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Relationships Between Saproxylic Beetle Microhabitat Occurrences and Forest State Indicators

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Abstract: The use of proxies in habitat assessments has become widespread in recent decades. We used forest state descriptive data from a large-scale project (SCP) as proxies to investigate the occurrence of habitats suitable for some protected saproxylic beetles. We searched for pre-defined tree-related microhabitats (TreMs) suitable for saproxylic beetles in 1 ha quadrats in the Börzsöny Mts., Hungary. We compared the frequency of each microhabitat type with the aggregated values of the forest state proxies. Our results suggest that the average number of snags with DBH = 21–50 cm and the frequency of lying deadwood with Ø > 35 cm can adequately represent the occurrence of all beetle microhabitats studied. In most cases, the frequency of plots with species richness of live canopy trees with DBH > 35 cm and the amount of lying dead wood were also good indicators. The TreM indicators of the SCP alone can detect the presence of specialist beetles requiring cavities. The stands with a better forest state had more protected saproxylic beetles. The practical implementation of our work is based on the optimization of the resources required for monitoring. In surveys prepared to cover large areas, it is easier to monitor the habitat of saproxylic beetles with the help of individual proxies.

Keywords: tree-related microhabitats; Natura 2000; forest state proxy; deadwood; habitat tree; veteran tree

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1. Introduction

European forests were structurally more diverse in their original natural state regardless of whatever theories we accept about their pre-human appearance. Some suggest that the original natural vegetation of temperate forests in Central and Western Europe was probably a park-like landscape [1] or closed stands with gap dynamics [2,3]. Their diversity was maintained by biotic and abiotic natural disturbances of varying intensities. Over the last few hundred years, forests have undergone drastic transformations: the structural richness of the original vegetation has been impoverished by human impacts. Mostly open forests have been replaced by closed, dark, monocultivated stands, and the occurrence of light-dependent species has declined [4]. This forestry practice, including the felling of veteran trees, the removal of deadwood, and the disappearance of large-diameter trees, has greatly reduced the tree-related microhabitats (TreMs) associated with them [5]. The progressive technical development in forestry and the recurrent disturbances caused by production and the most common rotation forest management had increasing negative effects on biodiversity [6–8]. European forests managed by rotation forestry systems are characterized by even-aged stands, short rotation times compared to the natural lifespan of tree species, low tree species richness, homogenous structure, and a low amount and heterogeneity of TreMs, such as large-diameter deadwoods or veteran trees. However, many of these TreMs may preserve high biodiversity, including thousands of forest specialist species and special habitat types [9].

The decaying parts and the cavities of habitat trees can persist for a long time and provide continuous habitats for saproxylic beetles and other invertebrates [10]. Nowadays, veteran trees are rarely found in closed forests treated with intensive forest management but are more common in forests with low levels of canopy closure and in wood pastures, providing habitats for heliophilic and thermophilic saproxylic species [11]. There are also forest stands containing veteran trees that have been spontaneously reforested due to abandonment of grazing and silvicultural interventions. The survival of veteran trees in such sites depends on their abandonment and the canopy closure of the stand. The dynamics of communities living on veteran trees under closed stands are shifting towards extinction debt [5]. The continuous development of veteran trees into standing dead trees and later lying deadwoods is also valuable, as large-diameter deadwood is mostly not present in sufficient quantities in commercial forests [12]. These results suggest that species associated with open canopies or large-diameter deadwood are at higher risk of extinction than other specialists [5].

The saproxylic communities that use these TreMs have declined and are now among Europe's most threatened biodiversity elements [13], despite the fact that a quarter of the species in forest communities are saproxylic [14]. Many saproxylic beetles are listed as species of community interest under the Habitats Directive [15]. Their distribution and population dynamics need to be monitored, thus receiving special attention. Some of these species are also identified as flagship and umbrella species [16]. Only a few saproxylic beetle species have been selected as an indicator of habitat quality within the Natura 2000 system [17]. Therefore, in addition to species under Natura 2000 protection, it is worthwhile to consider less intensively researched species that are included in other types of protection lists (e.g., national protection, Red List) [18].

In many cases, we do not have enough information on the habitat requirements of protected species [19]. Deadwood characteristics, like amount [17,20], type (standing or lying [19], species composition [21], decaying stage [22,23], diameter distribution [24], and the presence of habitat or cavity-bearing tree [25,26] could be important. Differences in saproxylic community composition between deadwood types are magnified by higher trophic level specialists [19]. Indirect factors influencing the organization of deadwood species assemblages are canopy closure [13,27], temperature [17,21], moisture [24], management characteristics (deadwood retention) [19], and habitat continuity [28].

Forest stand scale studies have most often shown that managed forests have lower saproxylic abundance [13], diversity [22], and different composition [29] than unmanaged forests. This may be due to the fact that even under close-to-nature forest management practices, habitat trees may be felled and deadwood removed [30]. However, others have found that managed forests have higher saproxylic diversity than unmanaged forests. In managed forests, more species are associated with fresh deadwood [29], whereas in unmanaged forests, more rare, protected species can be found [21]. In any case, the presence and characteristics of forest structure elements can provide more reliable information on species richness than management intensity [29]. Due to the high number of saproxylic species, their habitat requirements are also diverse. The presence of habitat trees [25] and an adequate quantity, quality, and continuity of deadwood ensure their high species richness [24]. These criteria are often integrated into some monitoring programs [31–33]. The monitoring of species of community interest as defined in the EU Habitats Directive should be a priority. In addition to these, many other protected species are less researched due to their rare occurrence and invasive sampling methods. In many cases, only the amount of deadwood is used as an indicator, and the presence of the protected species in them is rarely investigated [34].

For better-known taxa, it is possible to formulate precise habitat criteria. Recognition of these types can be used to estimate whether the protected species is likely to occur in a study area [35]. They can also be interpreted as indirect indicators (proxies) and highlight the most important criteria. The presence of species can also be confirmed by further specific surveys (e.g., observation, trapping, bark peeling, exit hole examinations, etc.). Larval galleries and adult insect exit holes in wood and bark serve as prominent evidence of the presence of various species [36]. Despite this, these features are rarely utilized in entomological research [37]. These methods can be even better than traditional techniques (e.g., flight traps), as other methods are not proof of colonization [38]. Within the families *Cerambycidae* and *Buprestidae*, multiple studies have been carried out on several species by surveying species-specific exit holes [39–43]. The size and shape of the exit holes are useful, even for examining population attributes [37]. Their presence might indicate beetle communities with similar habitat requirements. The functional role of saproxylic beetles is rarely addressed [30]. However, functional studies based on communities are more useful because they also help to interpret the consequences of (local) species extinctions [44].

In this paper, we examined which stand-scale indicators are able to predict the presence of the studied habitats suitable for some protected saproxylic beetles as proxies. In order to achieve this, we also demonstrated a newly developed TreM classification method. Our goal is to identify the most important general predictors and the differences between the forest stand types and the examined species based on forest state indicators.

2. Methods

2.1. Forest State Data

The SCP ("Swiss Contribution Project"—"Multi-purpose assessment serving biodiversity conservation in the Carpathian region of Hungary") field surveys were carried out in 3 landscape units of Hungary (Börzsöny, Mátra, and Aggtelek Mts.) between 2014 and 2016. Extensive data collection was carried out on 500 m^2 circular plots along a 50, 70, or 100 m grid. At the plot level, data were collected on canopy closure, tree stand composition, DBH class distribution, standing and lying dead trees with their decay stage, and the occurrence of TreMs (Table 1). The "route" is a sampling unit used to describe a few stand characteristics that can be observed along a straight line connecting two plots. On the route, we registered large (DBH > 50 cm) outstanding living or dead trees, which were at least 30 cm larger than the average diameter of neighboring trees. In this paper, we have only highlighted the components used in this research; the full list and detailed methodology are available in [45]. In this manuscript, we present and evaluate the survey data collected in the Börzsöny Mts.

Table 1. Definition and explanation of relevant SCP variables. Legend: FWD and CWD: Fine and Coarse Woody Debris; DBH: Diameter at Breast Height; TreM: tree-related microhabitat.

Sampling Unit	Variable	Details
Route	Presence of outstanding large veteran trees	Alive/dead/both; DBH > 50 cm
Plot	Canopy closure	Closure of trees above 2.5 m in height with 5% precision
	Tree species composition in diameter classes	Cover in broad categories (0%–5%, 6%–20%, 21%–50%, 51%–100%), in diameter classes (DBH = 0–8, 9–20, 21–35, 36–50, >50 cm) above 2.5 m, per species
	No. of standing dead trees and snags	In diameter classes above (dead tree) and below (snag) 2.5 m (DBH = 9–20, 21–50, >50 cm)
	Decay stage of standing dead trees	Fresh/mixed/decayed categories in case of two diameter classes (DBH = 21–50, >50 cm)
	Lying deadwood	FWD (Ø = 0–8 cm) and CWD (Ø > 8 cm) diameter and quantity (m^3 classes) in 9 categories
	Decay stage of CWD	Fresh/mixed/decayed categories for two diameter classes (Ø = 8–35, >35 cm)
	No. of TreM categories	The occurrence of 12 categories: root plate, residual pile, new stump, old stump, trunk base rot hole, trunk rot hole, stem breakage, bark loss, bark shelter, bird breeding cavity on living tree, bird breeding cavity on dead tree, deadwood on living tree

2.2. Study Area

The study area is located in the Börzsöny Mts. The bedrock is mainly andesite of volcanic origin. The highest peak is 939 m. The average annual mean temperature is 7.5–9.0 °C [46], and annual precipitation is 600–850 mm [47]. The vegetation of the mountain range is characterized by stands of sessile oak (*Quercus petraea* (Matt.) Liebl.) and Turkey oak (*Quercus cerris* L.) on the lower elevations. Above these, hornbeams (*Carpinus betulus* L.) and sessile oaks predominate. In higher areas, on north-facing slopes, and in valleys, European beech (*Fagus sylvatica* L.) dominates. Most of the forests in the mountain range are under active silvicultural management. The forests are managed according to a uniform shelterwood system [48]. Smaller areas are also managed by selection cutting, and there are some protection forests [49].

The selection of sampling sites for the saproxylic beetle survey was based on SCP data. Only mature oak and beech-dominated stands were selected (their admixing ratio is greater than 50%), and their quality (good, medium, poor) was also specified based on the deadwood's amount and quality. These categories were roughly equally represented in the sampling areas. The sampling units were 1 ha large quadrats, surrounded by 4 SCP plots in a 100 m grid (Figure 1). At least 3 out of 4 SCP plots had to meet the mentioned habitat criteria. A total of 155 quadrats were surveyed.

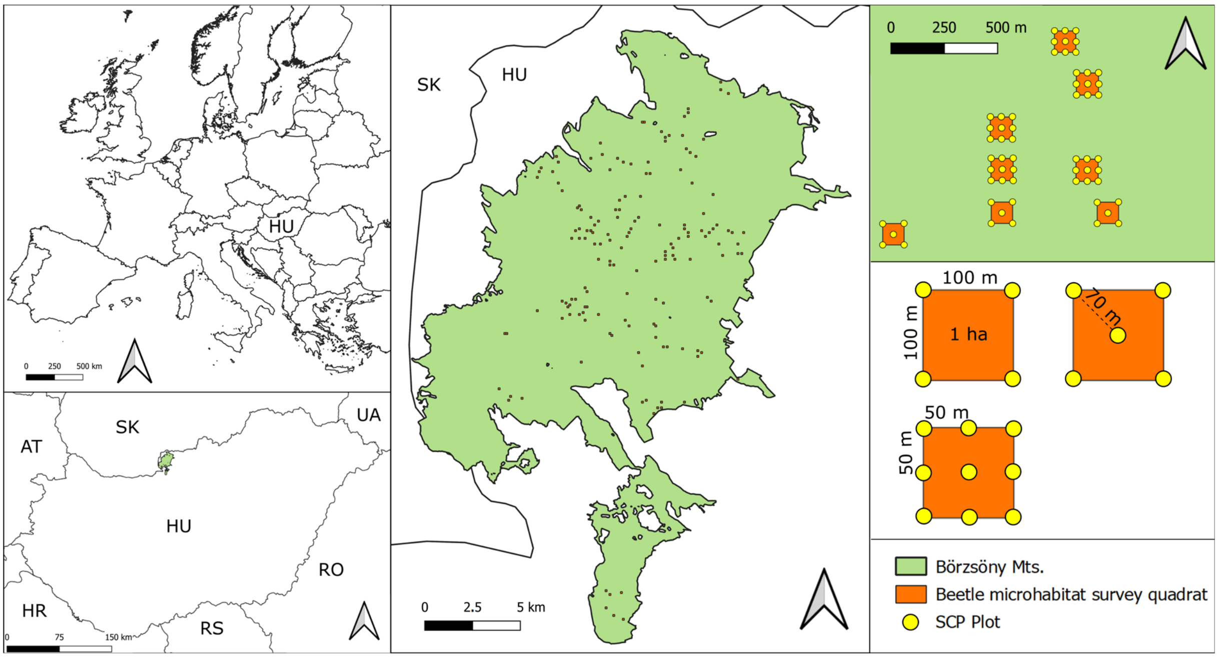

Figure 1. Study areas in the Börzsöny Mts. Spatial location of saproxylic beetle sampling quadrats and SCP plots. Four (100 m), five (70 m), or nine (50 m) SCP plots were contained in each beetle quadrat, depending on the density of the SCP sampling grid.

2.3. Saproxylic Beetle Data Collection

We studied 10 beetle taxa: *Cerambyx cerdo* Linnaeus, 1758; *Rosalia alpina* Linnaeus, 1758; *Limoniscus violaceus* P.W.J. Müller, 1821; *Cucujus cinnaberinus* Scopoli, 1763; *Sinodendron cylindricum* Linnaeus, 1758; *Lacon querceus* Herbst, 1784; *Eurythyrea quercus* Herbst, 1780; *Gasterocercus depressirostris* Fabricius, 1792; *Ampedus* spp.; and *Protaetia* spp. The species-specific habitat requirements, the occurrence of life traces along their development, the commonly used monitoring methods, and stand-scale predictors of their occurrence are summarized in Supplementary File S1. These taxa are protected in Hungary [50], and several of which are listed in the appendices of the Habitats Directive [15] and/or in the European Red List [18]. An important consideration was that these species should well characterize the physiognomy of the habitat tree or deadwood and the decay stage and be suitable for the descriptive designation of microhabitat types.

Based on the habitat requirements and life history characteristics of the presented saproxylic beetles and our preliminary experience, we defined 10 species-specific TreM types associated with them (Figure 2). The aim of defining these TreM types was to obtain the same amount of information as presence–absence data so that these species, which are mostly hidden, often occur in small numbers, and are found in adult form for a short period of time, can be found. The search for these species' adults and larvae often involves the partial destruction of the habitat. If the carefully formulated characteristics of the microhabitats (Figure 2, Supplementary File S1) were met, it was considered an occurrence. The definitions were developed based on our previous research (partly) in this area [51–53]. Data collection took place in 2021, between 10 June and 1 September. During the detailed investigation of the sampling quadrats, the pre-defined TreM types were recorded. Where such microhabitats were found, more detailed surveys were carried out to confirm the actual presence of the beetles. To perform this, several techniques were used simultaneously: searching for adults, larvae (even by invasive methods) and remains, detection of life traces (exit holes), and breeding the larvae to tenerals. In all cases, we recorded data from microhabitats matching the definitions, even if the saproxylic beetles we were looking for were not present. To ensure correct identification, additional species-specific criteria had to be met as follows:

- Cerambyx-type tree. Since *Aegosoma scabricorne* Scopoli, 1763 can also cause similar exit holes—although its habitat is basically different—we only recorded the large holes on the bark surface of oak trees.
- Gasterocercus-type tree. As there are other species of insects, especially wasps, that leave similar life traces—circular holes of the same diameter—we only recorded the trees in which we found the remains of *G. depressirostris* imago in one of the holes.
- Lacon-type cavity. The structure of the debris, the typical fungus (*Laetiporus sulphureus* Bull. (Murrill))-infested wood, its color, and the presence of the associated species, especially *Pentaphyllus* spp., are together considered an *L. querceus* occurrence.
- Cucujus-type dead tree. It was recorded if there was minimal debris under the moist bark, with life traces of associated species, e.g., *Hololepta plana* Sulzer, 1776 or the shedding remains of the target species.
- Limoniscus-type cavity. The most typical associated species (within the same microhabitat) is the *Ischnodes sanguinicollis* Panzer, 1793. If it was present, it means that the cavity is probably occupied by *L. violaceus* too, but the characteristics of the cavity make it clear enough that it is suitable for it.
- Protaetia-type cavity. Not all suitable cavities were considered colonized by these species, but only those with large quantities of species-specific feces, larval, shedding, or imago remains were found.
- Rosalia-, Ampedus-, and Sinodendron-type TreMs. The exit holes and other life traces found in the defined TreM types (Figure 2) within the study area are sufficient evidence of the presence of the species on their own, as they cannot be confused with any other species.

In addition, we also recorded non-species-specific microhabitats (barkless and intact standing and lying deadwood over an 8 cm diameter, new and old stumps). All 16 (10 species-specific + 6 general) microhabitat types were recorded in the 1 ha quadrats.

In all cases, quantitative data interpreted on an ordinal scale were also recorded (Table 2). Since further calculations require at least an interval scale, we interpreted the abundance data using interval midpoints.

2.4. Analysis

2.4.1. Data Preparation

For each quadrat, the number of microhabitat types and the number of microhabitats were collected. From these, a dataset was created that included all microhabitat types surveyed and one that included only the species-specific microhabitat types.

For the survey quadrats, it was necessary to aggregate the values for the SCP plots. Based on the descriptions of microhabitats and our experience, we included all relevant variables assessed by SCP in our analyses. Some variables could be averaged due to their nature, while in some cases, data could be aggregated by frequency (proportion of plots in the quadrat). We calculated average canopy closure, average native tree species number, average native admixed tree species number, average tree species number with DBH = 36–50 cm and DBH > 50 cm (also for admixed species), average non-native and invasive tree species number, average pseudospecies number (number of non-empty elements in tree species × diameter classes matrix), the average number of DBH classes, the average number of standing dead trees and stumps in different diameter classes (Ø = 9–20, 21–50, >50 cm), the average number of all standing deadwood, the average number of TreM categories (Table 1), and the average volume of deadwood (m^3/ha). Frequencies were calculated for additional variables. These were the frequency of fresh, mixed, and decayed standing dead trees with DBH = 21–50 cm and DBH > 50 cm, the frequency of plots containing only FWD (lying dead wood with Ø < 8 cm) and CWD Ø = 8–35 cm and Ø > 35 cm), the frequency of plots with CWD of fresh, mixed, and decayed classifications for the Ø = 8–35 cm and Ø > 35 cm diameter classes, and the frequencies of live, dead, and both classifications or large veteran trees recorded on the route.

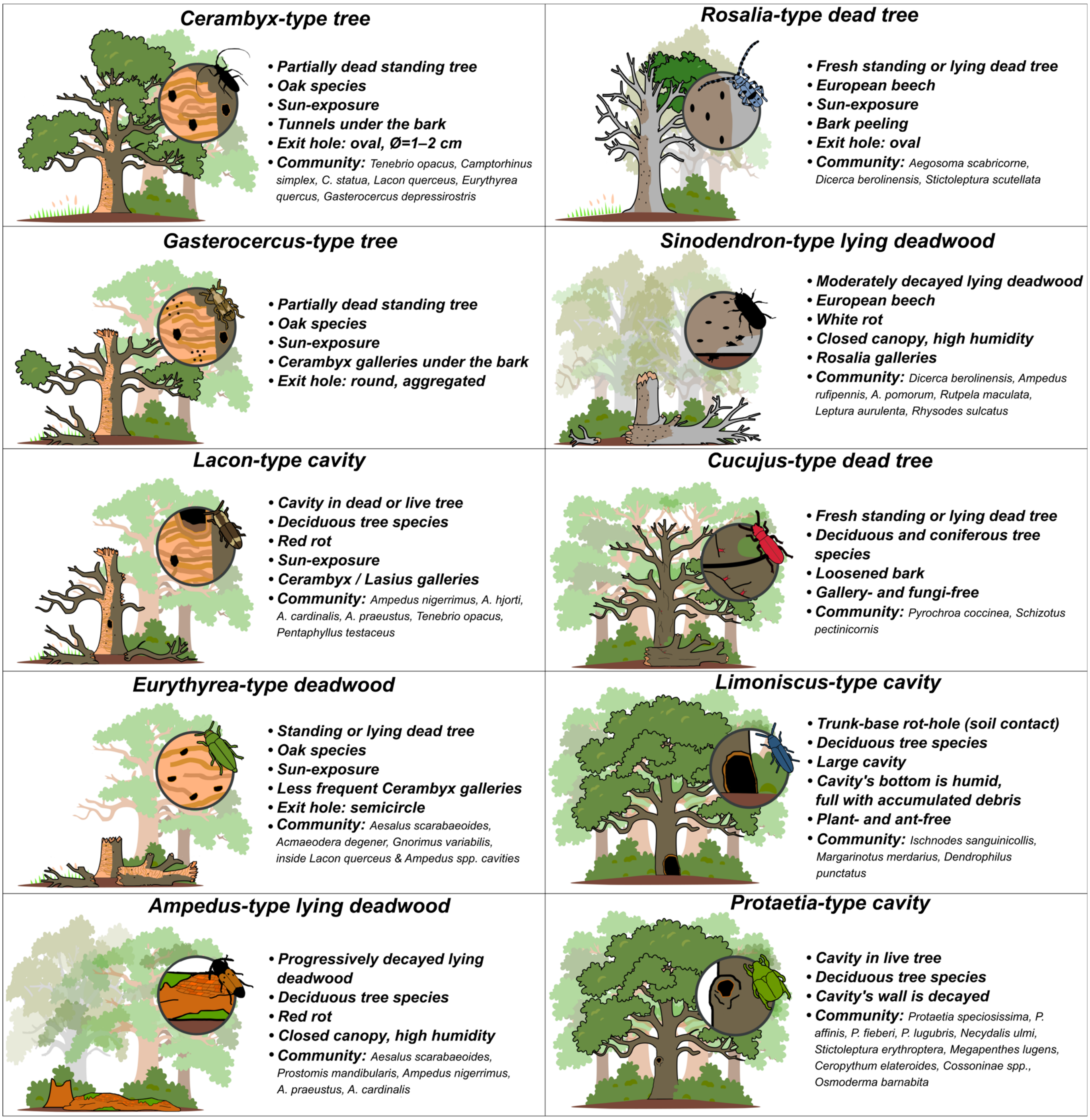

Figure 2. Characteristics and potential species pool of the 10 pre-defined tree-related microhabitat (TreM) types. Abbreviations have been used in the names of the types (e.g., Lacon-type cavity = Lacon querceus-type cavity) so that they can be considered species-specific microhabitats (with the exception of *Protaetia* and *Ampedus* spp.).

Table 2. Scales used for data recording.

Occurrence of Each TreM Type (No.)	Interval-Scale Midpoint (No.)
0	0
1	1
2–5	4
6–10	8
10–25	18
>25	30

2.4.2. Variable Selection

We excluded some variables from further analysis by exploring the number of cases. In the SCP data aggregated to quadrats, we found that the following variables occurred in statistically insignificant numbers of cases: the number of invasive tree species, the frequency of a mixed decay class of DBH > 50 cm standing deadwood, the frequency of large live and dead trees on the route, the number of non-native and invasive species, the frequency of DBH > 50 cm standing dead trees and snags, and the frequency of fresh and decayed DBH > 50 cm standing dead trees.

Despite excluding variables with a small number of cases, 36 variables remained. Due to the high number of potentially confounding explanatory variables for forest structural descriptors, we have implemented a random forest or random decision forests technique, which is an ensemble learning method for classification [54]. Using this method, we have constructed a collection of decision trees to estimate the mean decrease in accuracy of the relative importance of predictors in relation to the selected response variables for the number of beetle microhabitats. We have set the selection threshold to the first breakpoint in the decreasing order of predictors according to their relative importance. Forest stand descriptors in relation to the number of saproxylic beetle microhabitats are given in descending order of their relative variance importance (Supplementary File S2).

- Avg. No. of snags with DBH = 21–50 cm;
- Avg. No. of TreM categories;
- Avg. volume (m^3) of CWD;
- Freq. of decayed CWD with 35 cm < Ø;
- Freq. of CWD with 35 cm < Ø;
- Avg. No. of DBH > 50 cm tree species;
- Avg. No. of DBH classes;
- Avg. No. of DBH = 36–50 cm tree species;
- Freq. of outstanding live trees;
- Freq. of routes without outstanding trees;
- Freq. of CWD with Ø = 8–35 cm.

2.4.3. Statistical Analysis

To explore the relationship between the occurrence of saproxylic beetle microhabitats (as abundance site matrix) and the selected forest structural variables (Supplementary File S2), we applied Redundancy Analysis (RDA, [55]). This technique is frequently used in ecological and environmental research to understand the influence of predictor variables (forest state variables) on the variation in response variables, such as microhabitat numbers. The species with less than 10 occurrences were excluded from these analyses. We paid attention to the characteristics (oak or beech forests in a bad, moderate, or good state) of the study sites. During the RDA analyses, all the predictors were included based on variable selection by the random forest algorithm for the number of beetle microhabitats, and then we used a backward selection for the most adequate model in terms of the number of model parameters. A conditional random forest algorithm was used based on 5000 trees built using sample splitting, and the fraction was set at 0.632 as the portion of observations to draw without replacement. The analyses were carried out in R 4.4.1 [56] using the Vegan package (version 2.6-4, [57]).

The occurrence of species-specific and all microhabitats in beech and oak-dominated forests was also examined separately. For this purpose, we did not use the random forest variable selection results. In addition, the relationships between the number of species-specific microhabitats and forest state indicators were examined separately. During the species-specific analysis, we used variable selection based on experts' judgment; only those explanatory variables that could influence species occurrence based on their microhabitat descriptions were examined (Figure 2). Further results can be obtained from these detailed analyses. Spearman rank correlation tests were performed for these analyses, and the results were presented as correlation heatmaps. We applied this method to reveal meaningful relationships between different variables or different groups of variables. Exploring the relationship between variables can endeavor towards new insight and identify interdependencies. With this approach, we can group the related variables to reduce the need for further separate analyses.

3. Results

3.1. Redundancy Analysis

In the RDA ordination, the eigenvalues associated with the first two gradients were 74.58 and 13.36. These axes explained 30% cumulative variance of the species dataset and 69.61% cumulative variance of the microhabitat–forest structure relationships. Few species were strongly associated with particular habitats and forest structural variables (Figure 3). The Eurythyrea-type microhabitat was associated with oak forests in a good state where lying decayed deadwood larger than 35 cm in diameter was dominant. Rosalia- and Sinodendron-type microhabitats were associated with beech forests in a good state. These forests were characterized by trees with DBH > 50 cm, snags between DBH = 21 and 50 cm, and the increased amount of average CWD volume. The Cerambyx-type microhabitat was located in the negative range on both the x and y axes; therefore, their associations were also negative. It was associated with oak and beech forests in a bad state. In these forests, there were outstanding large and veteran trees, and the frequency of lying deadwood between 8 and 35 cm in diameter was low (therefore, the frequency of other diameter classes was higher) (Figure 3).

3.2. Correlation Heatmaps

The correlations of the total number of microhabitats with forest state indicators showed similar results to the random forest (Figure 4). However, significant differences could be observed when categorized by forest type. All forest composition variables showed strong correlations for beech forests, while they were weaker or even the opposite in oak forests. In all cases, indicators related to thinner standing and lying deadwood showed a weak correlation with the occurrence of microhabitats. Regardless of stand type and its quality, the following indicators showed a stronger and significant ($p < 0.05$) correlation in all cases with the microhabitats:

- Avg. No. of DBH = 36–50 cm tree species;
- Avg. No. of DBH > 50 cm tree species;
- Avg. No. of DBH classes;
- Avg. No. of snags with DBH = 21–50 cm;
- Avg. volume (m^3) of CWD;
- Freq. of CWD with 35 cm < Ø;

- Freq. of decayed CWD with 35 cm < Ø;
- Freq. of outstanding live trees;
- Avg. No. of TreM categories.

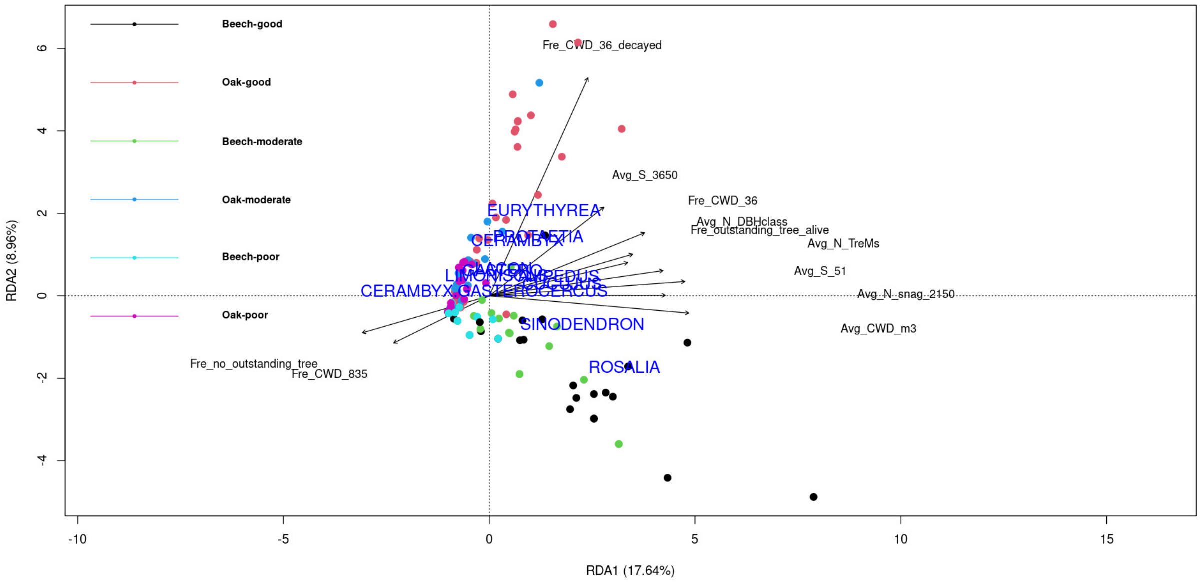

Figure 3. RDA tri-plot for the full model for saproxylic beetle microhabitats and forest structural descriptors. The arrows denote the changes in the forest's structural variables. Different colors represent habitats of different states and types.

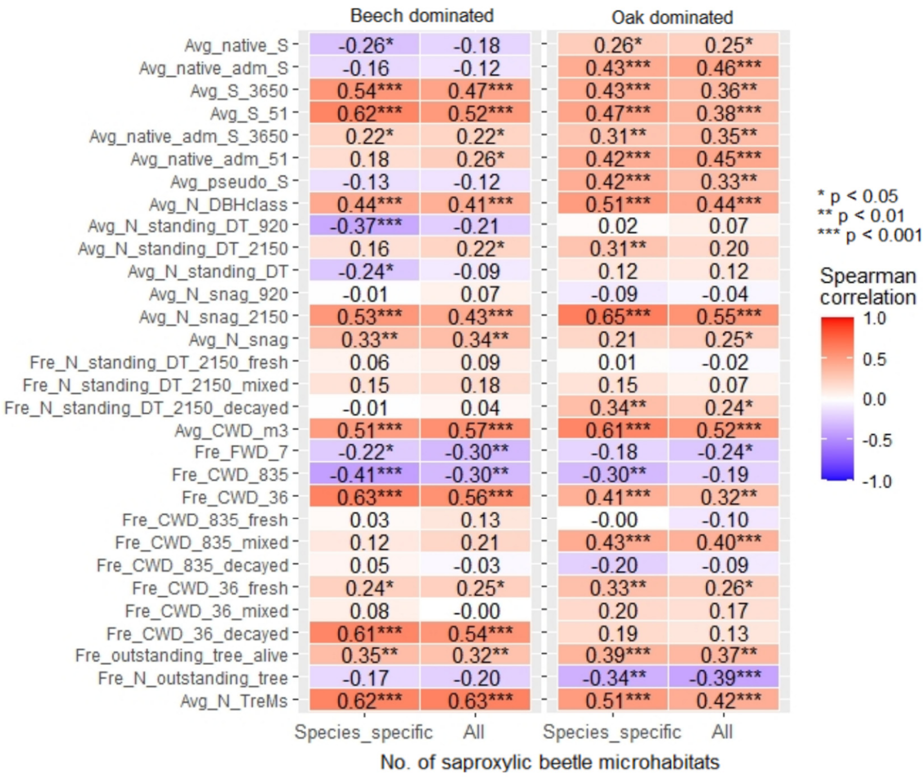

Figure 4. The relationship between species-specific and total (species-specific and general) microhabitat numbers and forest state indicators by forest stand type plotted on a correlation heatmap. Numbers indicate *r*-values. Legend: avg: average; fre: frequency; N: number; adm: admixed; S: species number; pseudo S: number of the non-empty elements of the species × DBH classes matrix; DT: dead tree; FWD and CWD: Fine and Coarse Woody Debris; TreMs = tree-related microhabitat categories; cav: cavity; numbers: DBH class limits (e.g., "920": DBH = 9–20 cm), the upper or lower limit for unique numbers (e.g., "36": >35 cm).

Species-specific microhabitats can be examined in detail to see what forest state indicators each species is associated with (Figure 5). In most cases, weak correlations are observed, but there are some variables that seem to be relevant for all species. The following indicators showed a significant ($p < 0.05$) and strong correlation in all cases with the microhabitats:

- Avg. No. of snags with DBH = 21–50 cm;
- Avg. volume (m^3) of CWD;
- Freq. of CWD with 35 cm < Ø;
- Freq. of trunk-based rot holes;
- Freq. of cavities.

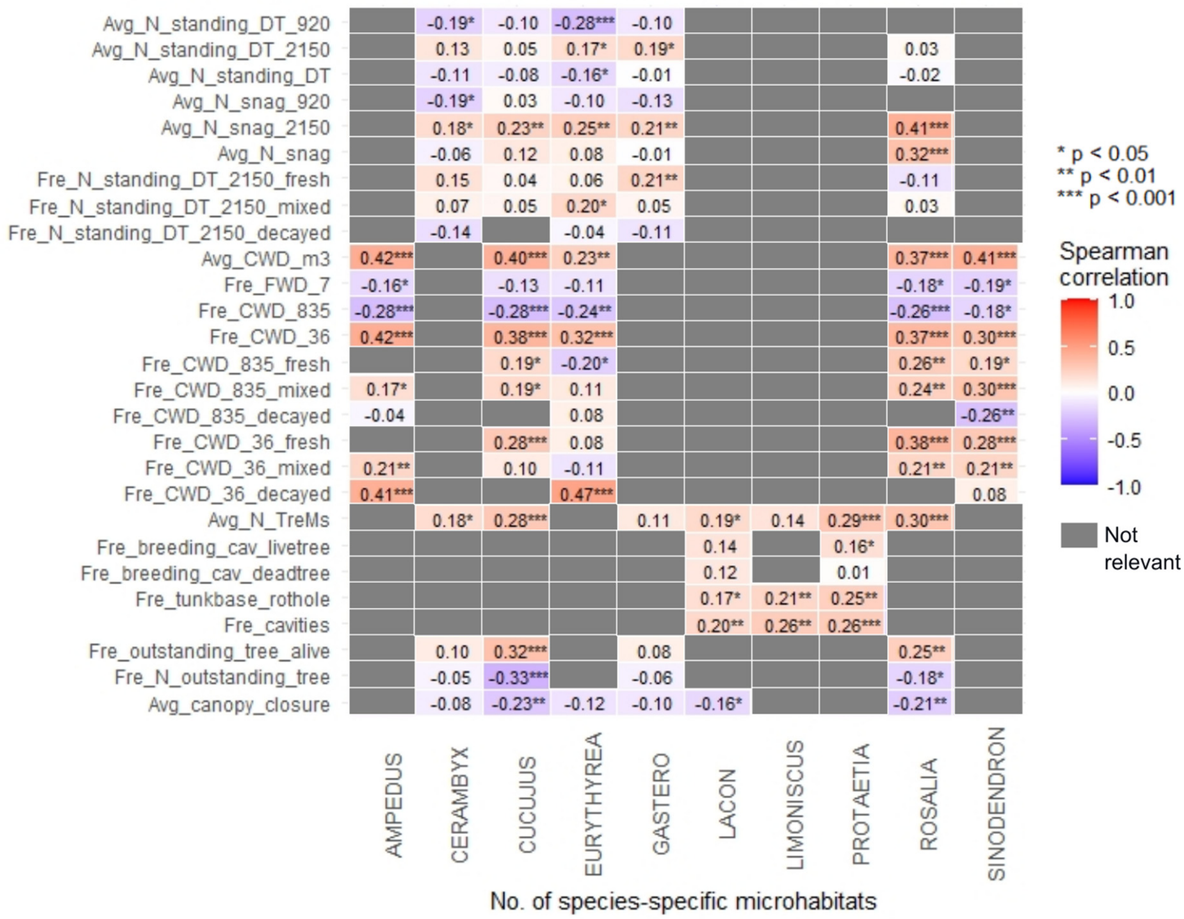

Figure 5. Detailed relationships between species-specific microhabitats and forest state indicators plotted on a correlation heatmap. Numbers indicate *r*-values. Gray areas mask relationships irrelevant to the studied microhabitat types. Legend: avg: average; fre: frequency; N: number; DT: dead tree; FWD and CWD: Fine and Coarse Woody Debris; TreMs = tree-related microhabitat categories; cav: cavity; numbers: DBH class limits (e.g., "920": DBH = 9–20 cm), upper or lower limit for unique numbers (e.g., "36": >35 cm).

4. Discussion

Our results suggest that combinations of forest state indicators collected at larger scales can be used indirectly (as proxies) to show the occurrence of saproxylic beetle habitats. The presence of species associated with cavities can also be predicted by the high occurrence of cavities in a stand. If the indicators are evaluated in terms of naturalness (presence of large trees, large amounts of standing dead trees, snags and CWD from large diameter classes, high TreM category occurrence rates), we showed that more saproxylic beetle microhabitats occurred in stands that were indicated by the SCP to be in a better state.

4.1. The Most Important Predictors

The main forest state indicators were well identified by the statistical procedures used and can, therefore, be considered sufficiently robust predictors. The most important variables include live trees, snags, and lying dead trees, but only if they are present in larger diameter classes. This draws attention to the habitat limitation of large-diameter trees. The condition and age of these trees will only be relevant for specific microhabitat requirements.

It should be emphasized that the DBH > 50 cm class is only available for living trees among the indicators included in this study. Many studies have found that large-diameter mature trees are good predictors of higher microhabitat diversity [58–61]. The taxa we studied also showed a strong correlation with the average number of large trees.

Large diameters were also possible in the case of dead trees. Still, the number of cases in the study areas was so small (less than 10 occurrences) that they would not have provided statistically reliable results. The exact requirements of deadwood characteristics are unclear as to the most effective way to increase the biodiversity of saproxylic species [22,24,62]. Some studies have found that above a certain (non-quantified) diameter range, no more species appear in deadwood [63,64]. Some species we have studied may also occur in thin-diameter trunks (e.g., *C. cerdo*: DBH > 10 cm—[65]). The correlation between the body size of saproxylic species and deadwood diameter may be explained by the fact that source limitation only allows for smaller body sizes [30]. As a result, trees with small diameters are suboptimal for them [66]. Furthermore, as these species do not typically occur in large numbers in such habitats, it is easy for data collectors to overlook smaller trees.

Other key variables included the amount of CWD. This is not a good indicator by itself [22] but can be used as additional information along with other characteristics [61,67]. Some authors found that the amount of deadwood lying in oak forests increased the number of generalist and specialist species [68].

In the literature, the most important predictor is very often the limitation of available light [64,69]. For the microhabitats we studied, we found a stronger negative correlation only for the occurrence of the Cucujus- and Rosalia-type microhabitats (Figure 5), which show a more open canopy in these quadrats than in others. The light requirements of these species are also revealed by previous research [69,70]. The Cerambyx–Gasterocercus–Lacon–Eurythyrea microhabitat types can be strung together into a sequence of developmental stages linked to a deadwood tree. There is no strong correlation with canopy closure in any of these cases. On average, these species occur in more closed forest stands, but locally, the lack of closure in the immediate vicinity of the microhabitats and/or the thicker branches of habitat trees overhanging the closed stand may ensure the presence of these species.

4.2. Differences Between Forest Stand Types

Because we have worked within a landscape unit, we do not consider macroclimatic effects to be a modifying factor in our study. Much of the cited literature on the examined beetles is from Central Europe, so the possible different occurrences under different macroclimatic conditions are less relevant to this study. Some authors even found that the variation between regions (as climatically allowed by the needs of the species) is less important than the preferred tree species and local site characteristics (deadwood, sun exposure) [71]. Nevertheless, there may be cases where the occurrence of beetles is influenced by the meso- and microclimatic conditions through the decaying processes [72]. In relatively dry habitats, even though the dead oaks are large, red rot always affects only a small part of them. As a result, there are forests (e.g., in the West Börzsöny Mts., too) that are very old and have dead wood but are free of beetles. These climatic considerations should also be taken into account while predictions are made.

Significant differences between quadrats classified as beech- and oak-dominated forests can be found when analyzing the relationships of the microhabitats present in them with forest state descriptors. Some of the explanatory variables appear to be universal and were also detected by the random forest analysis. For some variables, correlations with signs that are opposite to those expected are observed. Among the microhabitat types studied, the Rosalia and Sinodendron types are typically more associated with beech forests [65,73]. This was confirmed by the RDA tri-plot (Figure 3). The Cerambyx, Gasterocercus, and Eurythyrea types are more associated with oak forests [74]. The other five species-specific microhabitats may be associated with several types of deciduous trees but are often also found in oaks.

Oak-dominated forests often have a higher species richness than beech-dominated ones because of their higher light availability [75]. Changes in the number of tree species may have less impact in oak forests than in beech forests and are generally poorer in admixed tree species. Furthermore, many of the microhabitat types studied are associated with oaks, and the higher ratio of admixed tree species is at the expense of the proportion of oaks. This could lead to the result that the number of tree species in oak forests is negatively correlated with the number of microhabitats.

The reason for the negative correlation between the TreMs and the standing and lying deadwood is obvious. These were indicators of small diameter classes, so their absence (in favor of thicker diameter classes) is indicated by our results.

Microhabitats in oak stands were more strongly correlated with large live trees and (decayed) lying deadwood. This can be explained by the fact that oak-associated species generally require large trees, and among the studied microhabitats, the presence of decayed dead trees is relevant only in oak forests.

4.3. Differences Between Species

There are relevant differences between the occurrence of some species-specific microhabitats. Overall, both aspects of the analysis (the multivariate RDA and the correlation analysis by each TreM type) yielded important and complementary results. The habitats showing strong associations in the RDA mostly meet the preliminary expectations (both in terms of forest stand type and explanatory variables). The RDA also revealed explanatory variable interactions that are not apparent individually, as they are only indirectly related to the microhabitats studied (association of Sinodendron and Rosalia types with large living trees). The correlation tests revealed weaker but also important associations for some microhabitats (cavity-dependent species).

The frequency of Eurythyrea-type microhabitats shows a very strong association with the frequency of decayed, large-diameter CWD. The RDA analysis did not reveal a strong correlation with the amount of large-lying deadwood.

The Rosalia- and Sinodendron-type microhabitats are associated with large-diameter live trees, snags, and large amounts of lying dead wood, which is supported by the analyses of each TreM type separately.

The Cerambyx-type microhabitat is associated with large (DBH > 50 cm) trees in stands, where the average DBH is at least 30 cm smaller in diameter than the outstanding tree. In addition, this microhabitat is associated with oak forests of poor quality in terms of deadwood supply. This may be due to the intensive management of these oak stands, but the remaining veteran/retention trees can provide habitat for saproxylic species. These areas are also characterized by the absence of lying deadwood with a diameter of 8–35 cm. As the oak stands are in poor condition in terms of deadwood supply, the FWD (Fine Woody Debris, Ø < 8 cm) is likely to be dominant in these sites. Lying deadwood is indifferent to the *C. cerdo*, so this seems to be a result exclusively related to the specific situation we investigated. Correlation tests did not show an exceptionally strong association with any of the explanatory variables tested, so the association with veteran trees cannot be demonstrated per se.

The other microhabitats are associated with forest stands with similar characteristics according to the RDA. This result is nuanced by the analyses of each TreM type separately. The Ampedus- and Cucujus-type microhabitats are associated with high amounts of CWD and a higher frequency of decay stage, corresponding to their habitat requirement (decayed and fresh, respectively). The microhabitats associated with cavities (Lacon, Limoniscus, and Protaetia types) show a weak but significant correlation with the occurrence of cavities and rot holes recorded by SCP. This suggests that where these microhabitats are present, they are also found in higher proportions at the stand scale. Thus, we can potentially assume metapopulations, where the microhabitats are potentially suitable habitat patches that are either occupied or unoccupied by saproxylic species. According to Levins' model, unoccupied habitats are also necessary for the stable persistence of a population [76]. The continuous availability of microhabitats (in time and space) is particularly important for dispersal-limited species [77].

The detailed comparisons of the different analytical approaches above underline the need to carry out similar studies in multiple statistical aspects in each case; a multivariate analysis and a correlation study alone may not provide a complete picture of a studied phenomenon.

5. Conclusions

When planning a survey of an unknown area, it is advisable to use satellite imagery as a guide and to look for forest stands with varied canopy openness and high crown size diversity. These areas should be further selected by topography. Steep hillsides, where it is not worth carrying out silvicultural interventions, have a better supply of deadwood [78]. These areas are potential saproxylic hotspots [51]. When planning a survey in managed forests, the good deadwood supply, the presence of woody debris, and flowering herbaceous plants favored by saproxylic insects are also worth considering [51]. In addition, a good starting point can be the use of stand-scale proxy indicators that can predict the occurrence of the saproxylic beetles. For many countries, the National Forest Inventory (NFI) also records dead tree data [33], which, in addition to tree inventory data, could potentially provide a suitable selection for this purpose.

If the microhabitats are sufficiently well defined, the investigation of exit holes and other variables in the microhabitats does not necessarily need to be carried out by a specialist but can be performed by volunteers. By creating the possibility of citizen science, data on the species/community can be obtained over a much larger area. This would be particularly important for species of community interest in Natura 2000, for which country reports are required every 6 years. Species monitoring experts can target microhabitats registered by volunteers, or if volunteer surveyors send doubtless photographs, this may not even be necessary. Descriptive figures of the microhabitats and taxa we surveyed have been prepared specifically to be used for this purpose. In the LIFE project MIPP ("Monitoring of Insects with Public Participation") [79], data on species that we have studied (*C. cerdo*, *R. alpina*) were collected by volunteers [80]. A large number of observations were received [81], and their validity can be considered a success, as the data sent by laics were broadly consistent with the surveys by professionals [82]. Species were recorded during the MIPP, but using our method, one can also obtain additional information by searching microhabitats.

The next research step could be to test the predictions, i.e., to search for saproxylic beetle microhabitats in stands considered to be in a good state by the SCP proxy indicators.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f16020195/s1, Supplementary File S1: The investigated saproxylic beetle taxa and their habitat requirements [65,83–104]; Supplementary File S2: Variable selection with random forest.

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