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Drought-induced Forest Dieback Increases Taxonomic and Functional Diversity But Not Phylogenetic Diversity of Saproxyllic Beetles at Both Local and Landscape Scales

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Abstract

Context: Forest ecosystems worldwide 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 classic 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 dead tree crowns 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: In line with the habitat-amount hypothesis, taxonomic and functional diversity, but not phylogenetic diversity, of beetle assemblages significantly benefitted from forest dieback, at both local and landscape scales. Very few single or interaction effects were detected in the multiplicative models combining local and landscape variables, though a significant positive effect of landscape-scale dieback on the abundance of cavity- and fungus-dwelling species was consistent with a spill-over effect. Increased landscape-scale dieback also caused a functional specialisation of beetle assemblages, favouring those related to large-diameter, 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.

Introduction

Natural disturbances are major drivers of forest spatial and temporal dynamics (Pickett and White 1985; Kuuluvainen 2016; Bowd et al. 2021). Multiple disturbance complexes shape the structural heterogeneity of forests and generate key resources such as tree-related microhabitats, canopy gaps, and snags and logs, generally referred to as biological legacies (Franklin et al. 2000; Johnstone et al. 2016), which are colonized by diverse, and often specific communities (Swanson et al. 2011; Lachat et al. 2016; Kuuluvainen 2016). 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 (Siitonen 2001; Grove 2002). As a consequence, saproxylic beetles are at considerable risk

in intensively managed forests (Grove 2002), 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 and the number of tree-related microhabitats are likely to increase and this may favour saproxylic communities (Müller et al. 2010; Thorn et al. 2017; Sallé et al. 2020, 2021; Cours et al. 2021). Several local-scale (i.e. less than 0.5ha) 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 hypothesized that declining stands may improve habitat conditions for threatened forest communities such as saproxylic beetles (e.g. Müller et al. 2010; Kašák and Foit 2018; Sallé et al. 2021).

Most studies focus on the taxonomical responses of biological communities to forest dieback (Cai et al. 2021, but see Thorn et al. 2014; Kozák et al. 2020; Sire et al. 2021). 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. 2020).

Furthermore, many previous studies have highlighted the fact that the diversity and structure of local saproxylic beetle communities rely on local habitat conditions, though they may also depend on large scale, i.e. landscape, conditions (e.g. Økland et al. 1996; Gibb et al. 2006; Franc et al. 2007; Haeler et al. 2021). Sampling area size influences the detection of biodiversity responses to environmental conditions, a phenomenon known as “*the scale of effect*” (Jackson and Fahrig 2015) (Wiens 1989; Levin 1992; Percel et al. 2019). Insects are often highly mobile; they spread across landscapes in search of new resources, habitats and/or reproductive partners (Ranius 2006; Janssen et al. 2016; Komonen and Müller 2018) 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 (MacArthur and Wilson 1967; Fahrig 2013; 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 colonizing 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. However, few studies have monitored insect responses to forest disturbances at these various scales, and even fewer combine taxonomic, functional and phylogenetic responses (Kozák et al. 2020).

In our study, we assessed how multi-scale forest dieback shaped local saproxylic beetle assemblages. 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. 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 (Müller et al. 2010; Bouget et al. 2014; Seibold et al. 2016). We expected an increase in species richness resulting from the “*Species-Area Relationship*” (MacArthur and Wilson 1967) and an increase in abundance from the “*More-Individuals Hypothesis*” (Srivastava and Lawton 1998; Müller et al. 2018). We also expected contrasted responses according to functional guilds (e.g. trophic; Percel et al. 2019). Therefore, in this study, we addressed three major questions:

- i. Are the effects of forest dieback globally positive on the community metrics for saproxylic beetle assemblages?
- ii. How does large-scale dieback affect saproxylic beetles assemblages?
- iii. What are the main mechanisms driving the effects of forest dieback on saproxylic beetle assemblages?

Materials And Methods

2.1 Site description

A total of 56 plots were chosen in mountain 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). Forests occupied 50% of the Aure Valley and 75% of the Sault region. 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 ± 5%) of the forests on the Sault Plateau. Most of the forest stands surrounding our study plots were managed for wood 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. S3-5).

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. 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% salt 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 (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 xylofungicolous) and species rarity (rare vs. common) (Tab. 1; Bouget et al. 2005, 2019).

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 sites (geoservices.ign.fr). As NGI aerial photographs are taken approximately every five 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 4,256 polygons for four land cover classes: 1,743 polygons of dead crowns (41%), 1,606 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).

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 (Immitzer et al. 2016; De Luca et al. 2019). We used a minimum size of four pixels (4 m²). 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 designated several nested buffer zones around our study plots in order to describe forest dieback from the local to the landscape scale. The zones had radii of 25, 200, 500, 800, 1100 and 1500 m; we added the dead crown pixels in each of these buffer zones (Tab. 1).

2.4 Statistical analyses

Data analysis was conducted with R software 4.0.0 (R Core Team 2021). Firstly, we 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 species richness.

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) and 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*”. 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 sequences 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 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 658bp-long sequences ($N < 1\%$) whenever possible. The dataset of the records we used for phylogenetic diversity is publicly available at the following DOI: DS-PHYLOCOL XXX. 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 sites 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 “site” (i.e. Aure Valley or Sault Plateau) as a random variable. 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. site) and the sum of the dead crown pixels for a particular spatial scale. For each response variable, we selected the best-fitting error structure with the fitdistrplus 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, 1,100 m and 1,500 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 and performed AICc comparisons between the models to select the best landscape scale for each tested response variable. We checked for non-collinearity between local and landscape scales with the “check_collinearity” function from the performance R-package (Lüdecke et al. 2020) and always observed a variance inflation factor (VIF) below three. We then performed multiple regressions with generalized linear mixed models with “site” (Aure Valley or Sault Plateau) as a random variable and including as fixed variables, the measure of local dieback and the best landscape scale. 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 lowest AICc value) with a multiplicative interaction model (Equation 1). Since the 200-m scale was highly correlated with the 25 m-scale (Pearson’s $r = 0.82$, $P < 0.001$), we excluded this metric from our analysis (Fig. S8).

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

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 & 4) and that a significantly negative interaction term would support a dilutive/saturated effect and the habitat-patch hypothesis (Fig. 3d & 4; 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 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. The absence of an interaction effect would also support the habitat-amount hypothesis (MacArthur and Wilson 1967; Fahrig 2013; Seibold et al. 2017).

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 Local and landscape forest dieback

3.1.1 Validation of forest dieback metrics

To assess the relevance of the sum 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 (Drénou et al. 2013). The ARCHI protocol classifies trees in a gradient from healthy to dead, based on their architecture (Drénou et al. 2013). In our study, we applied the protocol to the 20 fir trees closest to each plot centre. We observed a significant relationship between the two variables (β -Estimate = 0.7; $P < 0.01$; Fig. S6), which indicates that our classification model of dead crown pixels and the sum 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 sum of dead crown pixels at the landscape scales (i.e. $R=200$ to 1500 m) with the European disturbance map edited by Senf and Seidl (2021), which is based on a time series analysis of the spectral band values of Landsat satellite photographs ($P < 0.001$; Fig. S7).

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. S1). Nevertheless, we found a positive relationship between total species richness and FRic (Fig. S1), but not with FDiv (Fig. S1) and FEve (Fig. S1). 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. S1) and a positive relationship between PSE and FEve (Fig. S1).

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 total species richness, abundance and richness of common species, and on abundance of rare species (Tab. 2; Fig.

S2). In contrast, rare-species richness did not respond to forest dieback at any scale (Tab. 2; Fig. S2). Almost no effect was detected in the multiplicative models. Nonetheless, the abundance of common species still responded positively to forest dieback at the local spatial scale, thus supporting a concentration effect. (Tab. 2; Fig. 3).

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 (Tab. 2; Fig. S2). In contrast, the richness of wood-eating species positively responded to both local- and landscape-scale dieback (Tab. 2; Fig. S2). In the multiplicative models, neither the abundance nor the species richness of wood-eating beetles significantly responded to forest dieback; this supports the habitat-amount hypothesis (Tab. 2; Fig. 3). Cavicolous and fungicolous species responded positively to forest dieback at the local and landscape scales, both in terms of abundance and richness, in the univariate models (Tab. 2; Fig. S2). In the multiplicative models, we detected a significant positive effect of dieback level at the landscape scale on fungicolous and cavicolous abundance in agreement with the spill-over effect (Tab. 2; Fig. 3).

3.4 Response of phylogenetic diversity to dieback

In both the univariate and multiplicative models, none of the phylogenetic diversity metrics responded to forest dieback at either the local or landscape scale. (Tab. 3; Fig. S2).

3.5 Response of functional diversity to dieback

In the univariate models, we observed positive effects for both local and landscape forest dieback on FRic and for landscape dieback only on FDiv; we observed negative effects for landscape forest dieback on FEve (Tab. 3). Concerning substrate metrics, we only noted a positive effect of forest dieback on the mean community preference for deadwood diameter (CWM DW diameter) and for deadwood decay (CWM DW decay) at the landscape scale (Tab. 3; Fig. S2). We observed parallel negative effects for forest dieback at the landscape scale on the functional dispersion of deadwood diameter preference (FDis DW diameter; Tab. 3; Fig. S2) and positive effects, also at the landscape scale, on the functional dispersion of deadwood decay preference (FDis DW decay; Tab. 3; Fig. S2). With the multiplicative models, a negative effect of landscape dieback and a positive interaction effect between local and landscape dieback on FEve were detected (Tab. 3). Concerning substrate traits, we observed a positive response of CWM DW diameter and a negative response of FDis DW diameter to landscape scale dieback (Tab. 3). In contrast, the functional traits canopy opening preference and body size did not respond to forest dieback in either the univariate or multiplicative models (Tab. 3).

Discussion

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 forest dieback had an overall positive effect on the taxonomic diversity of saproxylic beetles, at both local and landscape scales. 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 (Müller and Bütler 2010; Lassauce et al. 2011; Bouget et al. 2014; Thorn et al. 2018; Godeau et al. 2020; Sallé et al. 2020, 2021; Haeler et al. 2021).

4.2 Large-scale effects of forest dieback

Our results highlight the relevance of the landscape scale (i.e. from 500 m to 1500 m) when considering the effect of forest dieback on local saproxylic beetle communities. With the exception of the 200 m scale, which was strongly correlated with the local scale, we noticed that the best landscape scales (i.e. with the lowest AICc) for measuring the impact of dieback on saproxylic beetle diversity were the larger scales, i.e. 1100 m and 1500 m (except for wood-eating species richness; Tab. 2 & 3). 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 (Økland et al. 1996; Gibb et al. 2006; Franc et al. 2007; Sverdrup-Thygeson et al. 2014; Haeler et al. 2021). 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; Seibold et al. 2016; Kozel et al. 2021). Furthermore, our results showed positive responses to forest dieback at the landscape scale for most of our variables (except for rare species richness, wood-eating species abundance, phylogenetic diversity metrics, and CWM and FDis of canopy closure preference and mean size body; Tab. 2 & 3). 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).

Furthermore, we observed a significant landscape effect of forest dieback on the abundance of both cavicolous and fungicolous species (Tab. 2). The increasing severity of forest dieback in the surroundings of the local sites induced a spill-over effect on the abundance of these two substrate guilds. These results 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; Ojeda et al. 2007; Larrieu et al. 2018; Speckens 2021).

We did not observe any significant interaction between local and landscape forest dieback (Tab. 2). According to Seibold et al. (2017), the lack of interaction between these two spatial scales should support the habitat-amount hypothesis since the amount of habitat at both scales is merely additive (Fig. 4). 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 (Tab. 2; Fig. S2). 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, unless there is a spill-over effect (see cavicolous and fungicolous species, Tab. 2; Bouget and Parmain 2016).

Forest dieback at the landscape scale also had effects on the functional diversity metrics, mainly FDiv and FEve which did not respond to local forest dieback (Tab. 3). In another study, based on data from the same Pyrenean plots and from plots located in Bavarian mountain forests (Cours et al. 2021), we hypothesized that the severity of the local forest dieback in Bavaria was correlated to dieback severity at the landscape scale, as sudden, large-scale 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 (Tab. 3; Gámez-Virués et al. 2015; Cours et al. 2021).

4.3 Contrasting responses of different biodiversity dimensions to forest dieback

We did not detect any response to forest dieback for phylogenetic diversity. However, PSE was negatively correlated with FDiv and positively correlated with FEve, both of which were influenced by landscape forest dieback (Tab. 3; Fig. S1-2). Therefore, forest dieback did not seem to induce any loss or gain in the range of evolutionary history occupied by saproxylic beetle assemblages, or if so, only indirectly by influencing functional diversity. Nonetheless, the use of DNA barcodes alone may be insufficient to estimate real phylogenetic diversity and the inclusion of multigene phylogenies may better estimate phylogenetic diversity and its response to ecological processes (Liu et al. 2019). In contrast, taxonomic

and functional diversities were influenced by forest dieback (Tab. 2 & 3). Consequently, the diversity and quantity of habitats and resources released by forest dieback increased species richness and more heterogeneous functional assemblages, as suggested by the more-individuals and the habitat-heterogeneity hypotheses (Seibold et al. 2016), without significantly increasing phylogenetic diversity. Furthermore, phylogenetic response to disturbance may be such a long-term process that the effects of forest dieback on this component could not be observed in our study (Purschke et al. 2013). However, Kozák et al. (2020) 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 (Tab. 3). 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 (Thorn et al. 2018; Sallé et al. 2021; Cours et al. 2021). Here, we demonstrate that this probably stands true at larger spatial scales.

We observed a positive response to forest dieback for functional divergence (FDiv) and a negative response for functional evenness (FEve), but only at the landscape scale. When FDiv increases with the severity of forest dieback, this indicates that the dieback has made the arrangement of traits in the functional space wider (Mouillot et al. 2013). In parallel, when FEve decreases, it means that forest dieback leads to a less equal arrangement of traits in the functional space filled by the community (Villéger et al. 2008; Mouillot et al. 2013). Consequently, our results suggest that forest dieback at the landscape scale clustered the functional traits of local saproxylic beetle assemblages (decrease in FEve) into the extreme values of the functional spaces filled by these assemblages (increase in FDiv and FRic), and therefore led to local assemblage specialisation (Mouillot et al. 2013). Our results also suggest that forest dieback clustered the assemblages even more when it was severe at both the local and landscape scales, even if local dieback had no effect in the univariate and multiplicative models (positive synergistic effect in the multiplicative model; Fig. 4, Tab. 3). Therefore, forest dieback, especially at the landscape scale, seemed to promote and enhance local functional heterogeneity and thus diversify the functional niches of saproxylic beetles, at our study sites in the Pyrenean mountains. 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 plots were managed, and we found that forest dieback induced a functional heterogenisation accompanied by a specialisation of the studied assemblages at the boundaries of the functional space. We hypothesize 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 (Thorn et al. 2018; Kozák et al. 2020).

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; Tab. 3). 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; Tab. 3). 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 invaluable for biodiversity (Similä et al. 2003; Gossner et al. 2013; Lachat et al. 2013; Bouget et al. 2013; Kozák et al. 2020).

4.5 Application and conclusions

Our study revealed that the taxonomic and functional diversity of saproxylic beetle assemblages in Pyrenean mountain 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; Thorn et al. 2017, 2018; Sallé et al. 2020; Sallé and Bouget 2020). Our results lead us to consider unharvested declining forest stands as potentially relevant sites for biological conservation (Müller et al. 2010, 2019; Hlásny et al. 2021) because they favour the functional diversity, abundance and richness of saproxylic beetle species otherwise threatened in conventionally managed stands (Grove 2002). In line with the habitat-amount hypothesis supported by our results, 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 (Tab. 2 & 3). 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. 2021)

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Tables

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

Variable	Definition	Mean \pm CI 95%	Range (min - max)
Predictors			
Forest dieback severity			
25 m-scale	Sum of DCP within the 25 m radius.	59 \pm 23	0 - 375
200 m-scale	Sum of DCP within the 200 m radius.	3,239 \pm 1,131	8 - 15,799
500 m-scale	Sum of DCP within the 500 m radius.	20,801 \pm 7,047	126 - 81,369
800 m-scale	Sum of DCP within the 800 m radius.	52,105 \pm 17,310	349 - 209,221
1100 m-scale	Sum of DCP within the 1100 m radius.	94,175 \pm 30,291	732 - 351,300
1500 m-scale	Sum of DCP within the 1500 m radius.	165,980 \pm 51,111	1,307 - 583,590
Response			
Total species richness	Species richness of all saproxylic beetles	83 \pm 4	51 - 123
Common species			
Abundance	Abundance of common saproxylic beetles	715 \pm 122	120 - 2716
Richness	Species richness of common saproxylic beetles	70 \pm 4	43 - 105
Rare species			
Abundance	Abundance of rare saproxylic beetles	22 \pm 9	3 - 245
Richness	Species richness of rare saproxylic beetles	6 \pm 0.5	2 - 11
Wood-eating species			
Abundance	Abundance of wood-eating beetles	548 \pm 119	104 - 2589
Richness	Species richness of wood-eating beetles	31 \pm 2	16 - 50
Cavicolous species			
Abundance	Abundance of cavicolous beetles	50 \pm 8	8 - 143
Richness	Species richness of cavicolous beetles	11 \pm 1	3 - 21
Fungicolous species			
Abundance	Abundance of fungicolous beetles	242 \pm 29	41 - 622
Richness	Species richness of fungicolous beetles	33 \pm 2	17 - 47
Phylogenetic diversity			
SES Faith's PD	Faith's standardized phylogenetic diversity	-1.35 \pm 0.2	-3.0 - 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
Functional diversity (Villéger et al. 2008; Mouillot et al. 2013)			
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
CWM			
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 mean body size	4.9 \pm 0.4	2.9 - 9.9
FDis			
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 mean 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 \geq 3 in France.

Table 2. Results from the univariate (on left, column 3) and multiplicative interaction models (right-hand column) of the effects of local (R=25 m) and surrounding-landscape (highest scale of effect) dieback on the taxonomic diversity of saproxylic beetles.*

Response of local assemblage metrics	Effects	Simple effects			Interactive effects		
	Models	Univariate	Multi.	Mechanism	Multi.	Mechanism	
Total species richness	Local	3.1**	1.9 ^{ns}	HAH	-0.5 ^{ns}	HAH	
	Landscape 1100m	4.5***	1.6 ^{ns}	HAH			
Common species	Abundance	Local	3.9***	2.8*	Concentration	-1.4 ^{ns}	HAH
		Landscape 1500m	3.3**	1.2 ^{ns}	HAH		
	Richness	Local	3.1**	1.8 ^{ns}	HAH	-0.4 ^{ns}	HAH
		Landscape 1100m	4.6***	1.6 ^{ns}	HAH		
Rare species	Abundance	Local	5.4***	-0.5 ^{ns}	HAH	2.3 ^{ns}	HAH
		Landscape 1100m	5.6***	0.2 ^{ns}	HAH		
	Richness	Local	2.2 ^{ns}	1.7 ^{ns}	No effect	-0.9 ^{ns}	No effect
		Landscape 1100m	1.6 ^{ns}	0.6 ^{ns}			
Wood-eating sp.	Abundance	Local	3.5**	2.2 ^{ns}	HAH	-0.3 ^{ns}	HAH
		Landscape 1500m	2.1 ^{ns}	-0.3 ^{ns}	No effect		
	Richness	Local	4.4***	1.5 ^{ns}	HAH	0.3 ^{ns}	HAH
		Landscape 500m	3.8***	0.5 ^{ns}	HAH		
Cavicolous sp.	Abundance	Local	2.5*	0.4 ^{ns}	HAH	0.02 ^{ns}	HAH
		Landscape 1500m	5.9***	3.0**	Spill-over		
	Richness	Local	3.2**	1.3 ^{ns}	HAH	-0.4 ^{ns}	HAH
		Landscape 1100m	2.8*	0.9 ^{ns}	HAH		
Fungicolous sp.	Abundance	Local	2.1*	2.1 ^{ns}	HAH	-1.7 ^{ns}	HAH
		Landscape 1500m	3.7**	2.5*	Spill-over		
	Richness	Local	2.4*	2.3 ^{ns}	HAH	-1.4 ^{ns}	HAH
		Landscape 1100m	3.9***	1.9 ^{ns}	HAH		

* Effects were tested with generalized linear mixed models (with “site” as a random variable). Values shown are z.values from glmmTMB models. Colours represent the direction of the effect: green for a positive effect of dieback on the considered variable and grey when no significant effects were detected. “Multi.” = “Multiplicative model”; “HAH” = “habitat-amount hypothesis”; ^{ns} = P > 0.05; * = P < 0.05; ** = P < 0.01; *** = P < 0.001

Table 3. Results from the univariate (on left, column 3) and multiplicative interaction models (right-hand column) of the effects of local (R=25 m) and surrounding-landscape (highest scale of effect) dieback on saproxylic beetles (phylogenetic and functional diversity).*

Response of local assemblage metrics	Effects	Simple effects		Interactive effects	
	Models	Univariate	Multiplicative	Multiplicative	
Phylogenetical diversity	SES Faith's PD	Local	0.34 ^{ns}	0.81 ^{ns}	-0.65 ^{ns}
		Landscape 1500m	1.4 ^{ns}	0.36 ^{ns}	
	Variability	Local	0.01 ^{ns}	1.2 ^{ns}	-1.4 ^{ns}
		Landscape 1500m	0.3 ^{ns}	2.2 ^{ns}	
	Evenness	Local	-0.04 ^{ns}	0.8 ^{ns}	-0.7 ^{ns}
		Landscape 1500m	-0.7 ^{ns}	-0.2 ^{ns}	
Functional diversity	Richness	Local	4.2***	1 ^{ns}	0.7 ^{ns}
		Landscape 1500m	3.5***	0.4 ^{ns}	
	Divergence	Local	0.2 ^{ns}	-2.14 ^{ns}	1.8 ^{ns}
		Landscape 1500m	4.4***	0.87 ^{ns}	
	Evenness	Local	-0.3 ^{ns}	-1.7 ^{ns}	2.5*
		Landscape 1500m	-3.4**	-3.9***	
CWM	DW Diameter	Local	1.4 ^{ns}	-0.3 ^{ns}	-0.3 ^{ns}
		Landscape 1100m	4.5***	3.3**	
	DW Decay	Local	1.9 ^{ns}	-1.6 ^{ns}	2.2 ^{ns}
		Landscape 1500m	3.1*	0.8 ^{ns}	
	Canopy closure	Local	-0.03 ^{ns}	-0.02 ^{ns}	0.03 ^{ns}
		Landscape 1500m	-0.05 ^{ns}	-0.07 ^{ns}	
Body size	Local	0.14 ^{ns}	-0.12 ^{ns}	0.12 ^{ns}	
	Landscape 1500m	0.1 ^{ns}	-0.005 ^{ns}		
FDis	DW Diameter	Local	-1.8 ^{ns}	-1.0 ^{ns}	1.3 ^{ns}
		Landscape 1500m	-2.8*	-2.5*	
	DW Decay	Local	0.4 ^{ns}	-1.4 ^{ns}	1.2 ^{ns}
		Landscape 1500m	5.4***	1.2 ^{ns}	
	Canopy closure	Local	-0.09 ^{ns}	-0.13 ^{ns}	0.003 ^{ns}
		Landscape 1500m	-0.01 ^{ns}	0.05 ^{ns}	
Body size	Local	0.05 ^{ns}	-0.25 ^{ns}	0.16 ^{ns}	
	Landscape 1100m	0.25 ^{ns}	-0.01 ^{ns}		

* Effects were tested with generalized linear mixed models (with "site" as a random variable). Values shown are z-values from glmmTMB models. Colours represent the direction of the effect: green for a positive effect of dieback on the considered variable, red for a negative effect and grey when no significant effects were detected. DW = "dead wood"; ^{ns} = P > 0.05; * = P < 0.05; ** = P < 0.01; *** = P < 0.001

Figures

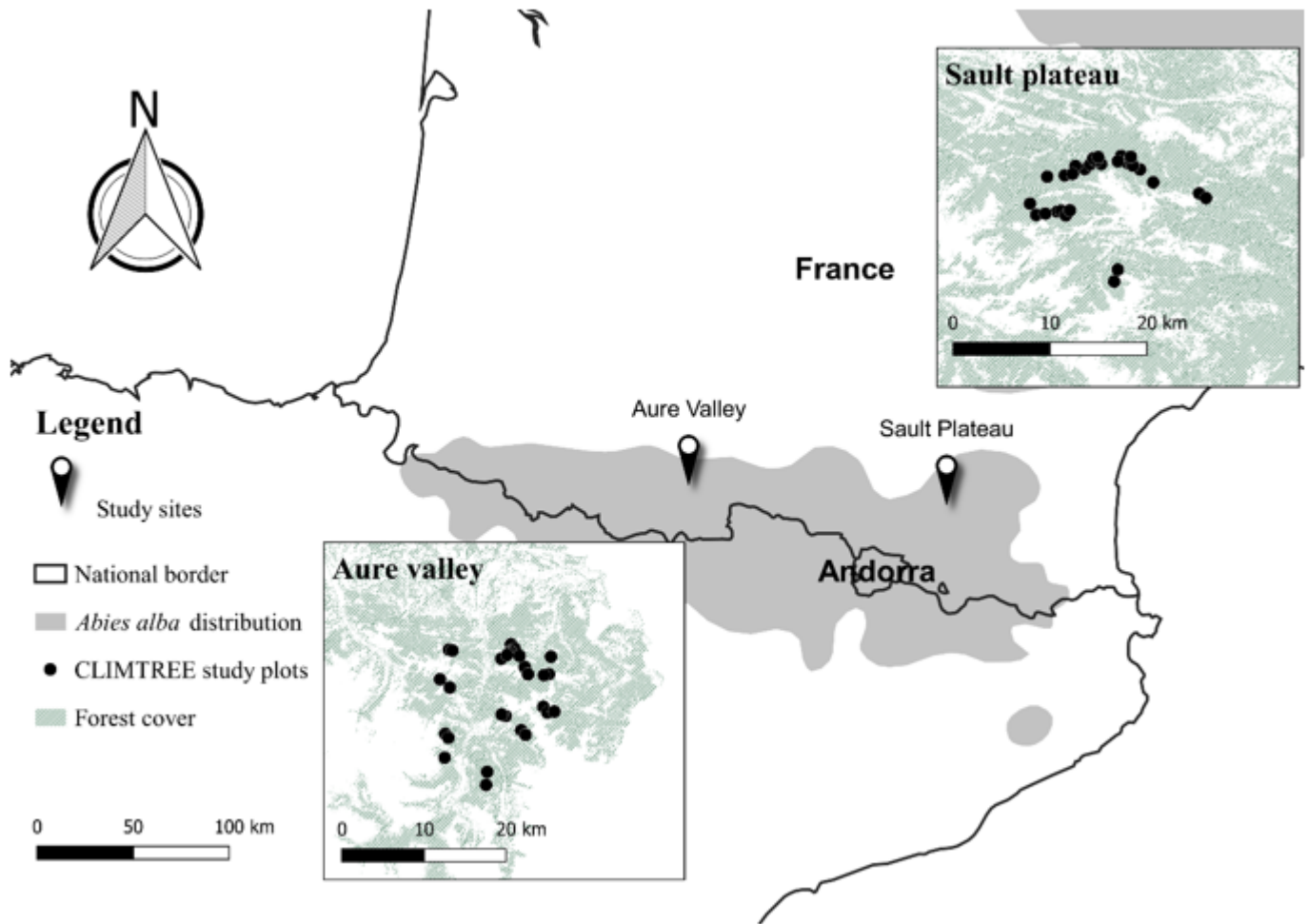


Figure 1

Map of the study sites. Grey areas correspond to *Abies alba* distribution (Source: EUFORGEN; Caudullo et al. 2020). Mapping was performed in QGIS 3.10.

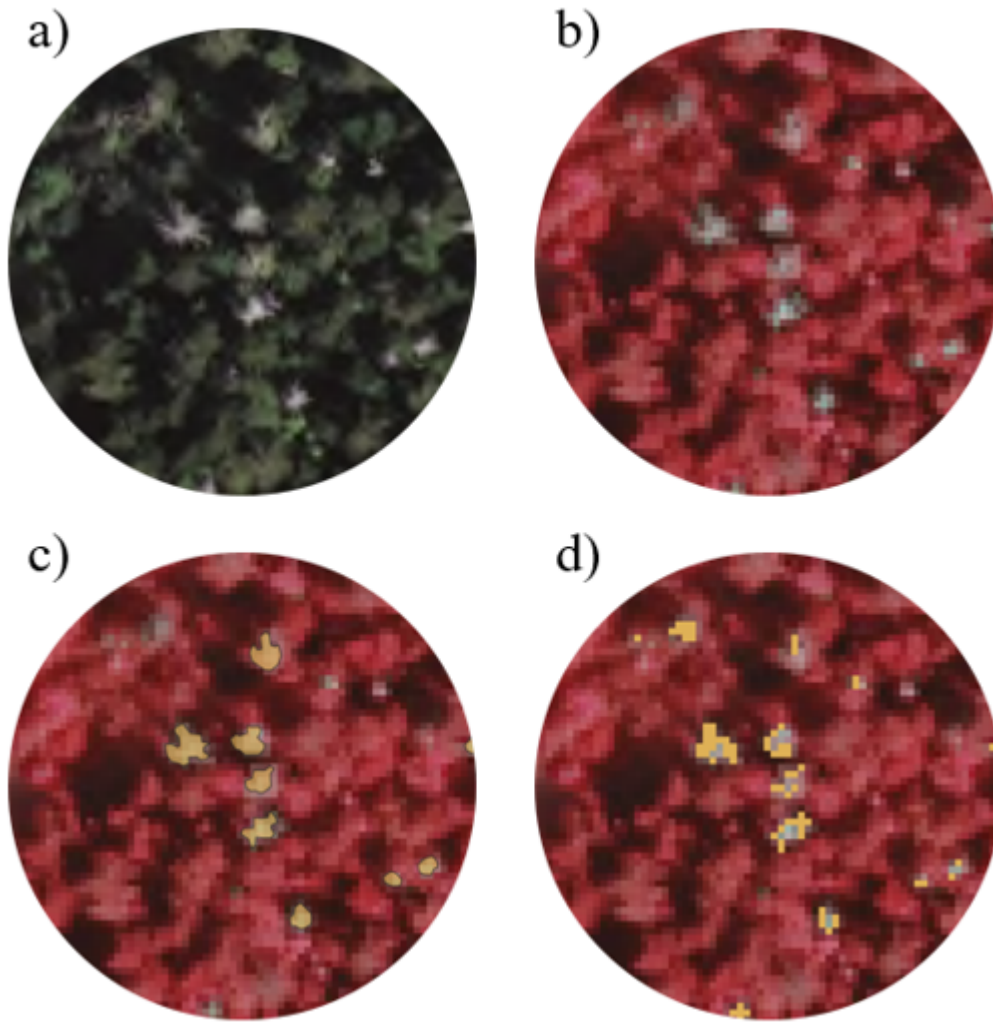


Figure 2

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 point: lat. 488182.46, lon. 6205612.67 (Lambert-93, EPSG:2154).



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) $\beta_1 > 0$ = 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 the habitat-amount hypothesis.

Supplementary Files

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