. Svoboda, H. Viiri, and R. Seidl. Bark Beetle Outbreaks in Europe: State of Knowledge and

- Ways Forward for Management. *Current Forestry Reports*, 7(3):138–165, Sept. 2021. ISSN 2198-6436. doi:10/gm6fkh. URL <https://doi.org/10.1007/s40725-021-00142-x>.
- M. Immitzer, F. Vuolo, and C. Atzberger. First Experience with Sentinel-2 Data for Crop and Tree Species Classifications in Central Europe. *Remote Sensing*, 8(3):166, Mar. 2016. doi:10.3390/rs8030166. URL <https://www.mdpi.com/2072-4292/8/3/166>.
- J. Inglada, A. Vincent, M. Arias, B. Tardy, D. Morin, and I. Rodes. Operational High Resolution Land Cover Map Production at the Country Scale Using Satellite Image Time Series. *Remote Sensing*, 9(1):95, Jan. 2017. doi:10/gfvcb. URL <https://www.mdpi.com/2072-4292/9/1/95>.
- H. B. Jackson and L. Fahrig. Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, 24(1):52–63, 2015. ISSN 1466-8238. doi:10.1111/geb.12233. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12233>.
- P. Janssen, E. Cateau, M. Fuhr, B. Nusillard, H. Brustel, and C. Bouget. Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodiversity and Conservation*, 25(6):1167–1185, June 2016. ISSN 1572-9710. doi:10.1007/s10531-016-1116-8. URL <https://doi.org/10.1007/s10531-016-1116-8>.
- P. Janssen, M. Fuhr, E. Cateau, B. Nusillard, and C. Bouget. Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biological Conservation*, 205:1–10, Jan. 2017. ISSN 0006-3207. doi:10.1016/j.biocon.2016.11.021. URL <http://www.sciencedirect.com/science/article/pii/S0006320716308540>.
- J. F. Johnstone, C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14(7):369–378, Sept. 2016. ISSN 1540-9295, 1540-9309. doi:10/f83hfj. URL <https://onlinelibrary.wiley.com/doi/10.1002/fee.1311>.
- J. Kašák and J. Foit. Shortage of declining and damaged sun-exposed trees in European mountain forests limits saproxylic beetles: A case study on the endangered longhorn beetle *Ropalopus ungaricus* (Coleoptera: Cerambycidae). *Journal of Insect Conservation*, 22(2):171–181, Apr. 2018. ISSN 1572-9753. doi:10.1007/s10841-018-0050-3. URL <https://doi.org/10.1007/s10841-018-0050-3>.
- S. W. Kembel, D. D. Ackerly, S. P. Blomberg, W. K. Cornwell, P. D. Cowan, M. R. Helmus, H. Morlon, and C. O. Webb. Picante: Integrating Phylogenies and Ecology, June 2020. URL <https://CRAN.R-project.org/package=picante>.
- A. Komonen and J. Müller. Dispersal ecology of deadwood organisms and connectivity conservation. *Conservation Biology*, 32(3):535–545, 2018. ISSN 1523-1739. doi:10/gdb8s3. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/cobi.13087>.

- D. Kozák, M. Svitok, M. Wiezik, M. Mikoláš, S. Thorn, A. Buechling, J. Hofmeister, R. Matula, V. Trotsiuk, R. Bače, K. Begovič, V. Čada, M. Dušátko, M. Frankovič, J. Horák, P. Janda, O. Kameniar, T. A. Nagel, J. L. Pettit, J. M. Pettit, M. Synek, A. Wieziková, and M. Svoboda. Historical Disturbances Determine Current Taxonomic, Functional and Phylogenetic Diversity of Saproxyllic Beetle Communities in Temperate Primary Forests. *Ecosystems*, 24:37–55, 2021. ISSN 1435-0629. doi:[10.1007/s10021-020-00502-x](https://doi.org/10.1007/s10021-020-00502-x). URL <https://doi.org/10.1007/s10021-020-00502-x>.
- P. Kozel, P. Sebek, M. Platek, J. Benes, M. Zapletal, M. Dvorsky, V. Lanta, J. Dolezal, R. Bace, B. Zbuzek, and L. Cizek. Connectivity and succession of open structures as a key to sustaining light-demanding biodiversity in deciduous forests. *Journal of Applied Ecology*, n/a(n/a), 2021. ISSN 1365-2664. doi:[10.1111/1365-2664.14019](https://doi.org/10.1111/1365-2664.14019). URL <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.14019>.
- M. A. Krawchuk, G. W. Meigs, J. M. Cartwright, J. D. Coop, R. Davis, A. Holz, C. Kolden, and A. J. Meddens. Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. *Frontiers in Ecology and the Environment*, 18(5):235–244, 2020. ISSN 1540-9309. doi:[10/gg2fd4](https://doi.org/10.1002/fee.2190). URL <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/fee.2190>.
- T. Kuuluvainen. Conceptual models of forest dynamics in environmental education and management: Keep it as simple as possible, but no simpler. *Forest Ecosystems*, 3(1):18, Aug. 2016. ISSN 2197-5620. doi:[10.1186/s40663-016-0075-6](https://doi.org/10.1186/s40663-016-0075-6). URL <https://doi.org/10.1186/s40663-016-0075-6>.
- T. Lachat, C. Bouget, R. Bütler, and J. Müller. Deadwood: Quantitative and qualitative requirements for the conservation of saproxyllic biodiversity. In *Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity*, page 92. European Forest Institute, 2013.
- T. Lachat, M. Chumak, V. Chumak, O. Jakoby, J. Müller, M. Tanadini, and B. Wermelinger. Influence of canopy gaps on saproxyllic beetles in primeval beech forests: A case study from the Uholka-Shyrokyi Luh forest, Ukraine. *Insect Conservation and Diversity*, 9(6):559–573, 2016. ISSN 1752-4598. doi:[10.1111/icad.12188](https://doi.org/10.1111/icad.12188). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/icad.12188>.
- E. Laliberté, P. Legendre, and B. Shipley. FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology, Aug. 2014. URL <https://CRAN.R-project.org/package=FD>.
- J. Lambert, C. Drenou, J.-P. Denux, G. Balent, and V. Cheret. Monitoring forest decline through remote sensing time series analysis. *GIScience & Remote Sensing*, 50(4):437–457, Aug. 2013. ISSN 1548-1603. doi:[10.1080/15481603.2013.820070](https://doi.org/10.1080/15481603.2013.820070). URL <https://doi.org/10.1080/15481603.2013.820070>.
- L. Larrieu, Y. Paillet, S. Winter, R. Bütler, D. Kraus, F. Krumm, T. Lachat, A. K. Michel, B. Regnery, and K. Vandekerckhove. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, 84:194–207, Jan. 2018. ISSN 1470-160X. doi:[10.1016/j.ecolind.2017.08.051](https://doi.org/10.1016/j.ecolind.2017.08.051). URL <http://www.sciencedirect.com/science/article/pii/S1470160X17305411>.

- S. A. Levin. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology*, 73(6):1943–1967, 1992. ISSN 1939-9170. doi:10.2307/1941447. URL <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.2307/1941447>.
- D. Lüdecke, D. Makowski, P. Waggoner, and I. Patil. Performance: Assessment of Regression Models Performance, May 2020. URL <https://CRAN.R-project.org/package=performance>.
- R. H. MacArthur and E. O. Wilson. *The Theory of Island Biogeography*. Princeton University Press, 1967. ISBN 978-0-691-08836-5.
- A. Magnusson, H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, N. Sadat, D. Lüdecke, R. Lenth, J. O’Brien, and M. Brooks. glmmTMB: Generalized Linear Mixed Models using Template Model Builder, Mar. 2020. URL <https://CRAN.R-project.org/package=glmmTMB>.
- N. G. McDowell, C. D. Allen, K. Anderson-Teixeira, B. H. Aukema, B. Bond-Lamberty, L. Chini, J. S. Clark, M. Dietze, C. Grossiord, A. Hanbury-Brown, G. C. Hurtt, R. B. Jackson, D. J. Johnson, L. Kueppers, J. W. Lichstein, K. Ogle, B. Poulter, T. A. M. Pugh, R. Seidl, M. G. Turner, M. Uriarte, A. P. Walker, and C. Xu. Pervasive shifts in forest dynamics in a changing world. *Science*, 368(6494):eaaz9463, May 2020. ISSN 0036-8075, 1095-9203. doi:10.1126/science.aaz9463. URL <https://www.sciencemag.org/lookup/doi/10.1126/science.aaz9463>.
- D. Mouillot, N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28(3):167–177, Mar. 2013. ISSN 0169-5347. doi:10.1016/j.tree.2012.10.004. URL <https://www.sciencedirect.com/science/article/pii/S0169534712002650>.
- J. Müller and R. Bütler. A review of habitat thresholds for dead wood: A baseline for management recommendations in European forests. *European Journal of Forest Research*, 129(6):981–992, Nov. 2010. ISSN 1612-4677. doi:10.1007/s10342-010-0400-5. URL <https://doi.org/10.1007/s10342-010-0400-5>.
- J. Müller, H. Bußler, M. Goßner, T. Rettelbach, and P. Duelli. The European spruce bark beetle *Ips typographus* in a national park: From pest to keystone species. *Biodiversity and Conservation*, 17(12):2979, May 2008. ISSN 1572-9710. doi:10.1007/s10531-008-9409-1. URL <https://doi.org/10.1007/s10531-008-9409-1>.
- J. Müller, R. F. Noss, H. Bussler, and R. Brandl. Learning from a “benign neglect strategy” in a national park: Response of saproxylic beetles to dead wood accumulation. *Biological Conservation*, 143(11):2559–2569, Nov. 2010. ISSN 0006-3207. doi:10.1016/j.biocon.2010.06.024. URL <https://www.sciencedirect.com/science/article/pii/S0006320710002909>.
- D. A. Nipperess and F. A. Matsen. The mean and variance of phylogenetic diversity under rarefaction. *Methods in Ecology and Evolution*, 4(6):566–572, 2013. ISSN 2041-210X. doi:10.1111/2041-210X.12042. URL <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.12042>.

- V. S. Ojeda, M. L. Suarez, and T. Kitzberger. Crown dieback events as key processes creating cavity habitat for magellanic woodpeckers. *Austral Ecology*, 32(4):436–445, 2007. ISSN 1442-9993. doi:[10.1111/j.1442-9993.2007.01705.x](https://doi.org/10.1111/j.1442-9993.2007.01705.x). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1442-9993.2007.01705.x>.
- B. Økland, A. Bakke, S. Hågvar, and T. Kvamme. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity & Conservation*, 5(1):75–100, Jan. 1996. ISSN 1572-9710. doi:[10.1007/BF00056293](https://doi.org/10.1007/BF00056293). URL <https://doi.org/10.1007/BF00056293>.
- S. J. Otway, A. Hector, and J. H. Lawton. Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology*, 74(2):234–240, 2005. ISSN 1365-2656. doi:[10.1111/j.1365-2656.2005.00913.x](https://doi.org/10.1111/j.1365-2656.2005.00913.x). URL <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2656.2005.00913.x>.
- A. Paletto, I. De Meo, P. Cantiani, and F. Ferretti. Effects of forest management on the amount of deadwood in Mediterranean oak ecosystems. *Annals of Forest Science*, 71(7):791–800, Oct. 2014. ISSN 1297-966X. doi:[10.1007/s13595-014-0377-1](https://doi.org/10.1007/s13595-014-0377-1). URL <https://doi.org/10.1007/s13595-014-0377-1>.
- S. T. A. Pickett and P. S. White. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, 1985. ISBN 978-0-12-554520-4. doi:[10.1016/C2009-0-02952-3](https://doi.org/10.1016/C2009-0-02952-3). URL <https://linkinghub.elsevier.com/retrieve/pii/C20090029523>.
- M. N. Price, P. S. Dehal, and A. P. Arkin. FastTree 2 – Approximately Maximum-Likelihood Trees for Large Alignments. *PLOS ONE*, 5(3):e9490, Mar. 2010. ISSN 1932-6203. doi:[10/cfmfnh](https://doi.org/10.1371/journal.pone.0009490). URL <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0009490>.
- R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, 2023. URL <https://www.R-project.org/>.
- T. Ranius. Measuring the dispersal of saproxylic insects: A key characteristic for their conservation. *Population Ecology*, 48(3):177–188, July 2006. ISSN 1438-3896, 1438-390X. doi:[10.1007/s10144-006-0262-3](https://doi.org/10.1007/s10144-006-0262-3). URL <http://doi.wiley.com/10.1007/s10144-006-0262-3>.
- S. Ratnasingham and P. D. N. Hebert. BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes*, 7(3):355–364, 2007. ISSN 1471-8286. doi:[10/cv9qqw](https://doi.org/10.1111/j.1471-8286.2007.01678.x). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1471-8286.2007.01678.x>.
- S. Ratnasingham and P. D. N. Hebert. A DNA-Based Registry for All Animal Species: The Barcode Index Number (BIN) System. *PLOS ONE*, 8(7):e66213, 8 juil. 2013. ISSN 1932-6203. doi:[10.1371/journal.pone.0066213](https://doi.org/10.1371/journal.pone.0066213). URL <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0066213>.

- A. Sallé and C. Bouget. Victims or perpetrators: Contribution and response of insects to forest diebacks and declines. *Annals of Forest Science*, 77(4):104, Oct. 2020. ISSN 1297-966X. doi:[10.1007/s13595-020-01009-0](https://doi.org/10.1007/s13595-020-01009-0). URL <https://doi.org/10.1007/s13595-020-01009-0>.
- A. Sallé, G. Parmain, B. Nusillard, X. Pineau, R. Brousse, T. Fontaine-Guenel, R. Ledet, C. Vincent-Barbaroux, and C. Bouget. Forest decline differentially affects trophic guilds of canopy-dwelling beetles. *Annals of Forest Science*, 77(3):86, Sept. 2020. ISSN 1297-966X. doi:[10.1007/s13595-020-00990-w](https://doi.org/10.1007/s13595-020-00990-w). URL <https://doi.org/10.1007/s13595-020-00990-w>.
- A. Sallé, J. Cours, E. Le Souchu, C. Lopez-Vaamonde, S. Pincebourde, and C. Bouget. Climate Change Alters Temperate Forest Canopies and Indirectly Reshapes Arthropod Communities. *Frontiers in Forests and Global Change*, 4:120, 2021. ISSN 2624-893X. doi:[10.3389/ffgc.2021.710854](https://doi.org/10.3389/ffgc.2021.710854). URL <https://www.frontiersin.org/article/10.3389/ffgc.2021.710854>.
- L. Samaniego, S. Thober, R. Kumar, N. Wanders, O. Rakovec, M. Pan, M. Zink, J. Sheffield, E. F. Wood, and A. Marx. Anthropogenic warming exacerbates European soil moisture droughts. *Nature Climate Change*, 8(5):421, May 2018. ISSN 1758-6798. doi:[10.1038/s41558-018-0138-5](https://doi.org/10.1038/s41558-018-0138-5). URL <https://www.nature.com/articles/s41558-018-0138-5>.
- G. Sangüesa-Barreda, J. J. Camarero, J. Oliva, F. Montes, and A. Gazol. Past logging, drought and pathogens interact and contribute to forest dieback. *Agricultural and Forest Meteorology*, 208:85–94, Aug. 2015. ISSN 0168-1923. doi:[10.1016/j.agrformet.2015.04.011](https://doi.org/10.1016/j.agrformet.2015.04.011). URL <http://www.sciencedirect.com/science/article/pii/S016819231500115X>.
- S. Seibold, R. Brandl, J. Buse, T. Hothorn, J. Schmidl, S. Thorn, and J. Müller. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29(2): 382–390, 2015. ISSN 1523-1739. doi:[10.1111/cobi.12427](https://doi.org/10.1111/cobi.12427). URL <https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/cobi.12427>.
- S. Seibold, C. Bässler, R. Brandl, B. Büche, A. Szallies, S. Thorn, M. D. Ulyshen, and J. Müller. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, 53(3):934–943, 2016. doi:[10/f8xb6d](https://doi.org/10.1111/1365-2745.12666).
- S. Seibold, C. Bässler, R. Brandl, L. Fahrig, B. Förster, M. Heurich, T. Hothorn, F. Scheipl, S. Thorn, and J. Müller. An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecology*, 98(6):1613–1622, 2017. ISSN 1939-9170. doi:[10.1002/ecy.1819](https://doi.org/10.1002/ecy.1819). URL <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.1819>.
- R. Seidl, D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T. A. Nagel, and C. P. O. Reyer. Forest disturbances under climate change. *Nature Climate Change*, 7(6):395–402, June 2017. ISSN 1758-6798. doi:[10.1038/nclimate3303](https://doi.org/10.1038/nclimate3303). URL <https://www.nature.com/articles/nclimate3303>.

- C. Senf and R. Seidl. Mapping the forest disturbance regimes of Europe. *Nature Sustainability*, 4(1):63–70, Jan. 2021a. ISSN 2398-9629. doi:10.1038/s41893-020-00609-y. URL <https://www.nature.com/articles/s41893-020-00609-y>.
- C. Senf and R. Seidl. Persistent impacts of the 2018 drought on forest disturbance regimes in Europe. *Biogeosciences*, 18:5223–5230, Sept. 2021b. ISSN 1726-4170. doi:10/gnkwg. URL <https://bg.copernicus.org/articles/18/5223/2021/>.
- J. Siitonen. Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. *Ecological Bulletins*, (49):11–41, 2001. ISSN 0346-6868. URL <https://www.jstor.org/stable/20113262>.
- M. Similä, J. Kouki, and P. Martikainen. Saproxylic beetles in managed and seminatural Scots pine forests: Quality of dead wood matters. *Forest Ecology and Management*, 174(1):365–381, Feb. 2003. ISSN 0378-1127. doi:10.1016/S0378-1127(02)00061-0. URL <https://www.sciencedirect.com/science/article/pii/S0378112702000610>.
- L. Sire, P. S. Yáñez, C. Wang, A. Bézier, B. Courtial, J. Cours, D. Fontaneto, L. Larrieu, C. Bouget, S. Thorn, J. Müller, D. W. Yu, M. T. Monaghan, E. A. Herniou, and C. Lopez-Vaamonde. Climate-induced forest dieback drives compositional changes in insect communities that are more pronounced for rare species. *Communications Biology*, 5(1):1–17, Jan. 2022. ISSN 2399-3642. doi:10.1038/s42003-021-02968-4. URL <https://www.nature.com/articles/s42003-021-02968-4>.
- V. Speckens. Effets des dépérissements forestiers sur le bois mort et les dendromicrohabitats, et les communautés de coléoptères saproxyliques associées. Rapport de stage Master2, Université de Picardie Jules Verne (UPJV), Amiens, Sept. 2021. URL <https://hal.inrae.fr/hal-03348947>.
- J. N. Stokland, J. Siitonen, and B. G. Jonsson. *Biodiversity in Dead Wood*. Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge, 2012. ISBN 978-0-521-88873-8. doi:10.1017/CBO9781139025843. URL <https://www.cambridge.org/core/books/biodiversity-in-dead-wood/32EA8DA79A503B95795384FFA5BC993D>.
- A. Sverdrup-Thygeson, L. Gustafsson, and J. Kouki. Spatial and temporal scales relevant for conservation of dead-wood associated species: Current status and perspectives. *Biodiversity and Conservation*, 23(3): 513–535, Mar. 2014. ISSN 1572-9710. doi:10.1007/s10531-014-0628-3. URL <https://doi.org/10.1007/s10531-014-0628-3>.
- M. E. Swanson, J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, 9(2):117–125, 2011. ISSN 1540-9309. doi:10.1890/090157. URL <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/090157>.
- S. Thorn, C. Bässler, T. Gottschalk, T. Hothorn, H. Bussler, K. Raffa, and J. Müller. New Insights into the Consequences of Post-Windthrow Salvage Logging Revealed by Functional Structure of Saproxylic

- Beetles Assemblages. *PLOS ONE*, 9(7):e101757, 2014. ISSN 1932-6203. doi:10/f6whv7. URL <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0101757>.
- S. Thorn, C. Bässler, M. Svoboda, and J. Müller. Effects of natural disturbances and salvage logging on biodiversity – Lessons from the Bohemian Forest. *Forest Ecology and Management*, 388:113–119, Mar. 2017. ISSN 0378-1127. doi:10.1016/j.foreco.2016.06.006. URL <http://www.sciencedirect.com/science/article/pii/S0378112716303036>.
- S. Thorn, B. Förster, C. Heibl, J. Müller, and C. Bässler. Influence of macroclimate and local conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic beetles and wood-inhabiting fungi. *Biodiversity and Conservation*, 27(12):3119–3135, Oct. 2018. ISSN 1572-9710. doi:10.1007/s10531-018-1592-0. URL <https://doi.org/10.1007/s10531-018-1592-0>.
- S. M. Vicente-Serrano, S. Beguería, J. I. López-Moreno, M. Angulo, and A. El Kenawy. A New Global 0.5° Gridded Dataset (1901–2006) of a Multiscalar Drought Index: Comparison with Current Drought Index Datasets Based on the Palmer Drought Severity Index. *Journal of Hydrometeorology*, 11(4):1033–1043, Aug. 2010. ISSN 1525-755X. doi:10.1175/2010JHM1224.1. URL <https://journals.ametsoc.org/jhm/article/11/4/1033/5202/A-New-Global-0-5-Gridded-Dataset-1901-2006-of-a>.
- S. Villéger, N. W. H. Mason, and D. Mouillot. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *Ecology*, 89(8):2290–2301, 2008. ISSN 1939-9170. doi:10.1890/07-1206.1. URL <https://onlinelibrary.wiley.com/doi/abs/10.1890/07-1206.1>.
- C. O. Webb and N. C. A. Pitman. Phylogenetic Balance and Ecological Evenness. *Systematic Biology*, 51(6):898–907, Dec. 2002. ISSN 1063-5157. doi:10.1080/10635150290102609. URL <https://doi.org/10.1080/10635150290102609>.
- J. A. Wiens. Spatial Scaling in Ecology. *Functional Ecology*, 3(4):385–397, 1989. ISSN 0269-8463. doi:10.2307/2389612. URL <https://www.jstor.org/stable/2389612>.