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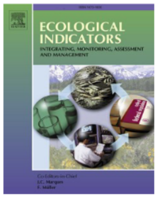

Rapid assessment of feeding traces enables detection of drivers of saproxylic insects across spatial scales

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ABSTRACT

Knowledge of habitat requirements of saproxylic insects and their response to habitat changes is critical for assessing the ecological impacts of forest management. Several studies have demonstrated a positive relationship of tree-species richness, deadwood volume, or structural diversity with saproxylic species diversity, while the relationship with the abundance of potential pest species have often been negative. A better understanding of which factors drive saproxylic insects' occurrence is therefore essential for deriving urgently needed thresholds for key habitat conditions. We tested a rapid assessment method applicable at large scale based on recorded feeding galleries and boreholes assessed during the Austrian National Forest Inventory to investigate the drivers and habitat thresholds of different saproxylic insect families; i.e. Buprestidae, Cerambycidae, Curculionidae, Siricidae, at multiple spatial scales; i.e. at the object, forest stand and landscape level. We modelled the relative abundance of all insects and these families considering nineteen explanatory variables using ordinal logistic regression models. Key habitat characteristics were identified using recursive partitioning. Our results revealed complex interactions among influencing factors at different spatial scales. We showed that deadwood volume was of surprisingly little importance. Instead, individual tree characteristics were of major importance, demonstrating the value of resource quality and variability. The abundance of all saproxylic insect families increased with advancing decomposition, on trees taller than 18 m, and above a living stand volume of 41 m^3ha^{-1}. Aiming to guide forest management, not only forest type-specific, but tree species-specific deadwood management is needed, taking into account site-specific conditions, including temperature and precipitation. For assessing temporal trends in insect colonization and habitat dynamics as well as the effects of forest management, we propose a continuous monitoring of insect traces, including living but weakened trees. This will allow for further thresholds that are urgently needed for maintaining biological diversity in forest ecosystems in the face of climate change.

1. Introduction

Deadwood, that is non-living woody biomass not contained in litter (IPCC, 2006), is an important driver of biodiversity in forests (Siitonen, 2001). More than 25 % of forest-related species rely on deadwood (Stokland et al., 2012), as it provides essential resources for obligate and facultative deadwood-dependent (i.e. saproxylic) species such as wood-decomposing fungi, insects, spiders, bryophytes, lichens, birds, bats, and other small mammals (Dittrich et al., 2014; Graf et al., 2022; Lassauce et al., 2011; Rimle et al., 2017; Shorohova and Kapitsa, 2014). Together with fungi, insects represent the most diverse saproxylic taxa and are important agents with regard to deadwood decomposition processes (Seibold et al., 2021). Different decomposition stages, size classes and different types of deadwood (e.g. snags, logs, crown deadwood, either

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sun-exposed or shaded) promote habitat heterogeneity and thus saproxylic diversity (Harmon et al., 1986; Ranius and Jansson, 2000).

A multitude of studies have investigated habitat preferences of saproxylic insects, and the results have been variable with respect to the degree of habitat specialization of saproxylic species (e.g. Komonen et al., 2016; Parisi et al., 2018; Seibold et al., 2016; Vanderwel et al., 2006). Nevertheless, there is widespread agreement on the differences in saproxylic species assemblages between broadleaved and coniferous tree species (Stokland et al., 2012) as well as on the decreasing importance of host species relatedness as wood decomposition progresses (Lee et al., 2014). In addition, some studies demonstrate a mostly positive relationship of saproxylic diversity with tree species richness, deadwood volume, and deadwood position (e.g. Bouget et al., 2021; Gossner et al., 2016; Jaworski et al., 2019; Sippola et al., 2002). The most common deadwood positions to be differentiated are standing and lying deadwood, with significant differences between both types found for temperate forests in North America (Ulyshen and Hanula, 2009) and France (Bouget et al., 2012). A qualitative characteristic of deadwood that has hitherto received comparatively little attention, but is of importance to saproxylic species, is bark cover (Dossa et al., 2016; Jones et al., 2020). A significant positive relationship between beetle richness and the amount of bark cover on standing and lying dead trees was demonstrated by McGeoch et al. (2007) specifically for spruce and pine dominated forests in Sweden.

Multiple drivers acting at different spatial scales are known to affect the diversity of saproxylic beetles. The characteristics of individual trees (e.g. species, position of deadwood, diameter) as well as of forest stands (e.g. canopy cover, deadwood volume) influence microclimatic habitat conditions by altering sun exposure, temperature and moisture over different spatial scales (Stokland et al., 2012), factors known to strongly influence the development and diversity of saproxylic beetle species (e.g. Gossner et al., 2016; Müller et al., 2020; Seibold et al., 2016). Lindhe et al. (2005), for instance, found species richness of saproxylic beetles in the Swedish hemi-boreal zone to increase with sun exposure, possibly associated with canopy openness. The same trend has also been observed for the richness and diversity of saproxylic beetles in coniferous, mixed spruce-fir-beech, and oak forests of Central Europe (Lettenmaier et al., 2022; Parisi et al., 2016; Vodka and Cizek, 2013). The positive influence of increasing resource availability (e.g. deadwood volume) on saproxylic taxa, including wood-inhabiting fungi, epixylic bryophytes and lichens, as well as saproxylic beetles, has been investigated and documented by numerous studies (e.g. Bouget et al., 2014; Haeler et al., 2021; Lassauce et al., 2011). Besides the amount of deadwood resources, The habitat-amount hypothesis challenges traditional concepts that explain species richness within habitats, such as the habitat-patch hypothesis, where species number is a function of patch size and patch isolation. It posits that effects of patch size and patch isolation are driven by effects of sample area, and thus that the number of species at a site is basically a function of the total habitat amount surrounding this site. We tested the habitat-amount hypothesis for saproxylic beetles and their habitat of dead wood by using an experiment comprising 190 plots with manipulated patch sizes situated in a forested region with a high variation in habitat amount (i.e., density of dead trees in the surrounding landscape). Although dead wood is a spatio-temporally dynamic habitat, saproxylic insects have life cycles shorter than the time needed for habitat turnover and they closely track their resource. Patch size was manipulated by adding various amounts of downed dead wood to the plots (~800 m^3 in total); dead trees in the surrounding landscape (~240 km2) were identified using airborne laser scanning (light detection and ranging). Over 3 yr, 477 saproxylic species (101,416 individuals) were recorded. Considering 20–1,000 m radii around the patches, local landscapes were identified as having a radius of 40–120 m. Both Seibold et al. (2017) further found the size of forest patches in Germany to be positively correlated with the richness of saproxylic beetles, but this could not be confirmed in case studies conducted in Swiss (Meyer et al., 2021) and Swedish forests (McGeoch et al., 2007). By contrast, increasing canopy cover and forest homogeneity - both in terms of tree species and structure - have been identified as factors negatively affecting deadwood-dependent insects, fungi, reptiles and amphibians in a global meta-analysis (Seibold et al., 2015). In addition, homogeneous and intensively managed forests are at risk of population outbreaks of insects as known from several bark beetle species associated with spruce or pine stands (Gandhi et al., 2022; Hlásny et al., 2019). Increased host tree susceptibility in homogenous monocultures is discussed as underlying mechanism (Jactel et al., 2021). If trees in such forests are stressed, this frequently allows bark beetles to overwhelm their defense mechanisms. Freshly felled trees, in combination with wind throws, provide large amounts of suitable breeding substrate and increase bark beetle populations to outbreak levels but also contribute to increases in deadwood stocks. This trend has intensified in recent years and is likely to increase as climate change progresses (Thom et al., 2017b). In Austria, for example, salvage logging accounted for 62 % of the total harvest in 2019, including damages caused by snow, storm and particularly by bark beetle mass proliferations (Glasberg and Strimitzer, 2020). The latter accounted for 4.7 million m^3 of timber in 2019, the second largest annual amount after World War II. In 2018, the amount was 5.2 million m^3, mainly of *Picea abies* ((L.) Karst.) and primarily caused by *Ips typographus* (Linnaeus, 1758) as well as *Pityogenes chalcographus* (Linnaeus, 1761) (Steyrer et al., 2020).

An adequate understanding of ecological factors at multiple spatial scales driving saproxylic insects' occurrence is necessary to derive urgently needed threshold values for key habitat features and conditions (Jaworski et al., 2019; Komonen and Müller, 2018; Oettel and Lapin, 2020). Spatial scales refer to different levels that can be summarized at individual trees (object-level), local forest stands (forest stand-level), and the larger regional context (landscape-level). Habitat features and conditions are often used as proxies for potential saproxylic activity because of the difficulty of surveying saproxylic fauna due to expertise required (Hopkins and Freckleton, 2002), but also for time and cost effectiveness, especially at large spatial scales. More precise, but still less costly than trapping, however, would be monitoring indirect activity, as is already well established for many vertebrates, e.g. counts of feces, tracks, or nests (Borrelli et al., 2020; Suárez-Tangil and Rodríguez, 2021; Walker et al., 2016). Yet, this has rarely been tested for invertebrates (Burns et al., 2014; Gollan et al., 2010; Schlick-Steiner et al., 2006). Developing a rapid assessment method for assessing saproxylic activity in deadwood by non-experts is therefore useful to support appropriate management activities related to biodiversity conservation and prevention of forest pest outbreaks.

Here, we assess how key habitat characteristics at multiple spatial scales influence the abundance of saproxylic insect families in Austrian forests using a large scale, rapid assessment method based on feeding galleries and boreholes on standing and lying deadwood. Specifically, we (1) quantified habitat availability and characteristics at the object, forest stand, and landscape levels, (2) identified factors affecting the abundance of individual saproxylic insect families, and (3) tested whether habitat thresholds could be inferred for individual families. Our hypothesis is that a rapid assessment method based on feeding galleries and boreholes of saproxylic insects allows identification of habitat characteristics important for saproxylic insects at object-, forest stand-, and landscape levels. Consequently, we hypothesize that (I) saproxylic insect abundance is primarily determined by deadwood resource availability and variability at object- and forest stand-level rather than landscape-level characteristics; (II) insect abundance varies among tree species and increase with resource availability, expressed in terms of tree size or deadwood volume; (III) an open canopy enhances insect abundance since canopy cover has been shown to affect saproxylic insects through changes in sun exposure (Bouget et al., 2014); and (IV) tree size, deadwood volume, and canopy cover show thresholds of rapidly increasing habitat availability and quality. The importance of habitat thresholds has been demonstrated, for example, for deadwood

volume in saproxylic species (Müller and Bütler, 2010).

2. Methods

2.1. Study area

Austria is a landlocked country in Central Europe with an area of about 8.34 million ha. Along with Slovenia, it is one of the most heavily forested countries in Central Europe, with a forest cover of almost 50 % (4.02 million ha), of which 84 % (3.36 million ha) are under management (BFW, 2022). Austrian forests span a wide range of elevations (120 m to 2,100 m a.s.l.) and climates (continental Pannonian, Alpine, and transitional central European climates) resulting in a considerable diversity of forest types (and thus tree species composition), ranging from temperate lowland forests to subalpine forests (Russ, 2019). The main tree species in terms of their share in growing stock include Norway spruce (*Picea abies* (L.) Karst.) (60.2 %), European beech (*Fagus sylvatica* L.) (10.3 %), European larch (*Larix decidua* Mill.) (7.1 %), Scots pine (*Pinus sylvestris* L.) (5.9 %), and silver fir (*Abies alba* Mill.) (4.3 %). The remaining share is accounted for by other coniferous (1.2 %) and broadleaved (10.9 %) species (BFW, 2022).

2.2. Habitat characteristics at object, forest stand and landscape level

For our study, we used data from the Austrian National Forest Inventory (NFI), which is the primary source of forest information at the national level for various purposes related to forestry as well as environmental planning and policy (Tomppo et al., 2010). Since 1961, the Austrian NFI has surveyed the domestic forest resources in eight survey periods and provides data on many forest-related key parameters, including various biodiversity indicators, such as standing and lying deadwood, as well as stand structure, tree and shrub species diversity. NFI data is collected on a network of permanent sample plots, arranged at the corners of square-shaped clusters with a side-length of 200 m. The clusters are located at the intersection points of a systematic 3.89 km × 3.89 km grid. The total grid consists of 5,582 clusters and therefore 22,236 sample plots, about half of which are located on forested land (Gschwantner et al., 2010).

Here, we used data from the eighth Austrian NFI (2016–2020). NFI data are gathered on sample plots, each consisting of a fixed-area circle of 300 m^2, angle-count sampling (Bitterlich, 1984, 1948), and a small fixed-area circle of 21.2 m^2 (Gschwantner et al., 2010) and summarized to object- (i.e. deadwood item), forest stand- (local) and landscape-related (regional) variables. Object-level variables refer to single standing sample trees and lying deadwood objects, forest stand-level variables to local forest stand characteristics, and landscape-level variables to a larger spatial scale of a region. A description and summary of all variables is provided in Table S1. For each standing tree and lying deadwood object, the tree species, diameter [mm], height or length [cm], decomposition stage and bark cover were assessed. The latter was summarized in three categories of less than 50 %, 50 to 99 % and 100 % bark cover. Stem volume was estimated for living and dead standing trees for each sample plot using the volume models described by Gabler and Schadauer (2008). Volume estimates for lying deadwood were obtained using Hubers' formula (Huber, 1828).

$$v = \frac{\pi}{4} d_{0.5l}^2 l \quad (1)$$

where: v = volume; $d_{0.5l}$ = mid diameter; l = length.

Each sample plot was further categorized in terms of canopy cover using four stand closure classes (gappy, open, light, closed) and forest type based on the current stand-characterizing tree species. The landscape-related slope steepness [%] was also recorded during the NFI survey (Hauk et al., 2020). Annual mean temperature [°C] and annual precipitation sum [mm], as well as summer mean temperature [°C] and summer precipitation sum [mm] for June to August, were derived by using daily measurements (2016–2020) from weather stations of the Central Institute for Meteorology and Geodynamics (ZAMG, 2020) and interpolated for the NFI plots. To investigate the potential influence of forest edges, we added information on the forest patch size [m^2] in which each sample plot is located and the distance to the nearest forest edge [m], derived from a high-resolution map of forest cover with a grid cell size of 1 m (BFW, 2020). In a pre-processing step, the forest cover map was polygonized and the area and perimeters were calculated for each forest patch. Forest patches were defined with a minimum size of 0.05 ha following the forest definition of the Austrian NFI (Hauk et al., 2020). The forest patch area was estimated using different spatial selection criteria depending on the type of intersection of a sample plot with the forest map. The following four intersection types were distinguished: (1) the plot intersects a forest patch, (2) the plot with a 10 m buffer intersects a forest patch, (3) the plot with a 10 m buffer intersects multiple forest patches, and (4) the plot does not intersect with a forest patch. The latter was not included in the analysis. To solve the problem of multiple intersections per sample plot (3), we applied the nearest neighbor criterion and selected the forest patch with the shortest distance to the plot centre. The distance to the nearest forest edge was determined using the nearest neighbor method. Forest patch boundaries were slightly simplified for this purpose: For each vertex or 10 m segment, a point vector was generated at the polygon boundary. In doing so, the nearest neighboring point on the forest patch border was determined for each sample plot, and the length of the connecting line was calculated. Missing results could be the result of inhomogeneities between in situ and remote sensing data sets.

2.3. Saproxylic insect survey

A rapid assessment of saproxylic insect occurrence was conducted systematically on two of four sample plots per NFI cluster, resulting in a total of 1,444 sample plots. All standing dead trees of at least 105 mm in diameter at breast height (dbh) were searched for insect traces up to a height of 2 m. In addition, the first six lying dead objects of at least 100 mm mid diameter were examined for insect traces. In order to allow family-level identification based on traces in deadwood, the assessment of bore holes and feeding galleries of saproxylic insects was limited to three decomposition stages. We focused on the habitat guild "fresh deadwood", according to Schmidl and Bussler (2004); (1) recently died, (2) intermediate, and (3) advanced were examined for boreholes or feeding galleries. The stages (4) severe and (5) very strong decomposed deadwood were not examined.

If bore holes were detected, a piece of bark was carefully lifted to better assess the holes or feeding galleries. The relative abundance of insect families was classified into two categories "rare", if a single and "frequent", if more than one borehole or feeding gallery was detected. For each sampled insect trace, the type of bore dust (mealy or chipsy) and the diameter of the boreholes or feeding galleries were categorized according to their location (only between bark and wood or also in wood) and size class (<5 mm or ≥ 5 mm) following the field instructions of the Austrian NFI (Hauk et al., 2020). In addition, photos were taken for later verification and documentation. We identified different saproxylic insect taxa belonging to the orders Coleoptera, Hymenoptera, and Lepidoptera based on this information and the recorded tree species. Identification was refined to the family or, where possible, the subfamily level.

2.4. Statistical analysis

For analysis, we prepared a tree-wise data set including relative abundances of insect traces (rare or frequent) per saproxylic insect family and forest stand-level, as well as landscape-level information. All analyses were performed in the R environment version 4.1.0 (R Core Team, 2021) using the packages ggplot2 (Wickham, 2016), MASS (Ripley et al., 2019), lme4 (Bates et al., 2021, Bates et al., 2015), domir

Table 1
Tree species, deadwood type and mean ± standard deviation (SD) of diameter (mm) and height or length (m), as well as the number of trees sampled as potential host trees for saproxylic insect occurrence during the Austrian National Forest Inventory (survey period 2016–2020).

Tree species	Deadwood type	Diameter (mm)		Height/length (m)		n
		mean	SD	mean	SD	
Abies alba	Lying	222	119	3.3	2.9	50
	Standing	308	287	17.3	11.8	13
Larix decidua	Lying	199	123	4.2	3.9	159
	Standing	225	119	19.2	7.0	50
Picea abies	Lying	172	91	2.9	3.3	1804
	Standing	176	124	13.8	7.4	475
Pinus sylvestris	Lying	176	85	3.5	3.5	98
	Standing	261	87	18.7	5.8	64
Pinus nigra	Lying	166	77	2.0	1.8	42
	Standing	262	104	15.2	2.5	4
Other coniferous	Lying	183	93	2.3	1.9	108
	Standing	239	159	12.8	3.4	5
Carpinus betulus	Lying	137	46	2.5	1.5	13
	Standing	127	89	11.6	5.3	6
Fagus sylvatica	Lying	166	75	3.2	3.5	240
	Standing	276	227	16.7	8.6	34
Fraxinus sp.	Lying	163	82	4.4	3.8	126
	Standing	228	142	20.2	7.6	50
Prunus sp.	Lying	171	65	3.7	4.6	14
	Standing	162	103	13.2	8.7	8
Populus sp.	Lying	228	130	5.9	4.9	24
	Standing	360	213	24.7	10.4	4
Quercus sp.	Lying	220	108	2.3	3.0	36
	Standing	215	150	17.1	9.5	15
Other broadleaved	Lying	144	39	3.9	3.2	127
	Standing	165	114	13.4	6.9	72
TOTAL		**179**	**104**	**5.8**	**6.8**	**3641**

(Luchman, 2020), and partykit (Hothorn et al., 2021).

We modelled the relative abundance of insect families considering nineteen explanatory variables. These were grouped into host tree characteristics (object level), (i) tree species, (ii) diameter, (iii) height or length, (iv) position of deadwood, (v) decomposition stage, and (vi) bark cover, forest stand characteristics (vii) forest type, (viii) canopy cover, (ix) the occurrence of habitat trees, (x) standing living volume, (xi) dead standing volume and (xii) dead lying volume, and landscape characteristics (xiii) temperature, (xiv) precipitation, (xv) forest edge effects, (xvi) distance to forest edge, (xvii) forest patch size, (xviii) slope steepness, and (xix) relief.

We used ordinal logistic regression models (function "polr" from the MASS package) to test the relationship between saproxylic family abundances and the nineteen tree, plot and landscape characteristics as explanatory variables without assessing variable interactions. Standing living volume, standing deadwood volume and lying deadwood volume were included as (log x + 0.01) transformed values. Models were tested for collinearity by means of variance inflation factors (VIF) and in case of variable combinations with high multicollinearity the less important variable was excluded. Final model selection was performed by single-term deletion with the "drop1" function (Bates et al., 2021, Bates et al., 2015). A term was considered significant if its Chi^2-statistic p-value was <0.05. To evaluate model performance, we plotted the single predictor variables against their smooths. Additionally, we calculated root mean squared error (RMSE) and Nagelkerke R^2 (Bo et al., 2006). On the basis of Nagelkerke R^2, a dominance analysis from the "domir" package was run to determine the relative importance of single variables and groups of object, forest stand, and landscape-level characteristics. We modelled the relative abundance of all saproxylic insects, the hymenopteran family Siricidae, and the Coleopteran families Cerambycidae, Buprestidae and Curculionidae. For the latter, separate models for the subfamilies of bark- and wood-breeding Scolytinae are provided in the supplementary material. Modelling was not possible for rarely recorded families, such as Lymexylidae, and Ptinidae.

Finally, we used recursive partitioning to derive thresholds for the most important habitat characteristics of the different saproxylic families to allow practical management recommendations. In doing so, the conditional inference tree method "ctree" from the partykit package was applied with a predefined minimum criterion = 0.95 as control parameter to determine the relationship between significant input

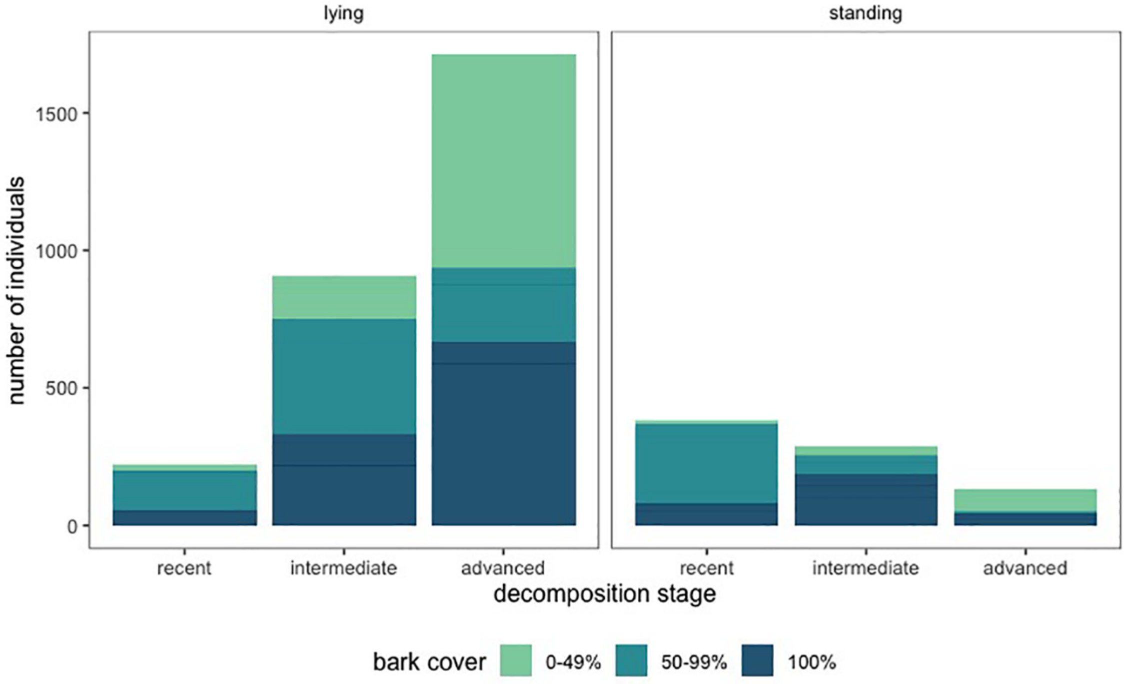

Fig. 1. Number of lying deadwood objects (n = 2,841) and standing dead trees (n = 800) recorded as potential host trees during the Austrian National Forest Inventory (2016–2020) in decomposition stages "recent" (wood hard, fine branches present), "intermediate" (wood hard, most fine branches absent) to "advanced" (wood softer, no branches remaining) and with bark cover classes 0–49 %, 50–99 %, 100 %.

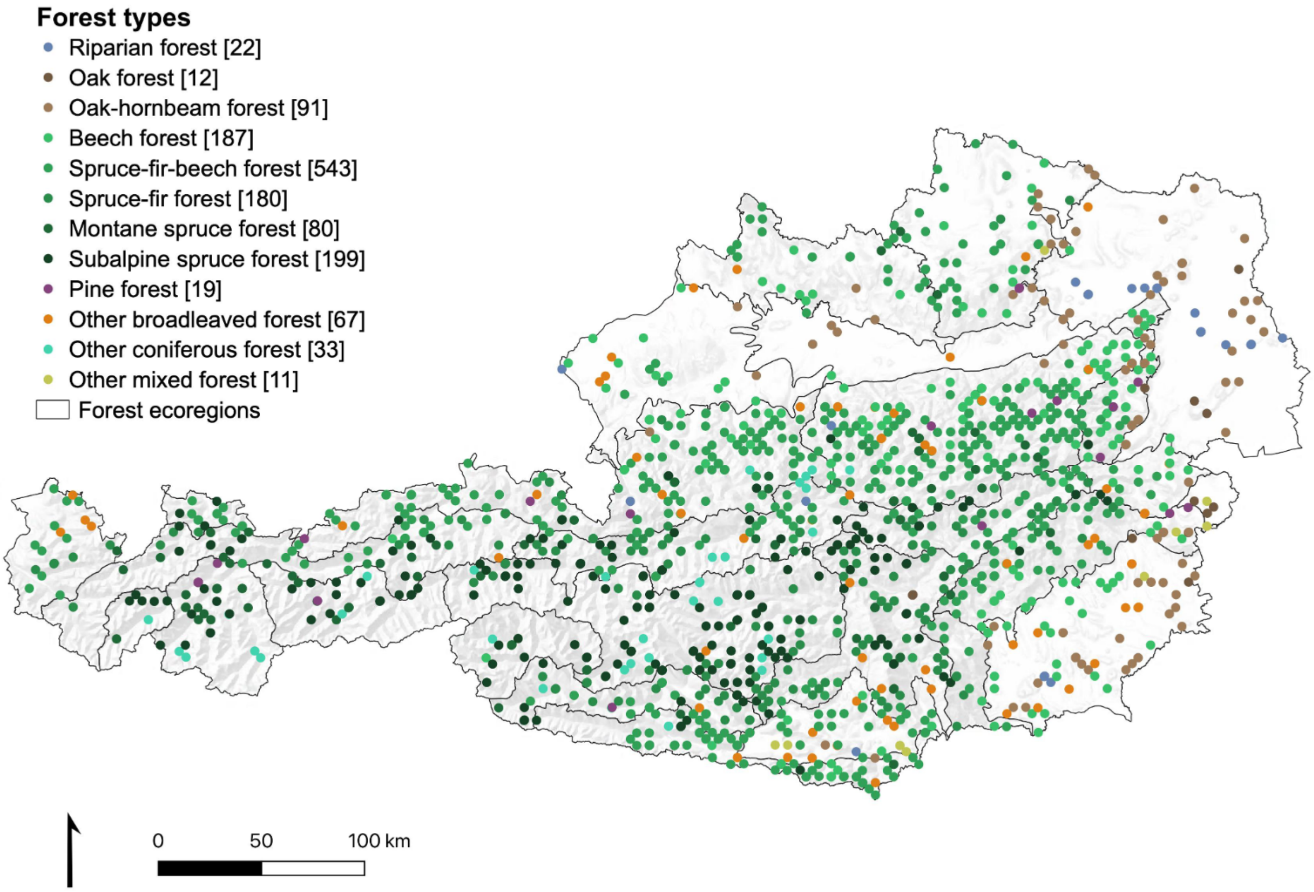

Fig. 2. Map of Austria showing forest ecoregions (according to Kilian et al. (1994)) and sample plots of the Austrian National Forest Inventory on which a rapid assessment of saproxylic insect traces was conducted during the observation period (2016–2020). Different colours indicate the respective forest type (n = 1,444 plots).

variables (habitat characteristics at object, forest stand and landscape level) and the response variable (insect family abundance). Trees were fitted using the Bonferroni correction. We created multivariate conditional inference trees (CTREEs) including all variables selected for the respective best regression model to account for interaction effects. Therefore, characteristics of the categorical variables ‘forest type’, ‘tree species’, and ‘relief’ were summarized as shown in Table S2 to obtain easily interpretable results. We chose 10-fold cross-validation to evaluate model prediction performance. Accuracy of classification was calculated as percentage of correct classification. CTREEs were constructed for all insects together, the hymenopteran family Siricidae, and the Coleopteran families Cerambycidae, Buprestidae and Curculionidae. Additionally, CTREEs were built for the Curculionidae subfamily bark- and wood-breeding Scolytinae.

3. Results

3.1. Habitat characteristics at object, forest stand, and landscape level

A total of 3,641 standing and lying deadwood objects in 1,444 NFI plots were examined for saproxylic insect occurrence. The most frequent species were the conifers *Picea abies* (n = 2,279), *Larix decidua* (n = 209), *Pinus sylvestris* (n = 162), and *Abies alba* (n = 63), along with the broadleaved *Fagus sylvatica* (n = 274). Details on all investigated tree species are presented in Table 1. Tree diameters and height (or length in case of lying objects) was on average (mean ± SD) 179 ± 104 mm and 5.8 ± 6.8 m, respectively.

Generally, lying deadwood objects (n = 2,841) were more numerous than standing dead trees (n = 800). The decomposition of lying trees was also more advanced than that of standing trees, where primarily recent or intermediate stages were recorded. Bark cover categories were evenly distributed across the categories “less than 50 %” (n = 1,088), “50 to 99 %” (n = 1,362) and “100 %” (n = 1,191). As decomposition progressed bark cover decreased, an observation that applies equally to standing and lying trees (see Fig. 1).

At forest stand level, twelve different forest types were distinguished. The distribution of NFI sample plots (n = 1,444) classified by forest types in Austria is illustrated in Fig. 2. Living wood volumes showed a heterogeneous distribution with a mean and standard deviation of 227.84 ± 268.52 m^3ha^{-1}. The per plot lying deadwood volume was twice as high as the standing deadwood volume, with 30.14 ± 42.55 m^3ha^{-1} and 16.43 ± 36.05 m^3ha^{-1}, respectively. The sampled trees were primarily in forests with closed (n = 2460, 68 %) to light (n = 818, 22 %) canopy cover; open (n = 289, 8 %) or clustered canopy (n = 74, 2 %) conditions occurred less frequently.

In accordance with Austria’s varied geomorphology, the sampled trees were predominantly found in relief sites on upper to lower slopes (n = 3419). Flat terrain (n = 200) and sites near streams (n = 22) occurred only rarely. The mean size and standard deviation of the forest patches is 13,783 ± 20,582 ha and showed a mean distance of 204 ± 184 m SD to the closest forest edge. For the observation period, we determined a mean annual temperature of 7.34 ± 2.06 °C and an annual precipitation sum of 1,229 ± 355 mm based on interpolations for the NFI plots. The mean values for summer temperature and sums of summer precipitation covered a range from 9.3 to 22.4 °C and 101 to 905 mm respectively.

Table 2
Total number of sample plots surveyed, and number as well as proportion of sample plots with insect traces [yes/no] per forest type.

Forest types	Total n of plots	n of plots with insect traces	Proportion of plots with insect traces
Spruce-fir-beech forest	543	378	69.6
Spruce-fir forest	180	133	73.9
Montane spruce forest	80	56	70.0
Subalpine spruce forest	199	159	79.9
Pine forest	19	14	73.7
Beech forest	187	110	58.8
Oak forest	12	7	58.3
Oak-hornbeam forest	91	51	56.0
Riparian forest	22	17	77.3
Other coniferous forest types	33	29	87.9
Other mixed forest types	11	5	45.5
Other broadleaved forest types	67	53	79.1
TOTAL	**1,444**	**1,017**	**70.4**

3.2. Traces of four saproxylic insect families

Overall, we found 2,770 insect traces belonging to the orders Coleoptera (n = 2,624, 94.7 %), Hymenoptera (n = 143, 5.2 %), and Lepidoptera (n = 3, 0.1 %). Wherever possible, identification was further refined to family or subfamily level, resulting in traces of the hymenopteran family Siricidae (n = 143), as well as of five Coleopteran families, namely Buprestidae (n = 127), Cerambycidae (n = 670), Curculionidae (n = 1,780), Lymexylidae (n = 33), and Ptinidae (Anobiidae) (n = 17). For Curculionidae, a refined assignment was possible, distinguishing between the subfamily Scolytinae and other subfamilies, as well as between bark-breeding (n = 1,392) and wood-breeding (n = 370) species. For the analysis, we focused on family-level information. However, we added additional analyses for bark- and wood-breeding Scolytinae in the supplementary material. Data on Lepidoptera were excluded from further analyses due to small sample size.

Insect traces were recorded on 1,017 out of 1,444 sample plots (70 %), with diverging proportions per forest type. Generally, the proportion of sample plots with insect traces was higher in forest types dominated by coniferous species (70–80 % of plots), than in those dominated by broadleaved species (56–59 %) except for riparian forests (77 %) and other broad-leaved forest types, as shown in Table 2.

Regarding tree species, we found that *A. alba* (75 %), *Populus* sp. (70 %), *Fraxinus* sp. (65 %) as well as *P. abies* (64 %) were mostly attractive to saproxylic insects. By contrast, *C. betulus* and *Quercus* sp. had the lowest percentage of insect traces with 40 % and 50 %, respectively. Interestingly, *A. alba* also had a high proportion of individuals with more than one insect trace, at 30 % (Fig. 3).

Individual insect families generally exhibited a similar distribution on standing and lying dead trees, except for Siricidae, which were mainly detected on lying trees (Fig. 4). It was hardly possible to identify host species preferences based on our chosen rapid assessment. However, family richness varied among tree species. Among standing dead trees, the lowest insect family richness was recorded on *C. betulus* and the highest on *F. sylvatica*. The latter was also true for *F. sylvatica* lying trees, while lying *Prunus* species harbored the lowest insect family richness. Interestingly, no Curculionidae were detected on standing *Pinus nigra* (Fig. 4). Traces of Curculionidae belonged mainly to the subfamily Scolytinae, as shown by their high proportion of traces (see Fig. S1a). Scolytinae traces were found on lying deadwood of all tree species and on standing dead trees of all species, except *P. nigra* and *C. betulus*. In contrast, traces of other Curculionidae were only found on standing *A. alba* and lying *P. nigra*. Traces of wood-breeding Scolytinae were most frequently detected on lying deadwood and on broadleaved tree species (*C. betulus*, *Quercus* sp., *F. sylvatica*, *Populus* sp.), while bark-breeding Scolytinae preferred *P. abies*, *Fraxinus* sp. and other coniferous trees as hosts (see Fig. S1b).

The overall and family-specific models revealed distinct patterns of influencing drivers relating to object, forest stand and landscape characteristics. An overview of significant model predictors is provided in Table 3 and full model details can be found in Table S3. The proportion of variance explained by all insects' model was 10 %, family models

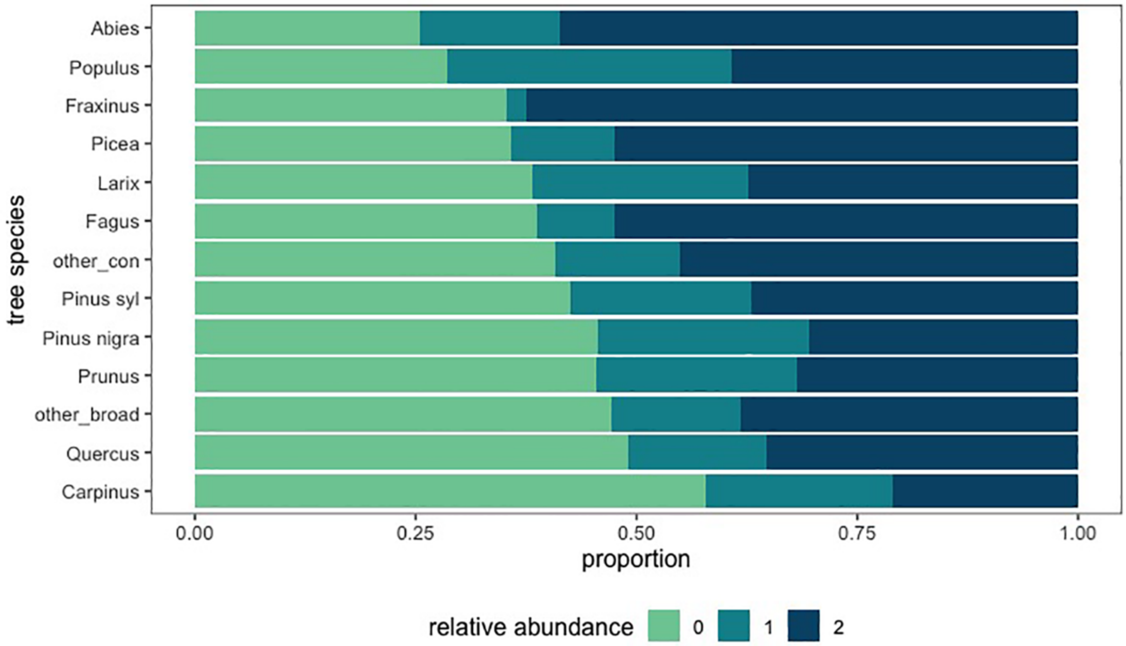

Fig. 3. Proportion of tree individuals with their relative abundance of insect traces (0 = no trace, 1 = one bore hole or feeding gallery, 2 = more than one bore hole or feeding gallery) per tree species. On 1,363 trees, no traces were found, while one trace was recorded on 472 trees and more than one trace on 1,806 individuals during the Austrian National Forest Inventory observation period 2016–2020.

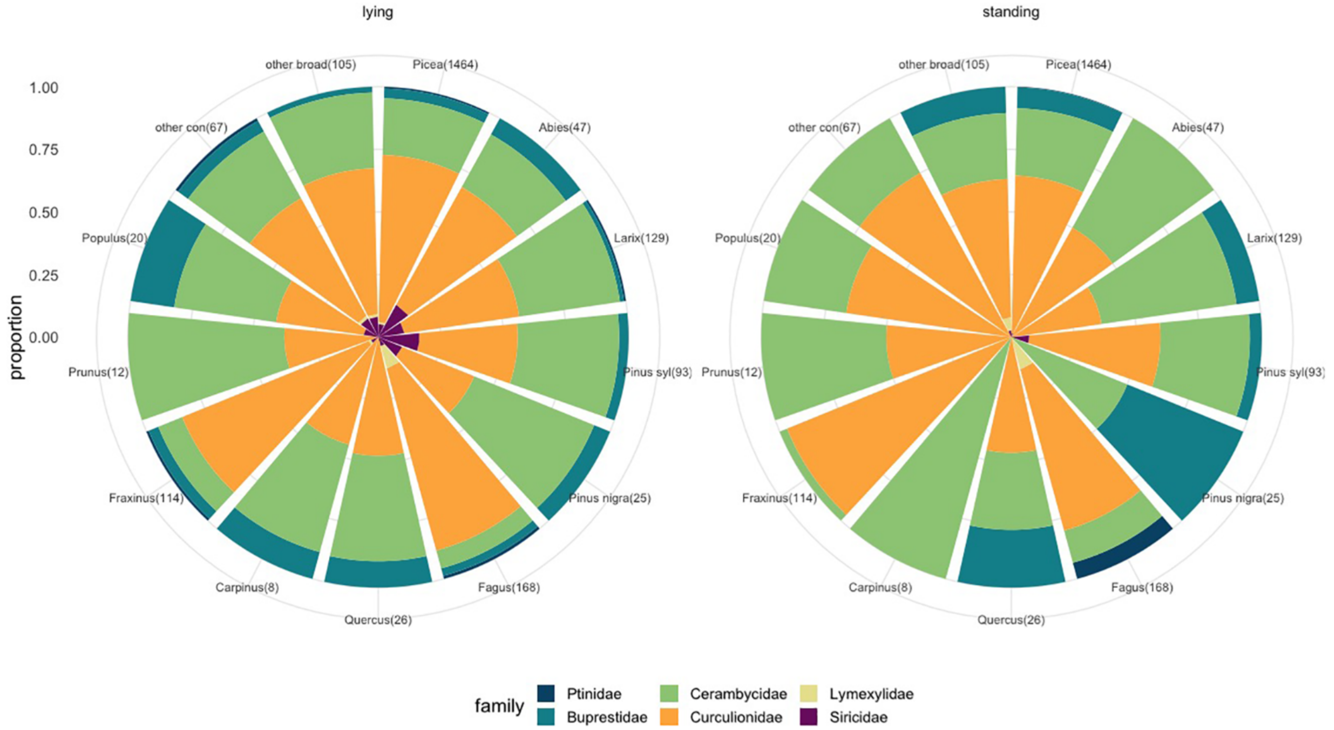

Fig. 4. Proportion of saproxylic insects identified at family level (belonging to the orders Hymenoptera and Coleoptera) and their proportion per tree species in standing (n = 444) and lying dead (n = 1,834) objects. The number in brackets refers to the respective number of objects per tree species.

Table 3
Relative importance of different spatial scales at the object, forest stand and landscape level and individual variables which were included in the final regression models of all insects, as well as the hymenopteran family Siricidae and the coleopteran families Buprestidae, Cerambycidae, and Curculionidae. For the latter further precise modeling was possible for the subfamily Scolytinae living in wood and bark. RSME and Nagelkerke pseudo R^2 values are provided to evaluate model performances. Relative dominance was calculated based on Nagelkerke R^2 values using the R package "domir". Details on full models and variable characteristics are provided in Table S3.

Models			**All**	**Siricidae**	**Buprestidae**	**Cerambycidae**	**Curculionidae**	**Scolytinae bark**	**Scolytinae wood**
Scales - relative importance		**object**	0.34	0.70	0.66	0.68	0.35	0.49	0.63
		forest stand	0.32	0.22		0.21	0.23	0.15	0.11
		landscape	0.34	0.09	0.34	0.11	0.42	0.36	0.26
Variables - relative importance	**object**	tree species	0.097	0.275		0.365	0.295	0.383	0.339
		diameter			0.140	0.070			
		height/length	0.046	0.051	0.204	0.040			
		position of DW		0.263					
		decomposition stage	0.193			0.104	0.061	0.028	
		bark cover		0.109	0.316	0.101		0.073	0.293
	forest stand	forest type	0.246	0.181		0.213	0.212	0.138	0.074
		canopy cover							
		layer composition							
		nr of habitat trees							
		living volume	0.046				0.017	0.015	
		standing dead wood volum	0.028						
		lying dead wood volume		0.024					0.032
	landscape	relief	0.071				0.073	0.045	0.048
		slope	0.136				0.164	0.115	0.153
		size of forest area				0.061			0.029
		edge effect (0,1)	0.021		0.190		0.018		
		distance to forest edge					0.029	0.026	
		mean annual temperature		0.044	0.151			0.053	
		mean summer temperature	0.036				0.037	0.056	0.031
		annual precipitation sum	0.080	0.052			0.095	0.070	
		summer precipitation sum				0.047			
Model performance		RSME	0.848	0.589	0.58	0.582	0.644	0.582	0.577
		R2	0.103	0.112	0.046	0.11	0.102	0.157	0.147

ranged from 6 % for Buprestidae to 11 % for Cerambycidae. Subfamily models for bark- and wood-living Scolytinae showed better performances with 15 %. Relative abundance of overall insect traces was mainly affected by tree species (relative importance: 10 %), and decomposition stage (19 %) at object scale, forest type (24 %) and resource availability (living volume (5 %)) at forest stand scale, slope (13 %) and annual precipitation (8 %) at landscape scale (see Table S3: Model "all"). The abundance of Siricidae, was significantly affected by

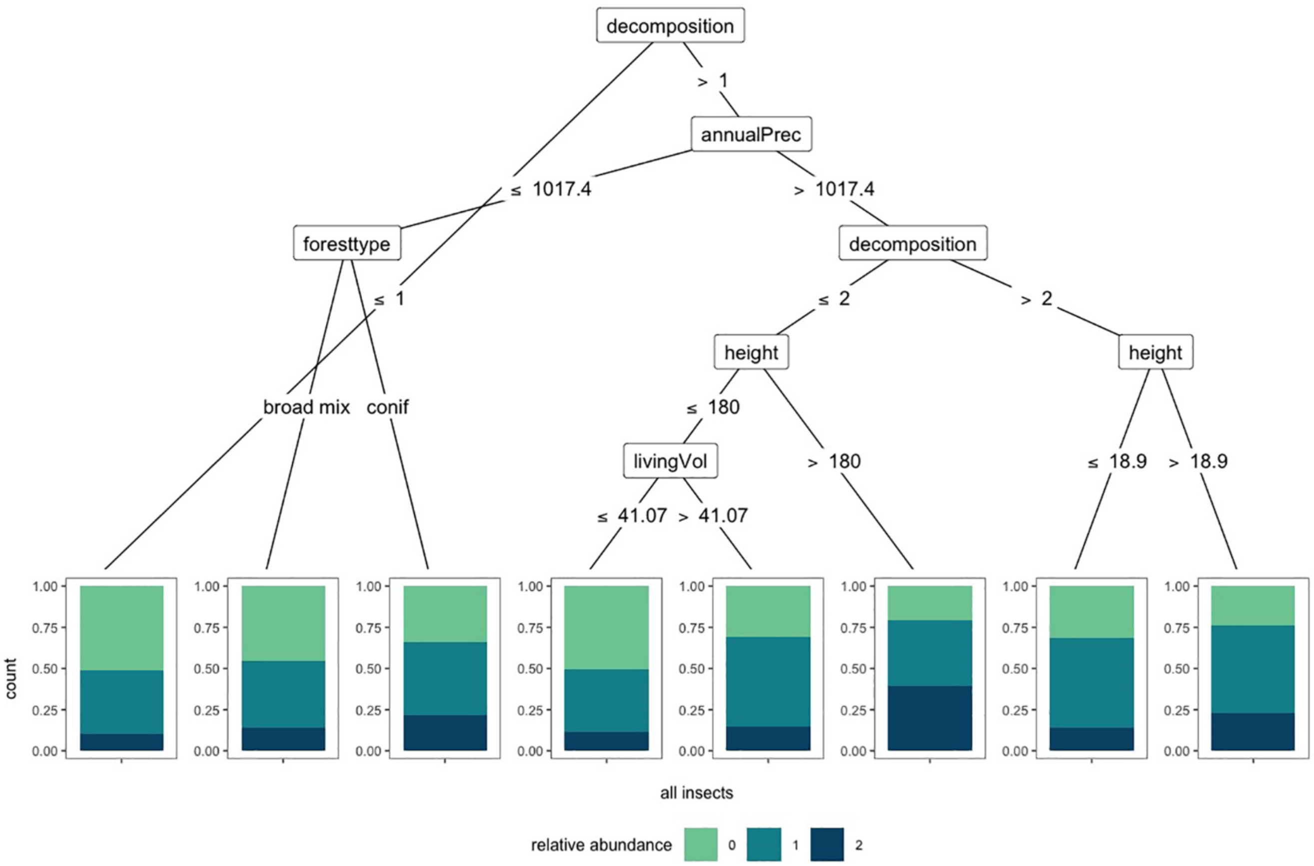

Fig. 5a. Multivariate conditional inference tree (CTREE) constructed from the variables selected for the final regression model for ***all* insects**. The nodes represent a split of the data into significantly different partitions. The significance of the split was predefined with a minimum p-value of 0.05 after Bonferroni correction. The y-axis shows the relative abundance probability (0 – absent, 1 – rare (one insect trace found), 2 – common (more than one insect trace found)). The variable values splitting the dataset are indicated on the tree branches: (a) decomposition: decomposition stage (1 – recent, 2 – intermediate, 3 – advanced), (b) annualPrec: annual precipitation sum in mm, (c) foresttype: forest types as broad(leaved), mix(ed), and conif(erous) forests, (d) height: height or length of the host tree (dm), (e) livingVol: living wood volume in m^3ha^{-1}. Model prediction performance was tested using 10-folds cross-validation with an average classification accuracy of 48.9 %.

tree species (27 %) and position of deadwood (26 %) at object level, being mainly found on coniferous tree species and in lying deadwood. Consequently, forest type (18 %) was a significant variable at forest stand level; traces were mainly found in coniferous forest types (spruce-fir, subalpine and other coniferous forest types). Trace detection of Buprestidae was enhanced at object level by declining bark cover (32 %) and increasing tree height (20 %). Forest stand characteristics were not significant. At landscape level, increasing annual temperature (15 %) and lack of edge effects (19 %) increased their abundance. Cerambycidae were mainly determined by object characteristics, namely tree species (36 %), its decomposition (10 %) and bark cover (10 %). Traces were more abundant with advancing decomposition and decreasing bark cover. Tree species were mostly *Pinus* and *Prunus* species (lowest probability on *F. sylvatica*). Tree species (29 %), along with forest type (21 %) and slope (16 %) were the most important variables in the Curculionidae model. Consequently, they were predominantly found on *Fraxinus* sp., or *P. abies* and *A. alba* in riparian or coniferous forests at either flat or steep slopes. Full model details for all families can be found in Table S3.

Detailed models on bark- and wood-breeding Scolytinae revealed additional insights. Among object characteristics tree species (39 %) and bark cover (7 %), at forest stand level forest type (14 %), and at landscape level slope steepness (11 %) and summer temperature (3 %) influenced bark-breeding Scolytinae strongest. Traces were found on coniferous (*P. abies, Larix decidua, Pinus* sp.) but also *Fraxinus* sp. with a higher bark proportion, since their traces disappear as bark detaches and decomposition progresses. The abundance was high in riparian forests, other broadleaved forests, spruce and spruce-fir forests at predominantly steep slopes and with increasing summer temperatures. By contrast, traces of wood-breeding Scolytinae were recorded predominantly on deadwood objects with detaching bark (29 %), which represented one of the most important drivers together with tree species (34 %), forest type (7 %) and slope (15 %). *Fraxinus* sp. and *F. sylvatica*, in particular, were colonized by wood-breeding Scolytinae, mainly in beech and spruce-fir forests with increasing summer temperatures and in flat terrain.

3.3. *Habitat thresholds for saproxylic families*

CTREE for all insects shows that for precipitation sums below 1,017 mm, insect traces were recorded more often in coniferous forest types than in mixed and broadleaved forest types as shown in Fig. 5a. At higher precipitation sum, insect abundance probability generally increased with intermediate decomposition and dead trees higher than 18.0 m or above a living stand volume of 41 m^3ha^{-1}. For deadwood in an advanced stage of decomposition, the threshold lies at a tree height of 1.8 m. The results indicate a complex interaction of variables.

Less complex trees were built for individual families. Trace detection of Siricidae increased on lying dead trees at annual precipitation sums of less than 1,099 mm and on trees higher 13.1 m. At higher precipitation totals, traces were found on objects with decreasing bark cover (see Fig. 5b).

Although Buprestidae abundance was generally low, traces were found more frequently on trees with lower bark cover (0–49 %). At

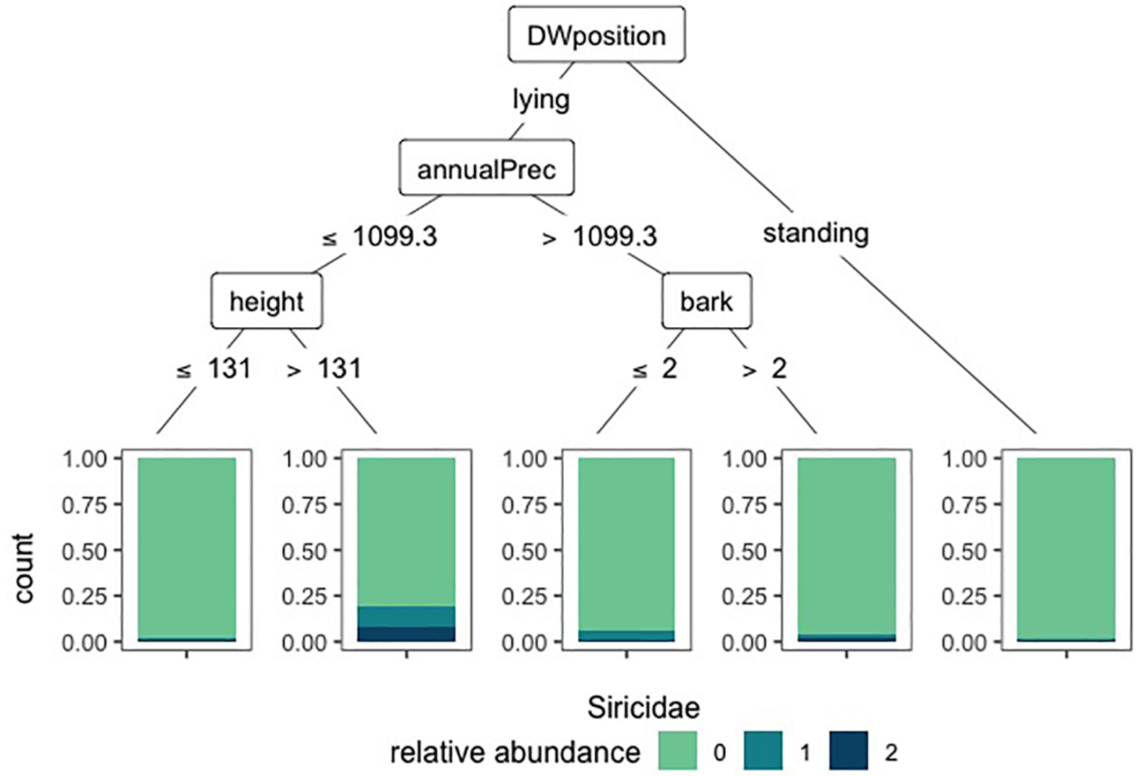

Fig. 5b. Multivariate conditional inference tree (CTREE) constructed from the variables selected into the final regression model for **Siricidae**. The nodes represent a split of the data into significantly different partitions. The significance of the split was predefined with a minimum p-value of 0.05 after Bonferroni correction. The y-axis shows the relative abundance probability (0 – absent, 1 – rare (one insect trace found), 2 – common (more than one insect trace found)). The variable values splitting the dataset are indicated on the tree branches: (a) DWposition: position of deadwood as lying or standing, (b) annualPrec: annual precipitation sum in mm, (c) height: height or length of the host tree (dm), (d) bark: bark cover (1 – 0–49%, 2 – 50–99%, 3 – 100%). Model prediction performance was tested using 10-folds cross-validation with an average classification accuracy of 96.1%.

higher bark cover, detection probability increased at mean annual temperatures above 6.7 °C (see Fig. 5c).

As bark cover decreased, trace detection of Cerambycidae was highest on trees with a diameter above 187 mm and in coniferous forests as shown in Fig. 5d. Below this threshold diameter, detection probability increased on conifers with advanced decomposition. At 100 % bark cover, abundance probability increased at summer precipitation sums greater than 694 mm.

Annual precipitation was the most important variable for Curculionidae providing the first and second split of the dataset (see Fig. 5e), with abundance highest at precipitation totals greater than 1,671 mm. At precipitation amounts less than 985 mm, traces were found primarily in flat terrain. As slope gradient increased, recent decomposition stages were decisive. At precipitation totals above 985 mm and below 1,671 mm, detection increased as decomposition progressed, and summer temperatures exceeded 14.1 °C. Further specification was possible for the subfamilies bark- and wood-breeding Scolytinae (see Fig. S2a and S2b). Bark-breeding Scolytinae were recorded predominantly on conifers in areas with annual precipitation totals above 1,523 mm and on steep slopes (>100 %). By contrast, wood-breeding Scolytinae were mainly detected on trees with low to moderate bark cover and on broadleaved species.

4. Discussion

Our study provides novel insights into the role of habitat availability and characteristics for saproxylic insects at different spatial scales in Austrian forests. Using a large-scale, rapid assessment of feeding galleries and boreholes, we quantified key habitat characteristics for saproxylic insects and provide thresholds for relative abundance of insect families at the interface of biodiversity conservation and forest protection. Our analyses of four insect families (and two subfamilies) revealed complex interactions among influencing factors at the object, forest stand, and landscape levels, and allowed the definition of thresholds demonstrating the value of the rapid assessment for future large-scale studies.

In line with our hypothesis (I), individual tree characteristics, such as tree species, decomposition stage, and bark cover were of major importance, demonstrating the value of resource quality and variability (e.g. Gossner et al., 2016; Oettel et al., 2020). We found, contrary to hypothesis II, that deadwood volume was of comparatively little importance although being a widely used indicator of forest biodiversity (e.g. Lassauce et al., 2011).

4.1. *Tree characteristics are the primary drivers of saproxylic families*

We found factors at all spatial scales to be important for the abundance of overall occurrence of insect traces. Closer examination of individual families revealed that tree characteristics, such as tree species, decomposition stage, and bark cover were most important for the majority of them (except Curculionidae being mainly driven by landscape characteristics). Further, stand level forest type and landscape characteristics, such as slope steepness, precipitation, and temperature were important drivers influencing all families except Buprestidae. For the latter, forest stand characteristics did not matter, while they responded significantly negatively to forest edge adjacency.

Insect traces varied among tree species, as hypothesized (II), with the highest numbers observed on broadleaved species *Populus* sp. and

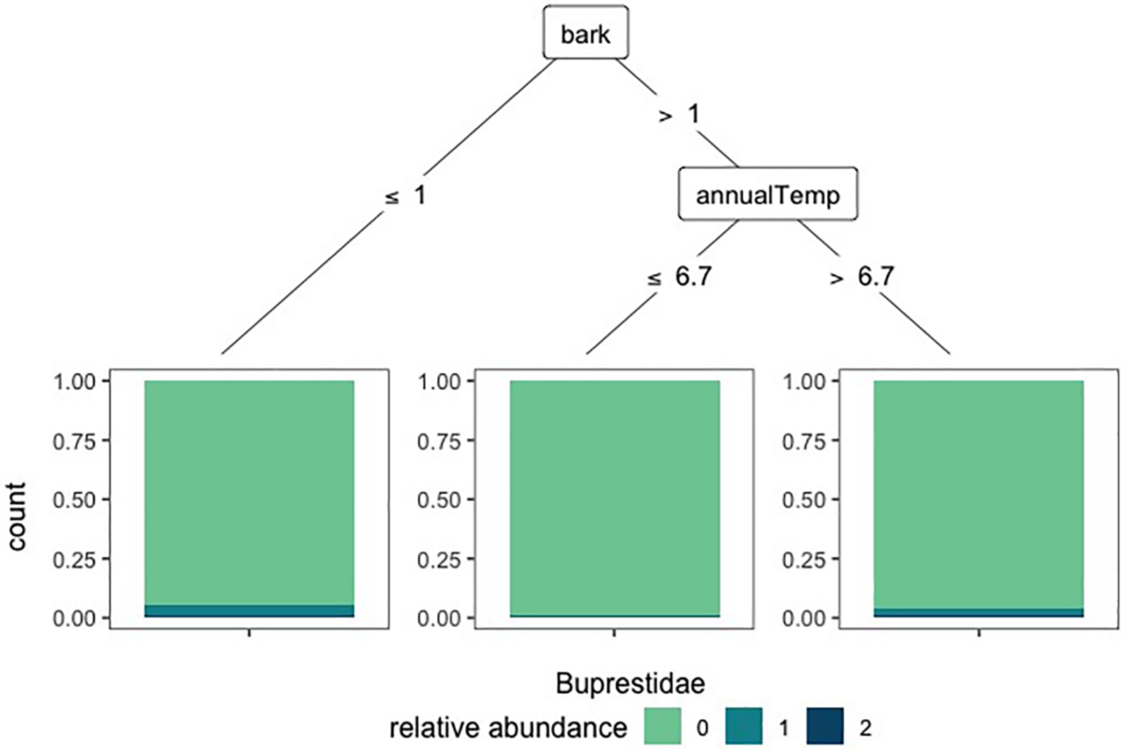

Fig. 5c. Multivariate conditional inference tree (CTREE) constructed from the variables selected for the final regression model for **Buprestidae**. The nodes represent a split of the data into significantly different partitions. The significance of the split was predefined with a minimum p-value of 0.05 after Bonferroni correction. The y-axis shows the relative abundance probability (0 – absent, 1 – rare (one insect trace found), 2 – common (more than one insect trace found)). The variable values splitting the dataset are indicated on the tree branches: (a) bark: bark cover (1 – 0–49%, 2 – 50–99%, 3 – 100%), and (b) annualTemp: mean annual temperature in °C. Model prediction performance was tested using 10-folds cross-validation with an average classification accuracy of 96.5%.

Fraxinus sp., as well as on coniferous species *Abies alba* and *Picea abies*. The high proportion of saproxylic species in *Populus* sp. is confirmed by other studies reporting on their ecological value. Vogel et al. (2020) have shown poplar deadwood to host the greatest saproxylic species richness in an experiment in German forests. In light of our focus on the habitat guild "fresh deadwood", our results further reflect very well the current European developments in the face of climate change, such as spruce stands decline related to outbreaks of *Ips typographus* populations (Kamińska et al., 2021; Netherer et al., 2019) and ash dieback caused by the invasive pathogen *Hymenoscyphus fraxineus* (Hultberg et al., 2020; Kjær et al., 2012; Mitchell et al., 2014), with weakened trees likely to be attacked by insects (Heinze, 2019). The high proportion of bark-breeding Scolytinae on dead *Fraxinus* trees in our dataset supports the study by Lenz et al. (2016) who found bark beetles such as *Hylesinus fraxini* as secondary pests on ash trees weakened by *Hymenoscyphus fraxineus* in forests of south-western Germany. The lowest number of traces was detected on *Quercus* sp. and *Carpinus betulus* trees. The comparatively low number of traces on oak is somewhat surprising, since common oak (*Quercus robur*) is known to host a high diversity of saproxylic beetles (Andringa et al., 2019; Brändle and Brandl, 2001; Vogel et al., 2021). In this way, Andringa et al. (2019) found high saproxylic family richness on deadwood of *Quercus robur* when comparing colonization of twenty different tree species in different stages of decomposition. However, the authors' experiment demonstrated a high variation in both family and species richness depending on the origin (the site where a tree grew) of individuals of a given tree species. Vogel et al. (2021) further found the highest alpha- and gamma-diversity in *Quercus petraea* branches of early decomposition stages. Local conditions related to factors known to influence saproxylic diversity, such as sun exposure, could also differ (Ranius and Jansson, 2000; Vogel et al., 2020). This indicates that varying environmental conditions leading to varying internal features, such as diameter and decomposition stage as well as interrelations among saproxylic species can lead to differences in colonization (Victorsson, 2012; Weslien et al., 2011). Family richness was highest on *F. sylvatica* trees and lowest on *C. betulus*. The latter contrasts Gossner et al. (2016) and Vogel et al. (2020), who found a high saproxylic beetle diversity on hornbeam. However, the number of objects examined in our study was quite low. In line with our findings, Walentowski et al. (2014) found a high saproxylic beetle diversity on beech compared to other species (*Populus, Salix, Picea, Tilia, Ulmus*) during investigations in German forests.

4.2. *The influence of availability and variability of resources*

In addition to tree species, decomposition stage (models: all, Cerambycidae, Curculionidae, bark-breeding Scolytinae) or bark cover (models: Siricidae, Buprestidae, Cerambycidae, bark- and wood-breeding Scolytinae) were relevant tree characteristics for colonization. Lee et al. (2014) emphasized the importance of decomposition in a study of beetle assemblages along a decomposition gradient in Alberta (Western Canada), since most species occur only within a narrow range of decomposition. In addition, Vanderwel et al. (2006) found a pattern of variation in species across decomposition stages, confirming that the habitat value of deadwood changes during decomposition. Bark cover, which is closely linked to decomposition, proved to be important for individual saproxylic families (models: Siricidae, Buprestidae, Cerambycidae, bark- and wood-breeding Scolytinae) feeding on phloem and xylem in trees (Ulyshen, 2016).

Jonsell et al. (1998) showed that in fact 31 % of saproxylic red listed invertebrates in Sweden are directly dependent on bark as habitat. Although many of them are not rare or threatened species, Gossner et al. (2016) pointed out that early successional beetles are important for

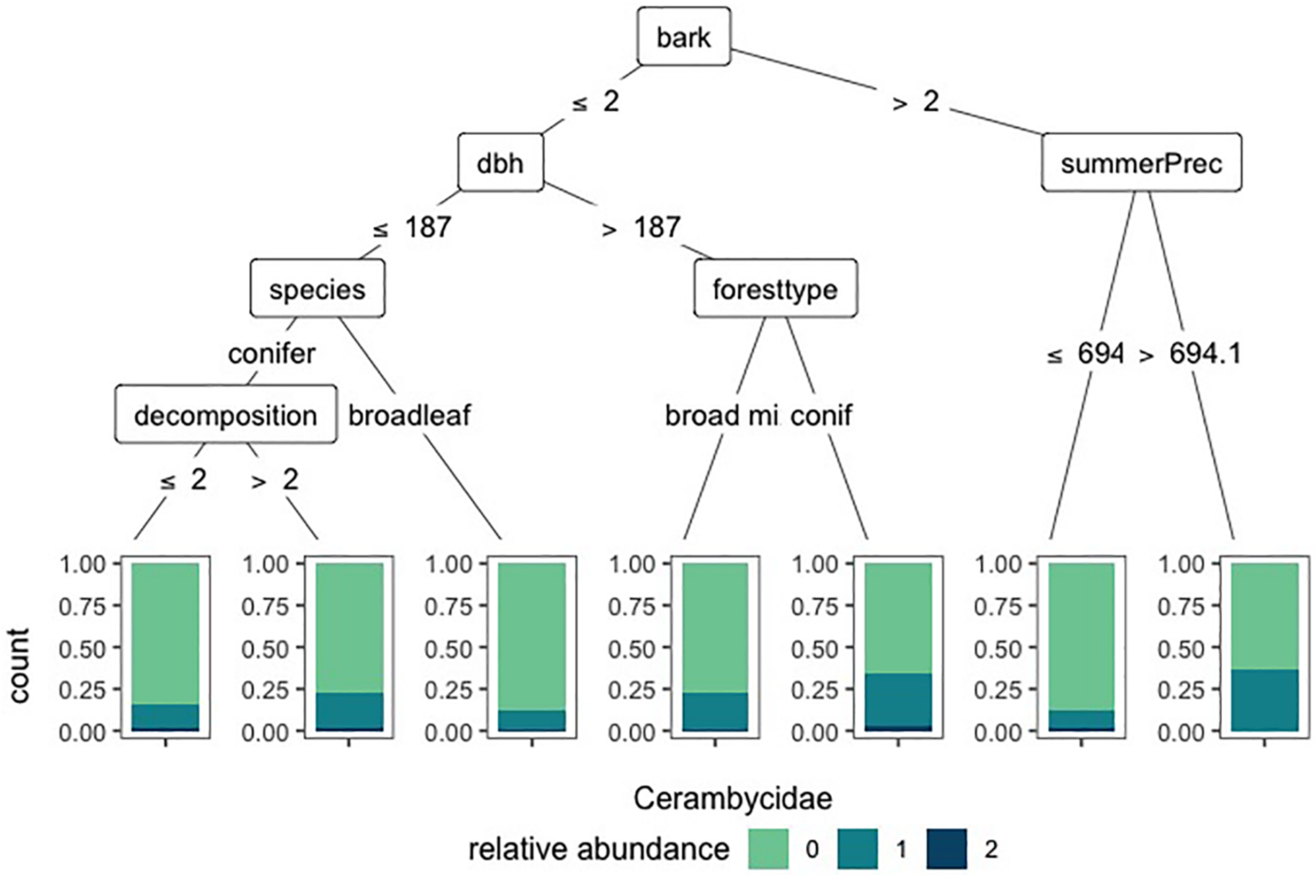

Fig. 5d. Multivariate conditional inference tree (CTREE) constructed from the variables selected for the final regression model for **Cerambycidae**. The nodes represent a split of the data into significantly different partitions. The significance of the split was predefined with a minimum p-value of 0.05 after Bonferroni correction. The y-axis shows the relative abundance probability (0 – absent, 1 – rare (one insect trace found), 2 – common (more than one insect trace found)). The variable values splitting the dataset are indicated on the tree branches: (a) bark: bark cover (1 – 0–49%, 2 – 50–99%, 3 – 100%), (b) dbh: diameter at breast height or mid diameter in mm, (c) summerPrec: summer precipitation sum (June to August) in mm, (d) species: tree species as conifer or broadleaf, (e) foresttype: forest types as broad(leaved), mix(ed), and conif(erous) forests, (f) decomposition: decomposition stage (1 – recent, 2 – intermediate, 3 – advanced). Model prediction performance was tested using 10-folds cross-validation with an average classification accuracy of 81.4%.

ecosystem functioning and conservation. They can create entrance ports for later successional species that are of conservation concern (Müller et al., 2008) or introduce fungi species (Stokland et al., 2012). For Buprestidae and Cerambycidae, our results indicated an increase in abundance with decreasing bark cover, although species of these families directly depend on bark as habitat. We believe that this relationship is due to a higher detection probability when bark is becoming detached. One survey, however, cannot adequately represent temporal succession of insect colonization. We therefore propose a continuous monitoring of insect traces, including also living but weakened trees. Regular monitoring activities, such as conducted by NFI, can help assess temporal trends in colonization development of saproxylic families in the context of forest stand characteristics, such as heterogeneity of tree species and structures, as well as individual tree characteristics, such as decomposition stage, bark cover, and tree fragmentation.

Our results show that resource variability is at least as important as availability. The hypothesis (I) that insect abundance increases with resource availability was only partly confirmed by our results. While tree characteristics, such as height (or length in case of lying trees) or diameter were significant variables in the model for all insects as well as for the families Siricidae, Buprestidae, and Cerambycidae, forest stand-related deadwood volume was of surprisingly low importance. In fact, only all insects together were significantly affected by standing deadwood wood volume, wood-breeding Scolytinae and Siricidae by lying deadwood volume. This contrasts with the results of many species-specific surveys from boreal, temperate, and Mediterranean forests in Europe indicating a significant effect of deadwood volume on saproxylic beetles (Brin et al., 2009; Della Rocca et al., 2014; Lassauce et al., 2011; Parisi et al., 2020). The latter even identified deadwood volume as the most important variable for saproxylic species richness. On the one hand, our focus on the habitat guild "fresh deadwood" could be an explanation for this finding. Some species primarily colonize living but weakened trees, as can be seen by the greater importance of living volume for all insects. On the other hand, our rapid family-level approach does not consider species richness or diversity, for which the later decomposition stages and large diameter deadwood, correspondingly the amount of deadwood, play a significant and often limiting role (Gossner et al., 2013; Parisi et al., 2020).

4.3. *Stand-scale canopy cover vs landscape-scale temperature*

Canopy cover has been identified as an important variable affecting saproxylic insects in several studies (e.g. Bouget et al., 2014; Lachat et al., 2016; Lindhe et al., 2005; Vogel et al., 2020), with more open conditions promoting microclimatic heterogeneity (Lettenmaier et al., 2022) and thus saproxylic insect abundance and diversity (Seibold et al., 2016). Surprisingly and contrary to our expectations (hypothesis III), canopy cover had no effect in our models. A reduced canopy cover is generally associated with increased sun exposure (Lindhe et al., 2005; Vogel et al., 2020) and consequently higher temperatures (Lettenmaier

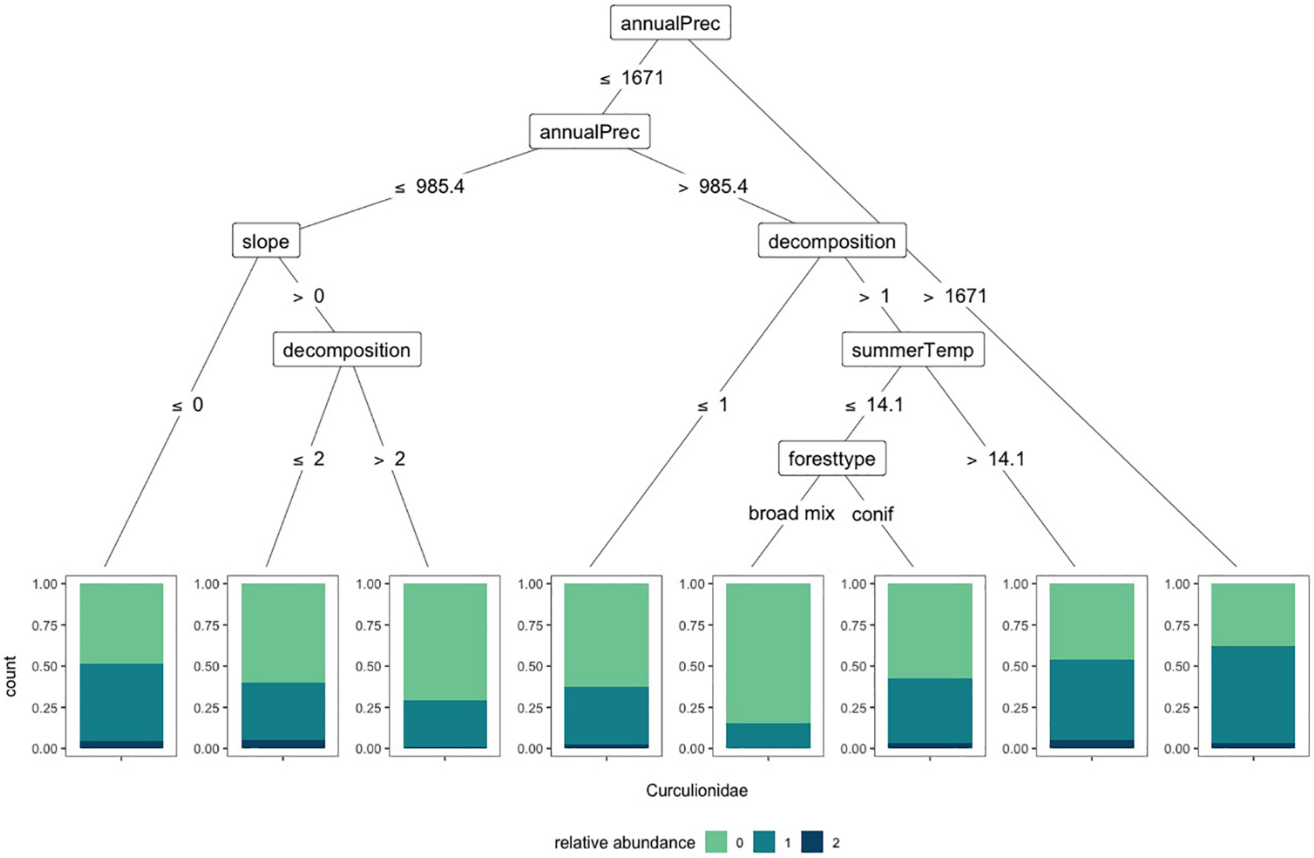

Fig. 5e. Multivariate conditional inference tree (CTREE) constructed from the variables selected for the final regression model for **Curculionidae**. The nodes represent a split of the data into significantly different partitions. The significance of the split was predefined with a minimum p-value of 0.05 after Bonferroni correction. The y-axis shows the relative abundance probability (0 – absent, 1 – rare (one insect trace found), 2 – common (more than one insect trace found)). The variable values splitting the dataset are indicated on the tree branches: (a) annualPrec: annual precipitation sum in mm, (b) slope: slope in grouped percentages 0–12, (c) decomposition: decomposition stage (1 – recent, 2 – intermediate, 3 – advanced), (d) summerTemp: mean summer temperature (June to August) in °C, (e) foresttype: forest types as broad(leaved), mix(ed), and conif(erous) forests. Model prediction performance was tested using 10-folds cross-validation with an average classification accuracy of 54.4%.

et al., 2022), which is known to have a positive effect on saproxylic species abundance and richness (Müller et al., 2015). The positive influence of temperature, however, was also evident in our results (models: all, Siricidae, Buprestidae, Curculionidae, bark- and wood-breeding Scolytinae). Rising temperatures in combination with acute drought have been reported to facilitate bark beetle outbreaks (Halsch et al., 2021; Hlásny et al., 2019; Netherer et al., 2019). However, precipitation was of low significance in our results. In our threshold analysis, bark-breeding Scolytinae were predominantly detected in areas with high precipitation totals and on steep slopes. We believe this is the result of lower forest management activities on such difficult to access sites. The Austrian Forest Act is very strict in terms of forest protection measures and felling of trees infested by bark beetles is mandated by the forestry authorities. This constitutes a difficult undertaking on steep and inaccessible terrain, however, and infested trees are often left standing on such sites.

4.4. Defining deadwood thresholds for forest management

The provision of thresholds serves as a basis for recommendations on the conservation of species or, in the case of mass outbreaks, their control through targeted conservation as well as forest management. A widely accepted and often cited threshold when it comes to deadwood dependent species is 20–50 m^3ha^{-1} for deadwood volume proposed by Müller and Bütler (2010), which should allow the majority of deadwood-dependent species to persist. However, many studies have confirmed that habitat quality and diversity are important in addition to deadwood volume (e.g. Andringa et al., 2019; Janssen et al., 2016; Sandström et al., 2019), and consequently call for further thresholds and more detailed management recommendations.

No thresholds are currently available for individual families. However, the reported values are in the range of those we found here for family richness. The abundance of all saproxylic insect families increases with progressing decomposition (intermediate to advanced decomposition stages), a minimum tree height of 18.0 m – a threshold that interestingly decreases with advancing decomposition to 1.8 m – and a living stand volume of greater than 41 m^3ha^{-1}. Living volume is important indicating the potential future habitat, since many early colonizers already colonize weakened trees, either directly or indirectly through fungal infestation.

For Siricidae, a threshold of 13.1 m tree height was determined to increase their abundance. A threshold of tree height was further determined for Siricidae, indicating that above 13.1 m tree height their abundance increased. Our values are similar to those published by Kärvemo et al. (2014) whose models show a positive correlation between tree height and bark beetle colonization above a threshold of 10–15 m tree height. For Cerambycidae, we were able to determine a threshold of 18.7 cm tree diameter, slightly below the threshold value of 22 cm proposed by Della Rocca et al. (2014) for saproxylic beetle richness in Italian floodplain forests.

The importance of diameter together with tree species, bark cover, and decomposition stage as host tree characteristics is evident in several

other studies (e.g. Gossner et al., 2016, 2013; Müller et al., 2015; Ulyshen and Hanula, 2009; Weslien et al., 2011). The importance of tree height has been less well pointed out so far (Kärvemo et al., 2014; Zumr et al., 2021). Zumr et al. (2021) rather generally recommended leaving high stumps in managed forests to increase saproxylic diversity. However, assuming that tree height is related to age, a number of studies show a positive relationship between stand age and saproxylic richness (e.g. Dollin et al., 2008; Irmler et al., 2010; Lassauce et al., 2013; Similä et al., 2002).

Landscape-related climatic thresholds were identified at an annual precipitation sum of 1,099 mm for Siricidae and of 985 mm for Curculionidae, below which abundance probability increased. Cerambycidae appeared to be more sensitive to summer precipitation, with their abundance probability increasing above 694 mm. The responses to precipitation may indicate an upper limit for annual precipitation above which conditions become unfavorable for saproxylic insects. A similar trend has been observed in an Austrian case study, with saproxylic beetle diversity responding negatively to increases in precipitation (Thom et al., 2017a). Buprestidae were sensitive to mean annual temperature and Curculionidae to mean summer temperature, occurring more frequently above 6.7 °C and 14.1 °C, respectively. Such positive responses to rising temperatures have also been reported by several other studies (e.g. Gossner et al., 2013; Lachat et al., 2012; Müller et al., 2015). Lachat et al. (2012) found higher saproxylic beetle richness in warm (mean annual temperature: 8.4 °C) compared to cool (mean annual temperature: 6.8 °C) beech forests. The value at cool sites is close to our reported annual temperature threshold. Following Müller et al. (2015), favorable temperatures can even buffer poor site conditions to a certain extend.

5. Conclusions

Our rapid assessment of feeding traces indicates a complex interplay of habitat characteristics at different spatial scales. While specific requirements of single species cannot not be considered, it allows to define thresholds of habitat characteristics for saproxylic insect families. Tree characteristics, forest type and site conditions affect all saproxylic insects, with thresholds being provided for tree height, dbh, living stand volume, or temperature and precipitation. Aiming to guide forest management at the interface of forest protection and biodiversity conservation, deadwood management should already consider the living stand. Avoiding population outbreaks of single species, not only forest type-specific, but also tree species-specific management is required. Finally, site-specific conditions, including temperature and precipitation should be taken into account. Ongoing monitoring of insect traces including living trees, observing temporal trends, as well as considering forest management impacts are therefore critical to define further thresholds and enable their validation.

CRediT authorship contribution statement

Janine Oettel: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Writing – original draft, Visualization, Writing – review & editing. **Martin Braun:** Formal analysis. **Gernot Hoch:** Conceptualization, Methodology, Writing – review & editing. **James Connell:** Methodology, Investigation. **Thomas Gschwantner:** Data curation, Methodology, Writing – review & editing. **Katharina Lapin:** Writing – review & editing. **Stefan Schöttl:** Formal analysis. **Katrin Windisch-Ettenauer:** Formal analysis. **Franz Essl:** Writing – review & editing, Supervision. **Martin M Gossner:** Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

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References

Andringa, J.I., Zuo, J., Berg, M.P., Klein, R., van’t Veer, J., de Geus, R., de Beaumont, M., Goudzwaard, L., van Hal, J., Broekman, R., van Logtestijn, R.S.P., Li, Y., Fujii, S., Lammers, M., Hefting, M.M., Sass-Klaassen, U., Cornelissen, J.H.C., 2019. Combining tree species and decay stages to increase invertebrate diversity in dead wood. For. Ecol. Manage. 441, 80–88. doi:10.1016/j.foreco.2019.03.029.

Bates, D., Maechler, M., Bolker, B., Walker, S., Haubo, R., Christensen, B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., Krivitsky, P.N., 2021. Package ‘lme4’.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 https://doi.org/10.18637/jss.v067.i01.

BFW (Bundesforschungszentrum für Wald), 2020. Erste hochgenaue Waldkarte der Waldinventur [WWW Document]. Erste hochgenaue Waldkarte der Waldinventur. URL https://www.bfw.gv.at/hochgenaue-waldkarte-waldinventur/.

BFW (Bundesforschungszentrum für Wald), 2022. Österreichische Waldinventur [WWW Document]. Waldinformationen aus erster Hand. Umfassend. Kompetent. Aktuell.

Bitterlich, W., 1948. Die Winkelzählprobe. Allg. Forst- und Holzwirtschaftliche Zeitung 59, 4–5.

Bitterlich, W., 1984. The relascope idea. Relative measurements in forestry. Commonwealth Agricultural Bureaux.

Bo, H., Jun, S., Palta, M., 2006. PSEUDO-R 2 in logistic regression model. Stat. Sin. 16, 847–860.

Borrelli, L., Minichino, A., Pace, A., Dipineto, L., Fioretti, A., 2020. Fecal sample collection method for wild birds-associated microbiome research: Perspectives for wildlife studies. Animals 10, 1–6. https://doi.org/10.3390/ani10081349.

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

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

Bouget, C., Brin, A., Larrieu, L., 2021. The use of sentinel logs to assess host shifts in early beetle colonisers of deadwood under climate-and forestry-induced tree species substitutions. Insect Conserv. Divers. 14, 117–131.

Brändle, M., Brandl, R., 2001. Species richness of insects and mites on trees: Expanding Southwood. J. Anim. Ecol. 70, 491–504. https://doi.org/10.1046/j.1365-2656.2001.00506.x.

Brin, A., Brustel, H., Jactel, H., 2009. Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in Maritime pine plantations. Ann. For. Sci. 66, 306. https://doi.org/10.1051/forest/2009009.

Burns, M.L., Smith, M., Slade, E.M., Ennos, R.A., 2014. The Saproxylic Activity Index: A New Tool for the Rapid Assessment of Deadwood Species during Forest Restoration. Open J. For. 04, 144–150. https://doi.org/10.4236/ojf.2014.42020.

Della Rocca, F., Stefanelli, S., Pasquaretta, C., Campanaro, A., Bogliani, G., 2014. Effect of deadwood management on saproxylic beetle richness in the floodplain forests of northern Italy: Some measures for deadwood sustainable use. J. Insect Conserv. 18, 121–136. https://doi.org/10.1007/s10841-014-9620-1.

Dittrich, S., Jacob, M., Bade, C., Leuschner, C., Hauck, M., 2014. The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. Plant Ecol. 215, 1123–1137. https://doi.org/10.1007/s11258-014-0371-6.

Dollin, P., Majka, C., Duinker, P., 2008. Saproxylic beetle (Coleoptera) communities and forest management practices in coniferous stands in southwest Nova Scotia, Canada. Zookeys 2, 291–336. https://doi.org/10.3897/zookeys.2.15.

Dossa, G.G.O., Paudel, E., Cao, K., Schaefer, D., Harrison, R.D., 2016. Factors controlling bark decomposition and its role in wood decomposition in five tropical tree species. Sci. Rep. 6 https://doi.org/10.1038/srep34153.

Gabler, K., Schadauer, K., 2008. Methods of the Austrian Forest Inventory 2000 / 02.

Gandhi, K.J.K., Miller, C.N., Fornwalt, P.J., Frank, J.M., 2022. Bark beetle outbreaks alter biotic components of forested ecosystems, Bark Beetle Management, Ecology, and Climate Change. Elsevier Inc. doi:10.1016/b978-0-12-822145-7.00008-8.

Glasberg, L., Strimitzer, L., 2020. Schadholz und Corona. Vienna.

Gollan, J.R., Smith, H.M., Bulbert, M., Donnelly, A.P., Wilkie, L., 2010. Using spider web types as a substitute for assessing web-building spider biodiversity and the success of habitat restoration. Biodivers. Conserv. 19, 3141–3155. https://doi.org/10.1007/s10531-010-9882-1.

Gossner, M.M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W., Müller, J., 2013. Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests. Conserv. Biol. 27, 605–614. https://doi.org/10.1111/cobi.12023.

Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan-Dewenter, I., Schulze, E.D., Weisser, W.W., 2016. Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity? Biol. Conserv. 201, 92–102. https://doi.org/10.1016/j.biocon.2016.06.032.

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

Gschwantner, T., Gabler, K., Schadauer, K., Weiss, P., 2010. National Forest Inventory Reports: Austria. In: National forest Inventories: Pathways for Common Reporting. Springer, Netherlands, pp. 57–71.

Haeler, E., Bergamini, A., Blaser, S., Ginzler, C., Hindenlang, K., Keller, C., Kiebacher, T., Kormann, U.G., Scheidegger, C., Schmidt, R., Stillhard, J., Szallies, A., Pellissier, L., Lachat, T., 2021. Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. Landsc. Ecol. 36, 89–104. https://doi.org/10.1007/s10980-020-01115-4.

Halsch, C.A., Shapiro, A.M., Fordyce, J.A., Nice, C.C., Thorne, J.H., Waetjen, D.P., Forister, M.L., 2021. Insects and recent climate change. Proc. Natl. Acad. Sci. U. S. A. 118, 1–9. https://doi.org/10.1073/PNAS.2002543117.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems. Adv. Ecol. Res. 15, 133–263. https://doi.org/10.1016/S0065-2504(03)34002-4.

Hauk, E., Niese, G., Schadauer, K., 2020. Instruktion für die Feldarbeit der Österreichischen Waldinventur 2016-2018 (2020). Vienna.

Heinze, B., 2019. Progressive mortality of Fraxinus species in Austria caused by Ash-dieback, in the context of Europe, in: BFW Praxisinfo 43. Vienna, Austria, pp. 7–12.

Hlásny, T., Krokene, P., Liebhold, A., Montagné-Huck, C., Müller, J., Qin, H., Raffa, K., Schelhaas, M.-J., Seidl, R., Svoboda, M., Viiri, H., 2019. Living with bark beetles: impacts, outlook and management options, From Science to Policy 8. European Forest Institute.

Hopkins, G.W., Freckleton, R.P., 2002. Declines in the numbers of amateur and professional taxonomists: Implications for conservation. Anim. Conserv. 5, 245–249. https://doi.org/10.1017/S1367943002002299.

Hothorn, T., Seibold, H., Zeileis, A., 2021. Package 'partykit ' A Toolkit for Recursive Partitioning.

Huber, F.X., 1828. Hilfstafeln für Bedienstete des Forst- und Baufaches zunächst zur leichten und schnellen Berechnung des Massengehaltes roher Holzstämme und der Theile derselben und auch zu anderm Gebrauche für jedes landesübliche Maaß anwendbar. München.

Hultberg, T., Sandström, J., Felton, A., Öhman, K., Rönnberg, J., Witzell, J., Cleary, M., 2020. Ash dieback risks an extinction cascade. Biol. Conserv. 244 https://doi.org/10.1016/j.biocon.2020.108516.

IPCC, 2006. IPCC Guidelines for National Greenhouse Gas Inventories, Prepared by the National Greenhouse Gas Inventories Programme. IGES, Japan.

Irmler, U., Arp, H., Nötzold, R., 2010. Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size. J. Insect Conserv. 14, 227–235. https://doi.org/10.1007/s10841-009-9249-7.

Jactel, H., Moreira, X., Castagneyrol, B., 2021. Tree Diversity and Forest Resistance to Insect Pests: Patterns, Mechanisms, and Prospects. Annu. Rev. Entomol. 66, 277–296. https://doi.org/10.1146/annurev-ento-041720-075234.

Janssen, P., Cateau, E., Fuhr, M., Nusillard, B., Brustel, H., Bouget, C., 2016. Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. Biodivers. Conserv. 25, 1167–1185. https://doi.org/10.1007/s10531-016-1116-8.

Jaworski, T., Plewa, R., Tarwacki, G., Sućko, K., Hilszczański, J., Horák, J., 2019. Ecologically similar saproxylic beetles depend on diversified deadwood resources: From habitat requirements to management implications. For. Ecol. Manage. 449, 117462 https://doi.org/10.1016/j.foreco.2019.117462.

Jones, J.M., Heath, K.D., Ferrer, A., Dalling, J.W., 2020. Habitat-specific effects of bark on wood decomposition: Influences of fragmentation, nitrogen concentration and microbial community composition. Funct. Ecol. 34, 1123–1133. https://doi.org/10.1111/1365-2435.13547.

Jonsell, M., Weslien, J., Ehnström, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodivers. Conserv. 7, 749–764. https://doi.org/10.1023/A:1008888319031.

Kamińska, A., Lisiewicz, M., Kraszewski, B., Stereńczak, K., 2021. Mass outbreaks and factors related to the spatial dynamics of spruce bark beetle (Ips typographus) dieback considering diverse management regimes in the Białowieża forest. For. Ecol. Manage. 498 https://doi.org/10.1016/j.foreco.2021.119530.

Kärvemo, S., Van Boeckel, T.P., Gilbert, M., Grégoire, J.C., Schroeder, M., 2014. Large-scale risk mapping of an eruptive bark beetle - Importance of forest susceptibility and beetle pressure. For. Ecol. Manage. 318, 158–166. https://doi.org/10.1016/j.foreco.2014.01.025.

Kilian, W., Müller, F., Starlinger, F., 1994. Die forstlichen Wuchsgebiete Osterreichs. FBVA-Berichte 82, 55–57.

Kjær, E.D., McKinney, L.V., Nielsen, L.R., Hansen, L.N., Hansen, J.K., 2012. Adaptive potential of ash (Fraxinus excelsior) populations against the novel emerging pathogen Hymenoscyphus pseudoalbidus. Evol. Appl. 5, 219–228. https://doi.org/10.1111/j.1752-4571.2011.00222.x.

Komonen, A., Müller, J., Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., Cizek, L., Frei, A., Holzer, E., Kadej, M., Kahlen, M., Köhler, F., Möller, G., Mühle, H., Sanchez, A., Schaffrath, U., Schmidl, J., Smolis, A., Szallies, A., Németh, T., Wurst, C., Thorn, S., Christensen, R.H.B., Seibold, S., Bouget, C., Nusillard, B., Pineau, X., Ricou, C., Jonsell, M., Hansson, J., Wedmo, L., waraich, Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., Sandström, J., Bernes, C., Junninen, K., Lõhmus, A., Macdonald, E., Müller, J., Jonsson, B.G., Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan-Dewenter, I., Schulze, E.D., Weisser, W.W., Hardersen, S., Curletti, G., Leseigneur, L., Platia, G., Liberti, G., Leo, P., Cornacchia, P., Gatti, E., Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J., Gossner, M.M., Falck, K., Weisser, W.W., Jaworski, T., Plewa, R., Tarwacki, G., Sućko, K., Hilszczański, J., Horák, J., Vanderwel, M.C., Malcolm, J.R., Smith, S.M., Islam, N., Chaudhary, A., Burivalova, Z., Koh, L.P., Hellweg, S., Ekbom, B., Schroeder, L.M., Larsson, S., Brin, A., Bouget, C., Valladares, L., Brustel, H., Sippola, A.L., Siitonen, J., Punttila, P., Similä, M., Kouki, J., Martikainen, P., Uotila, A., Ranius, T., Jansson, N., Jonsson, B.G., Kruys, N., Ranius, T., Bouget, C., Larrieu, L., Brin, A., Parisi, F., Frate, L., Lombardi, F., Tognetti, R., Campanaro, A., Biscaccianti, A.B., Marchetti, M., Sciarretta, A., Tognetti, R., Campanaro, A., Marchetti, M., Trematerra, P., Saint-Germain, M., Drapeau, P., Buddle, C.M., Provost, G. Le, Thiele, J., Westphal, C., Penone, C., Allan, E., Neyret, M., Plas, F. Van Der, Ayasse, M., Bardgett, R.D., Birkhofer, K., Blüthgen, N., Bolliger, R., Börschig, C., Busch, V., Chisté, M., Jung, K., Lange, M., Marzini, C., Overmann, J., Pa, E., Della, F., Stefanelli, R.S., 2016. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. For. Ecol. Manage. 22, 217–234. doi:10.1016/j.ecolind.2013.09.031.

Komonen, A., Müller, J., 2018. Dispersal ecology of deadwood organisms and connectivity conservation. Conserv. Biol. 32, 535–545. https://doi.org/10.1111/cobi.13087.

Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacsson, G., Müller, J., 2012. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecol. Indic. 23, 323–331. https://doi.org/10.1016/j.ecolind.2012.04.013.

Lachat, T., Chumak, M., Chumak, V., Jakoby, O., Müller, J., Tanadini, M., Wermelinger, B., 2016. Influence of canopy gaps on saproxylic beetles in primeval beech forests: a case study from the Uholka-Shyrokyi Luh forest, Ukraine. Insect Conserv. Divers. 9, 559–573. https://doi.org/10.1111/icad.12188.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol. Indic. 11, 1027–1039. https://doi.org/10.1016/j.ecolind.2011.02.004.

Lassauce, A., Larrieu, L., Paillet, Y., Lieutier, F., Bouget, C., 2013. The effects of forest age on saproxylic beetle biodiversity: Implications of shortened and extended rotation lengths in a French oak high forest. Insect Conserv. Divers. 6, 396–410. https://doi.org/10.1111/j.1752-4598.2012.00214.x.

Lee, S.I., Spence, J.R., Langor, D.W., Vanderwel, M.C., Malcolm, J.R., Smith, S.M., Islam, N., Kašák, J., Foit, J., Chaudhary, A., Burivalova, Z., Koh, L.P., Hellweg, S., Brin, A., Bouget, C., Valladares, L., Brustel, H., Sippola, A.L., Siitonen, J., Punttila, P., Similä, M., Kouki, J., Martikainen, P., Uotila, A., Jonsson, B.G., Kruys, N., Ranius, T., Parisi, F., Lombardi, F., Sciarretta, A., Tognetti, R., Campanaro, A., Marchetti, M., Trematerra, P., Sandström, J., Bernes, C., Junninen, K., Lõhmus, A., Macdonald, E., Müller, J., Jonsson, B.G., Hardersen, S., Curletti, G., Leseigneur, L., Platia, G., Liberti, G., Leo, P., Cornacchia, P., Gatti, E., Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan-Dewenter, I., Schulze, E.D., Weisser, W.W., Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J., Lange, M., Türke, M., Pašalić, E., Boch, S., Hessenmöller, D., Müller, J., Prati, D., Socher, S.A., Fischer, M., Weisser, W.W., Gossner, M.M., Learning, M., Cookbook, R., Ulyshen, M.D., Gossner, M.M., Falck, K., Weisser, W.W., Alexander, K.N.A., Saint-Germain, M., Drapeau, P., Buddle, C.M., Parisi, F., Pioli, S., Lombardi, F., Fravolini, G., Marchetti, M., Tognetti, R., Ramírez-Hernández, A., Martínez-Falcón, A.P., Micó, E., Almendarez, S., Reyes-Castillo, P., Escobar, F., Lindhe, A., Lindelöw, Å., Åsenblad, N., Jaworski, T., Plewa, R., Tarwacki, G., Sućko, K., Hilszczański, J., Horák, J., Pedlar, J.H., Pearce, J.L., Venier, L.A., McKenney, D.W., Ekbom, B., Schroeder, L.M., Larsson, S., Müller, J., Bußler, H., Kneib, T., Blazyte-Čereškiene, L., Karalius, V., Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S., Müller, J., Bouget, C., Nusillard, B., Pineau, X., Ricou, C., waraich, Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., Jonsell, M., Hansson, J., Wedmo, L., Sverdrup-Thygeson, A., Gustafsson, L., Kouki, J., Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., Ranius, T., Jansson, N., Profile, S.E.E., Ranius, T., Jansson, N., Isacsson, G., Brandl, R., Weisser, W.W., Bouget, C., Herv, E., 2014. Effects of forest management on ground-dwelling beetles (Coleoptera; Carabidae, Staphylinidae) in Central Europe are mainly mediated by changes in forest structure. For. Ecol. Manage. 6, 166–176. doi:10.1016/j.foreco.2014.06.012.

Lenz, H.D., Bartha, B., Straßer, L., Lemme, H., 2016. Development of ash dieback in South-Eastern Germany and the increasing occurrence of secondary pathogens. Forests 7. https://doi.org/10.3390/f7020041.

Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J., Hagge, J., 2022. Beetle diversity is higher in sunny forests due to higher microclimatic

heterogeneity in deadwood. Oecologia. https://doi.org/10.1007/s00442-022-05141-8.

Lindhe, A., Lindelöw, Å., Åsenblad, N., 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. Biodivers. Conserv. 14, 3033–3053. https://doi.org/10.1007/s10531-004-0314-y.

Luchman, J., 2020. Relative importance analysis with multivariate models: Shifting the focus from independent variables to parameter estimates. J. Appl. Struct. Equ. Model. 4, 1–20. doi:10.47263/JASEM.4(2)02.

McGeoch, M.A., Schroeder, M., Ekbom, B., Larsson, S., 2007. Saproxylic beetle diversity in a managed boreal forest: Importance of stand characteristics and forestry conservation measures. Divers. Distrib. 13, 418–429. https://doi.org/10.1111/j.1472-4642.2007.00350.x.

Meyer, S., Rusterholz, H.P., Baur, B., 2021. Saproxylic insects and fungi in deciduous forests along a rural–urban gradient. Ecol. Evol. 11, 1634–1652. https://doi.org/10.1002/ece3.7152.

Mitchell, R.J., Beaton, J.K., Bellamy, P.E., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Gimona, A., Harmer, R., Hester, A.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Kerr, G., Littlewood, N.A., Newey, S., Potts, J.M., Pozsgai, G., Ray, D., Sim, D.A., Stockan, J.A., Taylor, A.F.S., Woodward, S., 2014. Ash dieback in the UK: A review of the ecological and conservation implications and potential management options. Biol. Conserv. 175, 95–109. https://doi.org/10.1016/j.biocon.2014.04.019.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: A baseline for management recommendations in European forests. Eur. J. For. Res. 129, 981–992. https://doi.org/10.1007/s10342-010-0400-5.

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle Ips typographus in a national park: From pest to keystone species. Biodivers. Conserv. 17, 2979–3001. https://doi.org/10.1007/s10531-008-9409-1.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I.M.M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., Gossner, M.M., 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography (Cop.) 38, 499–509. https://doi.org/10.1111/ecog.00908.

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiß, I., Baldrian, P., Tláskal, V., Thorn, S., 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. Oikos 129, 1579–1588. https://doi.org/10.1111/oik.07335.

Netherer, S., Panassiti, B., Pennerstorfer, J., Matthews, B., 2019. Acute Drought Is an Important Driver of Bark Beetle Infestation in Austrian Norway Spruce Stands. Front. For. Glob. Chang. 2, 1–21. https://doi.org/10.3389/ffgc.2019.00039.

Oettel, J., Lapin, K., Kindermann, G., Steiner, H., Schweinzer, K.M., Frank, G., Essl, F., 2020. Patterns and drivers of deadwood volume and composition in different forest types of the Austrian natural forest reserves. For. Ecol. Manage. 463 https://doi.org/10.1016/j.foreco.2020.118016.

Oettel, J., Lapin, K., 2020. Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. Ecol. Indic.

Parisi, F., Lombardi, F., Sciarretta, A., Tognetti, R., Campanaro, A., Marchetti, M., Trematerra, P., 2016. Spatial patterns of saproxylic beetles in a relic silver fir forest (Central Italy), relationships with forest structure and biodiversity indicators. For. Ecol. Manage. 381, 217–234. https://doi.org/10.1016/j.foreco.2016.09.041.

Parisi, F., Pioli, S., Lombardi, F., Fravolini, G., Marchetti, M., Tognetti, R., 2018. Linking deadwood traits with saproxylic invertebrates and fungi in European forests – A review. IForest 11, 423–436. https://doi.org/10.3832/ifor2670-011.

Parisi, F., Frate, L., Lombardi, F., Tognetti, R., Campanaro, A., Biscaccianti, A.B., Marchetti, M., 2020. Diversity patterns of Coleoptera and saproxylic communities in unmanaged forests of Mediterranean mountains. Ecol. Indic. 110, 105873 https://doi.org/10.1016/j.ecolind.2019.105873.

R Core Team, 2021. R: A language and environment for statistical computing (version 4.1.0) [WWW Document]. R Found. Stat. Comput. Vienna, Austria. URL https://www.r-project.org/.

Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. 95, 85–94. https://doi.org/10.1016/S0006-3207(00)00007-0.

Rimle, A., Heiri, C., Bugmann, H., 2017. Deadwood in Norway spruce dominated mountain forest reserves is characterized by large dimensions and advanced decomposition stages. For. Ecol. Manage. 404, 174–183. https://doi.org/10.1016/j.foreco.2017.08.036.

Ripley, B., Venables, B., Bates, D.M., Horni, K., Gebhardt, A., Firth, D., 2019. Package 'MASS': Support Functions and Datasets for Venables and Ripley's MASS.

Russ, W., 2019. Mehr als 4 Millionen Hektar Wald in Österreich, in: Praxisinformation: Zwischenauswertung Der Waldinventur. Vienna, pp. 3–7.

Sandström, J., Bernes, C., Junninen, K., Lõhmus, A., Macdonald, E., Müller, J., Jonsson, B.G., 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. J. Appl. Ecol. 56, 1770–1781. https://doi.org/10.1111/1365-2664.13395.

Schlick-Steiner, B.C., Steiner, F.M., Moder, K., Bruckner, A., Fiedler, K., Christian, E., 2006. Assessing ant assemblages: Pitfall trapping versus nest counting (Hymenoptera, Formicidae). Insectes Soc. 53, 274–281. https://doi.org/10.1007/s00040-006-0869-6.

Schmidl, J., Bussler, H., 2004. Ökologische Gilden xylobionter Käfer Deutschlands. Naturschutz und Landschaftsplan. 36, 202–218.

Seibold, S., Ulyshen, M.D., Gossner, M.M., Thorn, S., Bässler, C., Müller, J., Brandl, R., 2015. Experimental studies of dead-wood biodiversity — A review identifying global gaps in knowledge. Biol. Conserv. 191, 139–149. https://doi.org/10.1016/j.biocon.2015.06.006.

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

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S., Müller, J., 2017. An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology 98, 1613–1622. https://doi.org/10.1002/ecy.1819.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R.S., Birkemoe, T., Boros, G., Brandl, R., Brustel, H., Burton, P.J., Cakpo-Tossou, Y.T., Castro, J., Cateau, E., Cobb, T.P., Farwig, N., Fernández, R.D., Firn, J., Gan, K.S., González, G., Gossner, M.M., Habel, J.C., Hébert, C., Heibl, C., Heikkala, O., Hemp, A., Hemp, C., Hjältén, J., Hotes, S., Kouki, J., Lachat, T., Liu, J., Liu, Y., Luo, Y.H., Macandog, D.M., Martina, P.E., Mukul, S.A., Nachin, B., Nisbet, K., O'Halloran, J., Oxbrough, A., Pandey, J.N., Pavlíček, T., Pawson, S.M., Rakotondranary, J.S., Ramanamanjato, J.B., Rossi, L., Schmidl, J., Schulze, M., Seaton, S., Stone, M.J., Stork, N.E., Suran, B., Sverdrup-Thygeson, A., Thorn, S., Thyagarajan, G., Wardlaw, T.J., Weisser, W.W., Yoon, S., Zhang, N., Müller, J., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8.

Shorohova, E., Kapitsa, E., 2014. Stand and landscape scale variability in the amount and diversity of coarse woody debris in primeval European boreal forests. For. Ecol. Manage. 356 https://doi.org/10.1016/j.foreco.2015.07.005.

Siitonen, J., 2001. Forest Managment, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Similä, M., Kouki, J., Martikainen, P., Uotila, A., 2002. Conservation of beetles in boreal pine forests: The effects of forest age and naturalness on species assemblages. Biol. Conserv. 106, 19–27. https://doi.org/10.1016/S0006-3207(01)00225-7.

Sippola, A.L., Siitonen, J., Punttila, P., 2002. Beetle diversity in timberline forests: A comparison between old-growth and regeneration areas in Finnish Lapland. Ann. Zool. Fennici 39, 69–86.

Steyrer, G., Cech, T.L., Fürst, A., Hoch, G., Perny, B., 2020. Waldschutzsituation 2019 in Österreich: Schäden durch Borkenkäfer weiterhin extrem hoch. Forstschutz Aktuell 33–44.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Deadwood. doi:10.1017/CBO9781139025843.

Suárez-Tangil, B.D., Rodríguez, A., 2021. Estimates of species richness and composition depend on detection method in assemblages of terrestrial mammals. Animals 11, 1–15. https://doi.org/10.3390/ani11010186.

Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N., Seidl, R., 2017a. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. J. Appl. Ecol. 54, 28–38. https://doi.org/10.1111/1365-2664.12644.

Thom, D., Rammer, W., Seidl, R., 2017b. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Glob. Chang. Biol. 23, 269–282. https://doi.org/10.1111/gcb.13506.

Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R.E. (Eds.), 2010. National Forest Inventories - pathways for common reporting, National Forest Inventories: Pathways for Common Reporting. Springer, New York. doi:10.1007/978-90-481-3233-1.

Ulyshen, M.D., 2016. Wood decomposition as influenced by invertebrates. Biol. Rev. 91, 70–85. https://doi.org/10.1111/brv.12158.

Ulyshen, M.D., Hanula, J.L., 2009. Habitat associations of saproxylic beetles in the southeastern United States: A comparison of forest types, tree species and wood postures. For. Ecol. Manage. 257, 653–664. https://doi.org/10.1016/j.foreco.2008.09.047.

Vanderwel, M.C., Malcolm, J.R., Smith, S.M., 2006. An integrated model for snag and downed woody debris decay class transitions. For. Ecol. Manage. 234, 48–59. https://doi.org/10.1016/j.foreco.2006.06.020.

Victorsson, J., 2012. Semi-field experiments investigating facilitation: Arrival order decides the interrelationship between two saproxylic beetle species. Ecol. Entomol. 37, 395–401. https://doi.org/10.1111/j.1365-2311.2012.01377.x.

Vodka, Š., Cizek, L., 2013. The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. For. Ecol. Manage. 304, 33–41. https://doi.org/10.1016/j.foreco.2013.04.007.

Vogel, S., Gossner, M.M., Mergner, U., Müller, J., Thorn, S., 2020. Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. J. Appl. Ecol. 57, 2075–2085. https://doi.org/10.1111/1365-2664.13648.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E., Thorn, S., 2021. Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches. Insect Conserv. Divers. 14, 132–143. https://doi.org/10.1111/icad.12442.

Walentowski, H., Müller-Kroehling, S., Bergmeier, E., Bernhardt-Römermann, M., Gossner, M.M., Reif, A., Schulze, E.D., Bußler, H., Strätz, C., Adelmann, W., 2014. Faunal diversity of fagus sylvatica forests: A regional and European perspective based on three indicator groups. Ann. For. Res. 57, 215–231. doi:10.15287/afr.2014.172.

Walker, F.M., Williamson, C.H.D., Sanchez, D.E., Sobek, C.J., Chambers, C.L., 2016. Species from feces: Order-wide identification of chiroptera from guano and other non-invasive genetic samples. PLoS One 11, 1–22. https://doi.org/10.1371/journal.pone.0162342.

Weslien, J., Djupström, L.B., Schroeder, M., Widenfalk, O., 2011. Long-term priority effects among insects and fungi colonizing decaying wood. J. Anim. Ecol. 80, 1155–1162. https://doi.org/10.1111/j.1365-2656.2011.01860.x.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis [WWW Document]. Springer-Verlag New York.

ZAMG, 2020. Climate Data [WWW Document]. URL https://www.zamg.ac.at/cms/en/climate/climate (accessed 12.17.20).

Zumr, V., Remeš, J., Pulkrab, K., 2021. How to increase biodiversity of saproxylic beetles in commercial stands through integrated forest management in central Europe. Forests 12, 1–19. https://doi.org/10.3390/f12060814.