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Tree Species Affect Beetle Diversity on the Common Deciduous Dead Wood in Lithuanian Unmanaged Forests

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Abstract: Beetles living in dead wood are species-specific, suggesting that beetle diversity may vary between different deciduous tree species. However, the patterns of diversity variation among deciduous trees are still poorly understood. In this study, we investigated the diversity of beetles associated with dead wood in the second decay stage in four protected areas of Lithuania, using trunk-emergence traps on *Alnus glutinosa* L., Gaertn. (black alder), *Betula* sp. L. (birch), *Fraxinus excelsior* L. (European ash), *Populus tremula* L. (European aspen), *Quercus robur* L. (common oak), and *Tilia cordata* Mill. (small-leaved linden). The findings of our study indicated variation in beetle diversity among the six tree species examined. We identified the greatest diversity of beetles in the decaying trunks of *Quercus robur*, followed by *T. cordata*, and *F. excelsior*. Our cluster analysis suggested a higher similarity in beetle diversity among tree species sharing the same type of bark; however, our db-RDA analysis showed that tree species explained more variance in the data than bark type. Our results support previous research highlighting the importance of dead wood species diversity in maintaining the diversity of beetles in forests. Within the context of current biodiversity decline, understanding the similarities or differences in beetle communities between tree species is key to tackling the loss of insect species.

Keywords: bark; broadleaved; Coleoptera; dead wood; diversity; second decay stage

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1. Introduction

Human activities have resulted in forest degradation [1], primarily occuring due to unsustainable exploitation, which involves excessive harvesting of forest products, wildfires, and the proliferation of invasive species or pests. Previous studies have shown that forest degradation can exacerbate biodiversity loss more than deforestation [2]. Forests degrade because of the loss of key ecological structures, such as dying trees and dead wood [3], which sustain diverse communities of arthropods and microorganisms important for nutrient recycling [4]. Current average volumes of dead wood are about 15.8 m^3 ha^{-1} in European forests, and 17.7 m^3 ha^{-1} in Lithuanian forests [5]. Despite its recent increase in almost all regions of Europe [5], dead wood volumes are still too low to ensure the protection of saproxylic beetles, which require at least 40–60 m^3 ha^{-1} for their conservation [6].

Saproxylic species are those dependent on dead and decaying wood for at least part of their lifecycle [7]. Dead wood hosts a range of various organisms such as lichens, fungi and insects, among which the majority consists of beetles (Coleoptera) [8]. For example, in German forests, 56% of forest beetles are regarded as saproxylic [9], and demonstrate varying degrees of affinity towards specific characteristics of dead wood [8]: wood moisture, diameter, tree species, decay stage, position, and type of wood (snags, logs, stumps), all of which can determine the composition of beetle communities or assemblages [10–17].

The importance of dead wood from different tree species in maintaining and preserving beetle diversity is often emphasized [18–20]. *Quercus* spp. L. (oaks) are regarded as biodiversity hotspot plants in Europe [18,21] because of the communities they sustain. The dead wood from oaks and other key plants, like *Tilia cordata* Mill. (small-leaved linden), *Alnus glutinosa* L. (black alder), Gaertn, *Fraxinus excelsior* L. (European ash), and *Populus tremula* L. (European aspen), is valuable for the survival of red-listed saproxylic beetle species [18,22–26]. Muñoz–López et al. [12] revealed that species and stage of decay of wood determine the composition and community structure of Coleoptera [12]. During early stages of decay, primary saproxyls show a strong specificity towards the plant's species or genera, whereas in later decay stages, the saproxylic species primarily rely on microhabitat features within the decayed wood that are not necessarily influenced by the tree species [27]. Supporting these findings, Jonsell [14] conducted a study in southern Sweden involving *P. tremula*, *Betula pubescens* Ehrh. (White birch), *Betula verrucosa* Ehrh. (Silver birch), *Quercus robur* L. (common oak), and *Picea abies* (L.) H. Karst. (European spruce), which demonstrated that beetle species display reduced specificity towards tree species as the wood undergoes advanced decay [14]. Other studies have also considered the relationship between tree species' phylogenetic relationships and the composition of their beetle communities. For example, Vogel et al. [18] showed that plant phylogenetic relationships explained the differences in beetle assemblages between broadleaved and coniferous tree species [18], similar to Kärvemo et al. [28], who found a congruent pattern between native and non-native tree species in Southern Sweden [28]. These findings demonstrate that beetle communities exhibit similarities among closely related plants that share common ecological traits [29]. This pattern corresponds to phylogenetic niche conservatism (PNC), which is the tendency of lineages to retain their niche-related traits through speciation events [30,31]. Understanding the mechanisms underlying the maintenance of such niches in beetle communities sheds light on the complex interactions between organisms and their environment, providing valuable insights into the processes underlying biodiversity and ecosystem dynamics.

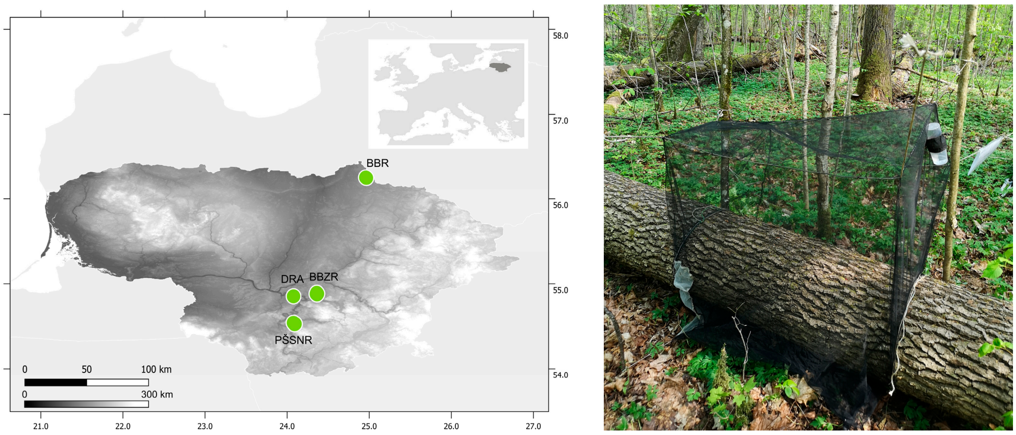
However, the composition of beetle communities is not always explained by decay stage or the plants' phylogenetic relationships, and other plant traits could be more important. In the Netherlands, the diversity of early decay stage in the dead trunk invertebrate community, including beetles, is better explained by the dissimilarity in bark traits among tree species, rather than by phylogenetic diversity of tree species [32]. The bark of dead wood helps to retain moisture inside the logs, providing a favorable environment for beetles to colonize the wood [12]. Variation in the density of bark pockets (space between bark and sapwood) and in the structure of the bark itself (coarse and fissured bark, sometimes specific to tree species) [33] creates different microhabitats that beetles exploit for shelter, food, and nesting sites [34,35]. Bark traits vary greatly among tree species and are potentially important for maintaining biodiversity; however, evidence of the ecological impacts of interspecific variation in bark traits on the assembly of dead wood invertebrate communities is lacking [32].

Our study explores potential drivers of beetle species assemblages, and it is the first of its kind in Lithuania. We leverage the most comprehensive list of collected beetles in Lithuania, generated during our previous studies [36], together with information on their ecology. We aim to compare the species diversity of beetles in six broadleaved tree species of early decaying dead wood while considering the influence of tree identity, relatedness, and bark type. We hypothesize that beetle diversity differs between the tree species. Since we focus on the second stage of decay (removing the effect of decay in beetle communities), we expect dead wood-dependent beetle communities to be similar between closely related tree species. Our research contributes to a broader understanding of conservation, ecosystem functioning, forest management practices, and evolutionary ecology. Our results aid in formulating effective strategies for biodiversity conservation and sustainable forest management.

2. Materials and Methods

We carried out our study in four protected areas in Lithuania, chosen due to the absence of human activity and the abundance of dead wood. To reduce spatial autocorrelation, we chose our study sites to be equidistant by up to ~200 km (Biržai Botanical Reserve (BBR) and Punios Šilas Strict Nature Reserve (PŠSNR)) and at least ~19 km (Dubrava Reserve Area (DRA) and Būda Botanical–Zoological Reserve (BBZR)) (Figure 1a, Table 1). Biržai Botanical Reserve is in the northern part of the country, and it was established to preserve the characteristic plant communities of the Biržai forest, which is dominated by pine (*Pinus* L.), oak (*Quercus* L.), birch, and aspen (*Populus* L.) tree species. The sites we surveyed in Biržai Botanical Reserve were characterized by two forest habitat types (EUNIS habitat classification): Fennoscandian hemiboreal natural old broad-leaved deciduous forests (*Quercus*, *Tilia*, *Acer*, *Fraxinus* or *Ulmus*) rich in epiphytes (9020), and Fennoscandian herb-rich forests with *Picea abies* (9050), with an average stand age of about 123 years [37]. Both Būda Botanical–Zoological Reserve and Dubrava Reserve Area are situated in central Lithuania. Due to its rich and fertile soils, the Būda Botanical–Zoological Reserve harbors a diverse array of rare flora and fauna, thriving within its characteristic biotopes, thus contributing to their preservation and conservation. The forest is characterized by ash (*Fraxinus* Tourn. ex L.) woodland, with oak, linden (*Tilia* L.), and alder (*Alnus* Mill.) trees interspersed with patches of hornbeam (*Carpinus* L.). Būda Botanical–Zoological Reserve forest sites surveyed were characterized by three forest habitat types: Fennoscandian hemiboreal natural old broad-leaved deciduous forests (*Quercus*, *Tilia*, *Acer*, *Fraxinus* or *Ulmus*) rich in epiphytes (9020), Fennoscandian herb-rich forests with *Picea abies* (9050), and Fennoscandian deciduous swamp woods (9080). The average age of the stand is about 103 years [37]. Dubrava is the only Reserve District in Lithuania where no deforestation has occurred since 1958. Spruce and pine stands dominate the forest, but alders, oaks, ashes, and aspens are also present. The Dubrava Reserve Area was characterized by several forest habitat types: Fennoscandian herb-rich forests with *Picea abies* (9050), Western Taiga (9010), and Active raised bogs (7110), which surrounded our study site. The average age of the stand is around 89 years [37]. Punios Šilas (Punia forest), in southern Lithuania, is one of Lithuania's most ancient forests and belongs to the Punios Šilas Strict Nature Reserve. While conifers predominate, deciduous tree species including linden, oak, and ash trees dominated our sites with Fennoscandian hemiboreal natural old broad-leaved deciduous forests (*Quercus*, *Tilia*, *Acer*, *Fraxinus* or *Ulmus*) rich in epiphytes (9020). The average age of the stands was about 112 years [37]. The four forests we studied are part of Natura 2000: the network of nature reserves in Europe that aims to safeguard biodiversity by protecting specific animal species and their natural habitats.

We analyzed beetle diversity in dead wood of six deciduous tree species: *A. glutinosa* (family: Betulaceae), *Betula* sp. (Betulaceae), *F. excelsior* (Oleaceae), *P. tremula* (Salicaceae), *Q. robur* (Fagaceae), *T. cordata* (Malvaceae) (Table 1). These broadleaved trees collectively contribute to approximately 44% of Lithuania's forested areas, as revealed in the most recent state accounting of Lithuanian forests [38]. Among these deciduous trees, *Betula* species comprise around 22% of the forest area, while *Populus tremula* stands occupy 4.6% and *Alnus glutinosa* covers 7.6% of the forested land, respectively. *Quercus robur* and *Fraxinus excelsior* occupy smaller portions, comprising only 2.2% and 0.9%, respectively. The remaining deciduous tree species encompass an insignificant 1.1% amount [38]. We visually analyzed the dead wood and identified tree species based on the bark. To avoid inaccuracies, we identified the birch trunks to the genus level, as distinguishing between the four *Betula* spp. that occur in Lithuania based on their bark is challenging. By focusing on deciduous trees, we targeted a more limited habitat, which could provide valuable insights into the dead wood-dependent beetle communities specific to this habitat type.



(**a**) (**b**)

Figure 1. (**a**) Map of Lithuania showing the survey sites (marked with green circles): BBR—Biržai Botanical Reserve, DRA—Dubrava Reserve Area, BBZR—Būda Botanical–Zoological Reserve, PŠSNR—Punios Šilas Strict Nature Reserve; the map is colored by elevation and the inset shows the location of Lithuania within Europe; (**b**) a trunk-emergence-type trap positioned on a wind-felled tree trunk of *Q. robur* within the Būda Botanical–Zoological Reserve, in 2020.

Table 1. The number of tree individuals (n), mean tree diameter (MTD), standard deviation (SD) of tree diameters, locality (Locality), and research year (Year) of the six researched tree species (Tree). To see abbreviations of locations, see Figure 1a.

Tree	n	MTD (cm)	SD (cm)	Locality	Year
Alnus glutinosa	9	24.0	2.1	BBR, BBZR	2018–2019, 2021
Betula sp.	9	26.0	4.2	BBZR, DRA, PŠSNR	2021
Fraxinus excelsior	12	27.2	3.0	BBR, BBZR	2018–2019
Populus tremula	9	27.8	4.1	BBZR, DRA	2018–2019, 2021
Quercus robur	9	36.8	8.6	BBZR, PŠSNR	2020–2021
Tilia cordata	6	32.5	8.6	BBZR, PŠSNR	2020

Over the course of the comprehensive four-year study, spanning from May to October to November 2018 and 2021, we installed 54 trunk-emergence-type traps (Figure 1b) on trunks for each of the six distinct tree species (Table 1). The trunks we selected were only wind-fallen trees, instead of cutting trees, to capture more natural beetle diversity. We exclusively researched the trunks that were in the second stage of wood decay, utilizing a combination of wood observing and the knife to determine their stage of decay [39,40]. The trunks of the second decay stage were weakly decayed and characterized by loose bark, fairly hard wood, and knife blade penetration into the wood by <2 cm [39,40]. The average diameter of the tree trunks we selected for the study ranged from 24.0 ± 2.1 cm (*A. glutinosa*) to 36.8 ± 8.6 cm (*Q. robur*) (Table 1). We constructed the tent-like traps following Halme et al. [41] and mounted them on trunks distant from each other by a minimum of approximately 25 m and a maximum of approximately 2 km within study site and year. The traps were made from of a polyester material that is permeable both to air and light, so as to create an environment as natural as possible for insects to emerge out of the dead wood inside the trap (Figure 1b). To install the traps properly on the tree trunk, the wind-fallen trees should have risen off the ground. We positioned the trunk-emergence traps on the middle sections of the trunks, with each trap covering one meter of the trunk to ensure equivalent sections were used in the study. We used ropes to attach the traps to nearby trees or sticks driven into the ground so that the material would not wrinkle and would be as smooth as possible. To ensure that the emerged insects did not escape from the trap and that insects from the environment did not enter the trap, we wrapped both ends of the trap tightly around the tree trunk. At the higher end of each trap, we affixed a plastic jar filled with >99% propylene glycol. Every two weeks, we collected emerged adult insects, after which Aistė Lekoveckaitė and Romas Ferenca selected and identified beetle specimens at the species or genus level using taxonomical keys [42,43]. We assigned species names by the current European system based on the Fauna Europaea database [44]. Identified specimens were deposited in the Tadas Ivanauskas Kaunas Zoological Museum and the Vilnius University Life Sciences Center Museum of Zoology.

To summarize beetle richness across different tree species, we calculated Hill numbers [45], including species richness (S), Shannon diversity index (H′), inverse Simpson's index (1/D), and Margalef's diversity index. We also produced sample-based rarefaction curves to visually compare beetle species richness among tree species and assess sampling effort [46]. The similarity of the beetle species assemblage in the six tree species was visualized using a non-metric multidimensional scaling (NMDS) ordination based on the Bray–Curtis similarity index. These analyses were conducted using Past4.07b software [47]. To assess which tree species similarity based on the occurrence of beetle species, we employed hierarchical cluster analysis as implemented in the vegan v.2.6-4 package [48] in R version 4.3.0 [49] using the Chao index, which accommodates variation in sample sizes.

We used non-parametric Kruskal–Wallis tests to assess the differences in beetle species richness and diversity among the different tree species, and conducted post hoc comparisons using the Dunn's tests to identify significant distinctions between tree species. All tests were two-tailed, where $p < 0.05$ was considered statistically significant. The tests were performed using Past4.07b [47]. To understand which proportion of the variance in beetle species assemblages is explained by tree species and bark type, we fit three distance-based redundancy analyses (db-RDA) where the explanatory variables were species tree, bark type, or both. In addition, we incorporated sampling year, trap number, and sample site as random variables in all models and used ANOVA to assess the significance of the models (999 permutations). We conducted the analyses using the *dbrda* function and Bray–Curtis distances, as implemented in the vegan v.2.6-4 package [48] in R version 4.3.0 [49]. To establish association links between deciduous tree species and beetle species based on association frequency, we generated network graphs using the bipartite v.2.18 package [50] in R software version 4.3.0 [49]. Given the number of beetle-plant interactions observed, we focused on the beetle species that account for 50% of the interactions that are not singletons (twelve beetle species), as well as beetles listed on the IUCN Red List of Saproxylic Beetles [51].

3. Results

A total of 6796 individuals belonging to 490 beetle species were identified (Table 2). More details are available in a full beetle species list in Table 2 of the publication by Lekoveckaitė et al. [36]. On average, each tree species yielded 1133 beetle specimens (SD = 412.39) and 180 species (SD = 28.22) (Table 2). The number of specimens collected from *Betula* sp., *P. tremula* and *A. glutinosa* showed comparable counts (ranging from 1347 to 1686), whereas the remaining three species (*T. cordata*, *Q. robur* and *F. excelsior*) exhibited lower numbers of beetles (ranging from 556 to 965) (Table 2). The range of richness values among the researched tree species was 67, with the highest richness being in trunks of *Q. robur* and the lowest richness recorded in trunks of *A. glutinosa* (Table 2).

The beetle species richness did not reach an asymptote in any of the tree species, suggesting that more species are expected to be discovered (Figure 2). The sample-based rarefaction rate also showed the *A. glutinosa* curve separated from the curves of the other tree species (Figure 2). The curves of the *T. cordata* and *Q. robur*, and *E. excelsior*, *Betula* sp., and *P. tremula* overlapped, according to their 95% confidence intervals (Figure 2).

Table 2. An absolute abundance (Beetle_ind.), richness (Taxa_S), Shannon's diversity index (Shannon_H'), inverse Simpson's index (1/D), and Margalef's index (Margalef) values for beetle fauna at the six tree species (Tree_species).

Tree_species	Beetle_ind.	Taxa_S	Shannon_H'	(1/D)	Margalef
Alnus glutinosa	1686	143	2.70	4.57	19.11
Betula sp.	1347	198	3.73	9.78	27.34
Fraxinus excelsior	965	162	4.14	26.52	23.43
Populus tremula	1383	205	4.08	19.40	28.21
Quercus robur	859	210	4.71	51.84	30.94
Tilia cordata	556	159	4.42	35.10	25.00
Mean (±SD)	1133 (±412.39)	180 (±28.22)	3.96 (±0.70)	24.54 (±17.34)	25.67 (±4.14)

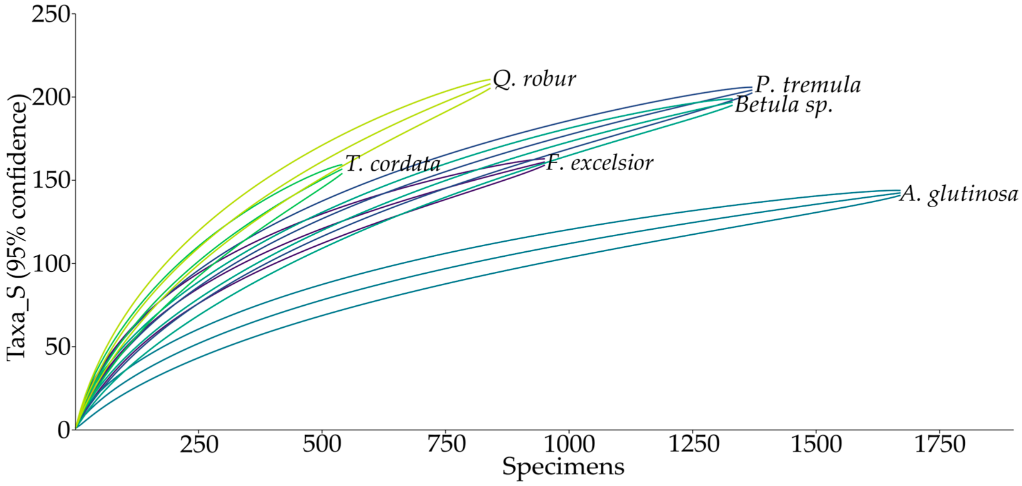


Figure 2. Sample-based species accumulation (rarefaction) curves, with 95% confidence intervals, of the beetle species' richness collected in six tree species.

The Hill numbers showed that the highest beetle species composition and diversity were in *Q. robur* trunks, while the lowest were in *A. glutinosa* (Table 2). The average Shannon's diversity index for beetle diversity in the dead wood trunks was 3.96 (SD = 0.70), the average inverse Simpson's index was 24.54 (SD = 17.34), and average Margalef's index was 25.67 (SD = 4.14) (Table 2).

Non-metric multidimensional scaling (NMDS; stress 0.3658) (Figure 3) reveals that the species composition of beetles in the dead wood of different tree species partly overlaps, with a tendency for tree species with smooth bark to share a more similar diversity of beetles as those with rough bark, which have a distinctive beetle diversity.

There was marginally non-significant difference in median beetle species richness across the tree species (Kruskal–Wallis χ^2 = 8.63, p = 0.1249). However, pairwise comparisons showed significant difference in median beetle species richness between *Q. robur* and *F. excelsior* (Dunn's post hoc p = 0.0496), and between *P. tremula* and *F. excelsior* trunks (Dunn's post hoc p = 0.0281), while marginally non-significant differences were observed between *P. tremula* and *A. glutinosa*, and between *Q. robur* and *A. glutinosa* trunks (Dunn's post hoc tests, p = 0.063, and p = 0.101, respectively) (Figure 4a).

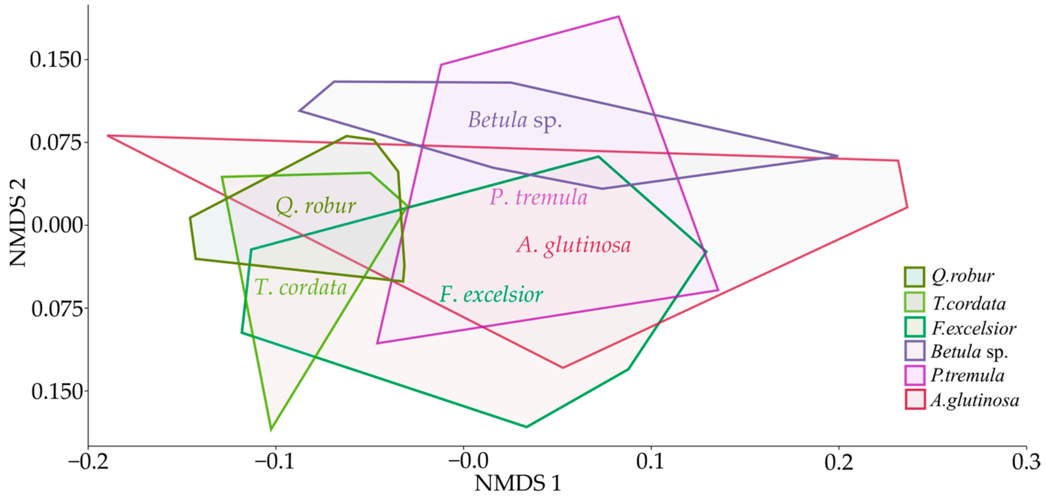
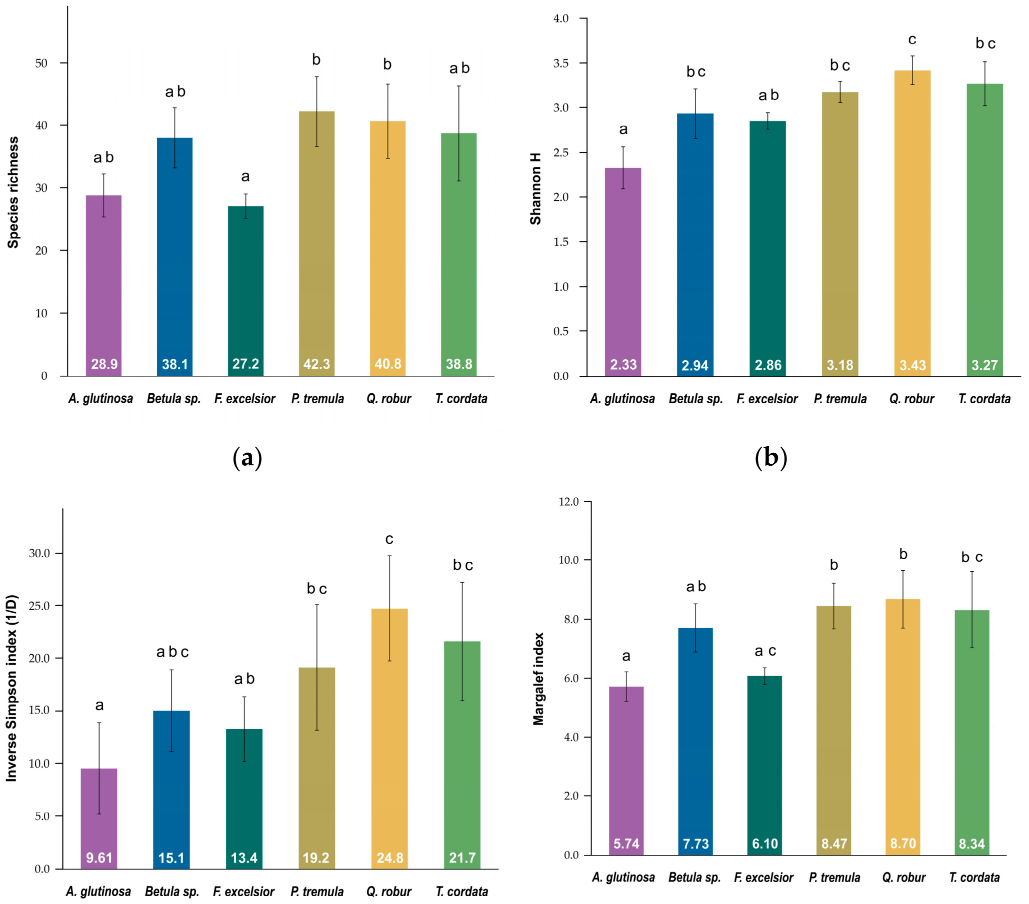


Figure 3. NMDS showing beetle assemblage across six deciduous tree species. Trees with rough bark are represented in green, while smooth-barked trees are denoted in purple.



(**a**) (**b**)

(**c**) (**d**)

Figure 4. Beetle species richness (**a**), Shannon's H diversity (**b**), inverse Simpson's (**c**), and Margalef's diversity (**d**) indices among the different tree species. Different letters indicate significant differences (Dunn's post hoc test, $p < 0.05$). Bars indicate means ± SE.

The observed median beetle diversity, measured by the diversity indices, was statistically significant across the tree species (Shannon: Kruskal–Wallis $\chi^2 = 17.62$, $p = 0.0035$, inverse Simpson: Kruskal–Wallis $\chi^2 = 11.95$, $p = 0.0355$, Margalef: Kruskal–Wallis $\chi^2 = 13.91$,

$p = 0.0162$). For all three diversity indices, statistical differences in diversity levels were observed between *Q. robur* and *F. excelsior*, *T. cordata* and *A. glutinosa*, *P. tremula* and *A. glutinosa* with the greatest difference between *Q. robur* and *A. glutinosa* (Shannon, Dunn's post hoc $p = 0.0003$; inverse Simpson, Dunn's post hoc $p = 0.0017$; Margalef, Dunn's post hoc $p = 0.0080$) (Figure 4b–d). Additionally, statistical differences were found between *Betula* sp. and *A. glutinosa* based on the Shannon diversity index (Dunn's post hoc $p = 0.0183$), and between *P. tremula* and *F. excelsior* based on Margalef diversity index (Dunn's post hoc $p = 0.026$) (Figure 4b,d).

The cluster analysis revealed that tree species can be grouped into two clusters based on the species composition of beetles (Figure 5). Group FQT contains *F. excelsior*, *Q. robur*, and *T. cordata*, with both Chao median and mean dissimilarity of 0.29. Group ABP contains *A. glutinosa*, *Betula* sp., and *P. tremula* with Chao median dissimilarity within the group of 0.28 and a mean of 0.32. The median and mean values between FQT and ABP members were 0.40. Among the tree species, *F. excelsior* and *T. cordata* exhibited the lowest dissimilarity in beetle occurrence (Chao distance 0.24), while the highest dissimilarity was observed between *Q. robur* and *A. glutinosa* (Chao distance 0.58), as indicated by height of the link (Figure 5).

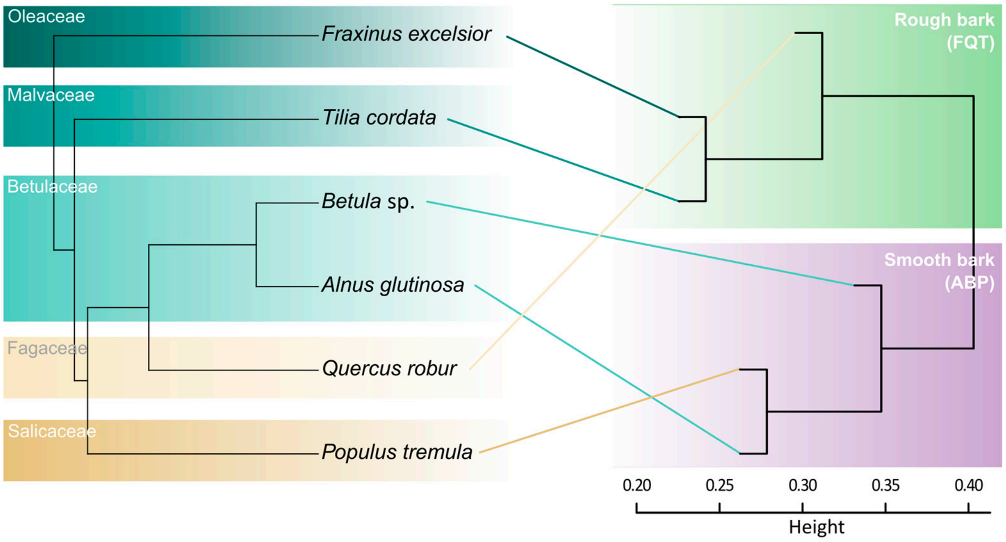


Figure 5. Tanglegram showing the phylogenetic relationships among the six tree species investigated in this study (left; modified from Durka and Michalski [52]) and the hierarchical clustering of tree species based on average beetle community similarities (Chao dissimilarity index). The lines connect the same species in the phylogeny and the hierarchical clustering. The hierarchical clustering resulted in two groups of plant species with similar beetle communities and similar bark types (smooth and rough).

The db-RDA models congruently showed that species trees explain a larger proportion of the variance in beetle species assemblages than bark type, although the effect of random and unaccounted variables is larger. For the model *species~bark type + random*, bark type explained 2.86% of the variance observed in the beetle community structure (ANOVA's Pr(>F) = 0.004). In the model *species~tree species + random*, tree species explained 13.01% of the variance (ANOVA's Pr(>F) = 0.001), same proportion explained by both explanatory variables in the model *species~tree species + bark type + random* (ANOVA's Pr(>F) = 0.001). In all models, the random variables accounted for 16.93% of the observed variance, with the remaining variance unexplained and ranging between 70.07% and 80.21% depending on the model.

The beetles network graph revealed that twelve beetle species accounted for half of the observed beetle species across the tree species; those beetle species were detected more often in the dead wood trunks of trees with smooth bark compared to those with rough bark

(Figure 6a). The network also showed that the most common beetle species are associated with *A. glutinosa* dead wood (Figure 6a). Among the Red Listed saproxylic beetle species, there was a tendency for the protected species to be most abundant in the dead trunks of *Q. robur* and *P. tremula* (Figure 6b).

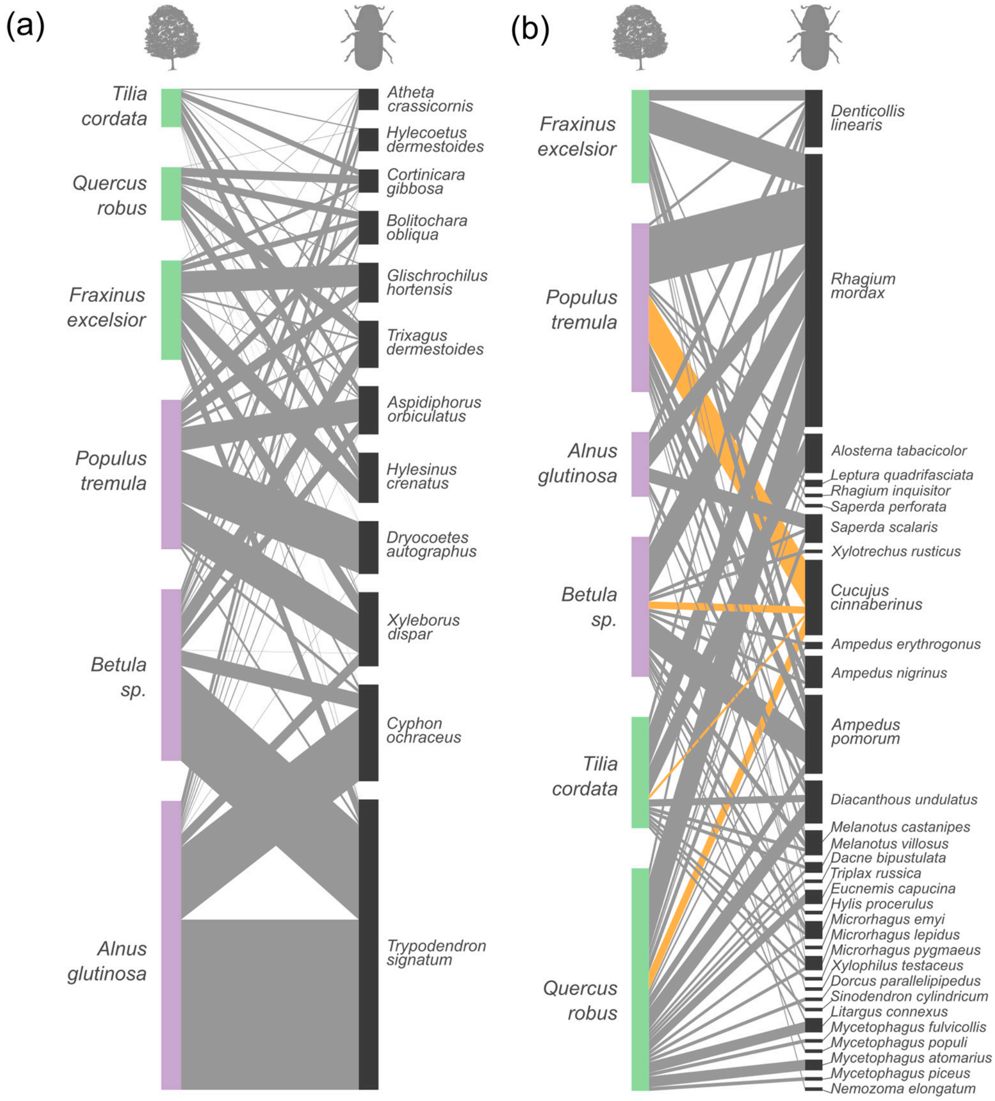


Figure 6. Beetle-plant bipartite networks among six deciduous tree species. Nodes on the left correspond to the sampled tree species (purple nodes denote trees with smooth bark while green nodes represent those with rough bark), and nodes on the right represent the beetle species, which include (**a**) the beetle species responsible for 50% of the observed interactions between beetles and beetles tree species, and (**b**) beetle species listed in the IUCN Red List of saproxylic beetles. The height of the bars and interaction lines is proportional to the observed frequency of the interaction. Orange highlights the interactions of the species listed in IUCN Red List of Saproxylic Beetles and Lithuania's Red Data Book. The tree silhouette was produced by Gabriela Palomo-Munoz and the beetle silhouette by Kristina Gagalova; both were downloaded from PhyloPic (https://www.phylopic.org/; accessed on 23 August 2023).

4. Discussion

In this study, we compared the species diversity of beetles inhabiting dead wood from six tree species of early decaying dead wood, and determined that wind-felled trunks in the second stage of decay exhibit distinct beetle diversity in Lithuania (Table 2, Figure 4). Variation in beetle species richness and diversity among the deciduous tree species was also observed in previous studies [15,18,25,26,53], supporting our findings. Moreover, our results align with those reported by Vogel et al. [18], who investigated saproxylic beetles in branch-bundles across a total of 42 European tree species, including the ones we researched. In both studies, *Quercus* spp. exhibits the highest diversity of beetles, followed by *T. cordata*. Furthermore, *F. excelsior* consistently demonstrates greater beetle diversity compared to *A. glutinosa* and *P. tremula* in both studies. After conducting Kruskal–Wallis tests, we identified statistically significant differences in beetle diversity among four tree pairs (Figure 4), emphasizing the influence of *A. glutinosa*, *Betula* sp., *F. excelsior*, *Q. robur*, and *P. tremula* tree species' composition on shaping beetle communities. Previous studies have also highlighted that a substantial proportion of beetle diversity overlap can be observed between *Betula* sp. and *P. tremula*, *P. tremula* and *Q. robur*, and *Q. robur* and *Betula* sp., surpassing a similarity value of 50% [25]. The same patterns were also found in our study.

Similar to Kärvemo et al. [28], and based on phylogenetic niche conservatism, we anticipated that closely related tree species would exhibit a similar beetle species composition, while distantly related species would display a different composition (Figure 5). This is because beetle species that are adapted to one tree species may already possess adaptations that allow them to thrive on a closely related tree species, which have similar traits [54]. For instance, we expected the beetle communities of *A. glutinosa* and *Betula* sp., belonging to the same family (Betulaceae), to exhibit more similarities, but our results did not support this hypothesis (Figure 5). Previously, the similarity of beetle species composition between *A. glutinosa* and *Betula* sp. was obtained by Jonsell et al. [26] in their cluster analysis; however, their study encompassed not only beetles (which accounted for more than half of the species studied), but also other saproxylic insect assemblages. A possible explanation for the lack of greater similarities among tree species based on the plant's phylogenetic distances could be attributed to differences in various environmental factors. When trunks from the same tree species are placed in different stands or environments with varying tree species' compositions, variations in their properties or characteristics can occur [55]. In our case, we studied dead wood of *A. glutinosa* in two protected areas: the Biržai Botanical Reserve and the Būda Botanical–Zoological Reserve, while *Betula* sp. wind-felled trunks were studied in the Punios Šilas Strict Nature Reserve, the Būda Botanical–Zoological Reserve, and the Dubrava Reserve Area. Additionally, the trees in the sites were surveyed in different years (Table 1).

Our cluster analysis results classified the six tree species into two clusters (groups ABP and FQT) (Figure 5), a grouping that is congruent with the structural differences in their bark surfaces. Our researched trunks of *F. excelsior*, *Q. robur*, and *T. cordata* are characterized by having rough bark surfaces, while *A. glutinosa*, *Betula* sp. and *P. tremula* have smoother bark surfaces. Previous research [32] has demonstrated that the greater the variation in bark surface between tree species, the greater the variation in the composition of faunal communities associated with those tree species despite decay stage. In line with this finding, we found that trees with rough bark tended to have more similar beetle species composition. However, beetle communities grouping by tree species bark type was only observed in the cluster analysis. The NMDS analysis did not clearly group the data based on bark type (Figure 3), and the high stress value indicated a poor representation. Additionally, the models we ran in db-RDA rejected our hypothesis by showing that tree species explain more variance in the data than bark type. A possible alternative explanation for the clustering based on bark type is the diameter of the tree trunks as a confounding factor. We observed that one cluster consists of trees with larger trunk diameters on average, while the other cluster comprises trees with smaller trunk diameters (Table 1). Other alternative explanations include the lack of more appropriate classifications for bark type that capture the true variation in the trait and other confounding variables inherent to the species trees. The distribution of beetle species by bark type may have been influenced by other variables (such as sun exposure, moss cover, fungal diversity, etc.) that were not included in the analysis, but have the potential to be addressed in the future. Finally, and based on the rarefaction curve (Figure 2), if a greater diversity of beetle species had been collected or if more tree species had been included in the study, it would be possible to obtain a more detailed understanding of how the variables influence beetle occurrence and abundance.

Out of the 490 identified species, twelve accounted for 50% of the beetles observed in all the surveyed trees (Figure 6a). Among them, three are considered as non-saproxylic: *Cortinicara gibbosa* (Herbst, 1793), *Trixagus dermestoides* (Linnaeus, 1766), and *Cyphon ochraceus* Stephens, 1830. Although *C. ochraceus* specimens are typically found outside of dead wood, our analysis showed it as one of the most common species in *A. glutinosa* and *Betula* sp. decaying trunks (Figure 6a). The feeding type of *C. ochraceus* is unknown [56], but considering its occurrence in *Betula* spp. dead wood in similar studies [56], we suggest that birches affect assemblages of those beetles in forest ecosystems. The remaining nine beetle species are regarded as saproxylic based on their lifestyle, as documented in previous studies [13,22,57,58]. Among those species, *Trypodendron signatum* (Fabricius, 1787), *Xyleborus dispar* (Fabricius, 1792), *Dryocoetes autographus* (Ratzeburg, 1837), and *Hylesinus crenatus* (Fabricius, 1787), which live beneath tree bark as xylophagous insects [57,59], were the most common species in our analysis. Surprisingly, *D. autographus*, typically associated with conifers, was notably prevalent in the trunks of *A. glutinosa* and *Betula* sp.

During four entomological seasons, we identified thirty-one beetle species that are included in the European Red List of Saproxylic Beetles [51] (Figure 6b). Those are all obligate saproxyls [57,59–61], and dead wood is mandatory for them. Except for *Xylophilus testaceus* (Herbst, 1806) (IUCN Red List Category (Europe)–Near Threatened (NT)) and *Cucujus cinnaberinus* (Scopoli, 1763) (NT), all the remaining species are listed as Least Concern (LC) on the European IUCN Red List of Saproxylic Beetles [62]. *C. cinnaberinus* is also the only one from our collected beetles that is included in the Red Data Book of Lithuania (IUCN category–endangered (EN)) [63]. We detected none of *C. cinnaberinus* specimens in trunks of *F. excelsior* and *A. glutinosa*, while it was the most abundant in *P. tremula* trunks (Figure 6b), which is one of the main preferred host tree species according to Vrezec et al. [64]. Among collected red-listed beetles, the most abundant in our sampling was *Rhagium* (*Megarhagium*) *mordax* (De Geer, 1775). It was common in all dead deciduous trees but showed greater abundance in *Q. robur* and *P. tremula*, demonstrating the importance of both smooth and rough bark tree surfaces for protected species (Figure 6b).

Understanding the dynamics of beetle communities in different tree species provides valuable information for conservation and management. Since Lithuania has experienced a consistent decrease in ash (as across Europe due to fungal infection caused by *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya [65]), and birch forests for almost a decade [66], with a particular decline observed in aspen forests in 2019–2022 [66], the insights from our research have implications for biodiversity conservation and sustainable forest management in the face of these environmental challenges.

5. Conclusions

Our findings highlight the significance of early decaying wood species diversity and reject the hypothesis that tree species with the same bark structure share similar beetle assemblages. In this context, maintaining the diversity of tree species regardless of bark type can contribute to the maintenance of both saproxylic and non-saproxylic beetle diversity in the forests and contribute to the conservation of a range of red-listed species. Further understanding of beetle community dynamics across different tree species, coupled with additional research that incorporates a broader range of variables, offers valuable insights for conservation and management efforts.

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