Article

The Structure of Saproxylic Beetle Assemblages in View of Coarse Woody Debris Resources in Pine Stands of Western Poland

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Abstract: Background: Resources of dying and dead trees, decaying fragments of stems, stumps and branches, i.e., coarse woody debris (CWD), are an important structural element of biocenoses and are drivers of biodiversity. The aim of this study was to describe assemblages of saproxylic beetles in pine stands of western Poland in view of dead wood resources. We present faunistic (species identity) and quantitative (species and individual counts) data from two types of stands: 1. unmanaged pine stands, in which no trees have been extracted for over 30 years, with processes connected with tree dying and self-thinning of stands being undisturbed, 2. managed pine stands, in which routine tending operations extracting trees are performed in accordance with forest management plans and naturally dying trees are removed in the course of tending and sanitary logging; Methods: Beetles were captured in the years 2013–2014 using window flight traps. Assemblages of saproxylic beetles were assessed based on the indices of dominance, diversity (the Shannon–Weiner index), and species richness (Margalef's index) as well as the estimated habitat fidelity index, feeding habits, and zoogeographical distribution. Similarity between the assemblages was evaluated applying cluster analysis. Dependence between dead wood resources and the diversity and species richness indices were analysed; Results: A total of 2006 individuals classified to 216 species were captured. Assemblages show considerable similarity on the local scale. Higher values of species diversity indicators were observed in unmanaged stands, in which no sanitation cuttings are performed; Conclusions: The decision to refrain from sanitation logging in pine monocultures results in increased CWD resources, which nevertheless does not lead to a marked increase in the values of biodiversity indicators. Unmanaged stands were characterised by a high share of zoophagous, mycetophagous, and saproxylic species. In contrast, managed stands were characterised by a high share of xylophagous beetles.

Keywords: deadwood; biodiversity; *Pinus sylvestris*; Coleoptera

1. Introduction

The present-day European forest management system is considered to be multifunctional (serving social, economic, and ecological functions) and sustainable [1]. A major objective of such a management is to preserve biodiversity. Forest habitats in Central Europe are characterised by high species diversity (with approx. 65% plant and animal species being forest species) [2,3]. Factors threatening species diversity include increased timber harvesting combined with reduced rotation, promotion of fast-growing species

regardless of habitat conditions, devastating management methods (e.g., large-area clear-cuts, deep ploughing, restrictive snag removal, cuttings performed regardless of local conditions, increased fertilisation), application of pesticides, selective breeding of forest trees, introduction of alien tree species, and afforestation excluding any open spaces [4].

Beetles (Coleoptera), particularly saproxylic species, i.e., those biologically associated with dying trees, are a diverse group both in terms of their ecology and taxonomy [5,6]. Some of them, including several species legally protected in Europe, constitute excellent indicators of biodiversity and the impact of forest management on forest ecosystems [7–15].

Protection of natural processes of tree dieback and reduced harvesting of snag as a biotope of many specific saproxylic species [16,17] seem necessary to preserve high species diversity. This need poses questions concerning the volume and quality of coarse woody debris left to decompose naturally, particularly in commercial forests [18]. The saproxylic fauna is modified not only by the obvious, significant role of CWD resources [19], but it is also influenced by the tree or wood species [20–23], humidity, insolation and type of the microhabitat [13,24,25], the geographical region and the size of the forest complex [26], as well as natural disturbances in bark beetle gradations [27], windthrows [28], and fires [29,30].

The problem of threshold dead wood resources in European forests has been discussed in detail [18,19]. Some sources of data indicate that a significant increase in species richness of saproxylic beetles is observed only at a very high accumulation of coarse woody debris on a regional scale [31–34].

In 2020 in Polish forests the mean CWD resources amounted to approx. $8.2 \text{ m}^3/\text{ha}$ [35], whereas as recently as in the years 2005–2009 it was on average $5.7 \text{ m}^3/\text{ha}$ [36,37]. Dead wood resources vary depending on the region. Thus, CWD resources are below the mean level in central Poland, where pine stands are dominant, while they are much greater in mixed broadleaf forests of southern Poland (where they range from 14.8 to $20.1 \text{ m}^3/\text{ha}$) [36].

A compromise needed to combine the sanitary regime in pine stands (as the most common type of commercial stands in the central, lowland part of Europe) with prescribed allocation of a portion of wood to be left in the forest to decompose naturally [34] may be attained only when considering a variety of aspects. A considerable role is played by the geographical location and the related climate, as well as the size of populations of harmful insects and the intensity of forest management in those forests [38]. The date of logging is also of importance, since it stimulates the population size in the case of bark beetles [39].

A considerable body of data on subcortical and saproxylic beetles of pine coniferous forests comes from Scandinavia. Among other things it was found that forest management significantly determines the composition and quantitative ratios of subcortical beetles [40]. The volume of dead wood resources does not always affect the species diversity or numbers of subcortical beetles [41], while the absence of dead trees of large diameters may result in the disappearance of species obligatorily associated with old trees and stands [42]. Seminatural pine forests are distinguished first of all by much greater CWD resources, which are also maintained in the first stages of succession of the young tree generation and such forest habitats are biotopes for threatened saproxylic species [43]. In order to protect saproxylic fauna it is important not always to increase the total volume of dead wood, but also its continuity and diversity in commercial forests, because each type of coarse woody debris (stumps, snag, branches, twigs) produces unique microhabitats [44–48].

Species diversity of saproxylic beetles in pine coniferous forests of Poland have been investigated depending on the method of forest management and the degree of ecosystem transformation [10].

Boggy pine forests as a refuge for saproxylic beetles were investigated in eastern Poland [49]. Obtained results indicate a local character of their assemblages and a significant role of commercial pine stands for the preservation of the natural habitat value and its high biodiversity.

Processes modifying the saproxylic fauna in hurricane-damaged pine coniferous forests were observed in the Puszcza Piska Forest [50]. Analyses showed no statistically

significant differences in saproxylic beetle assemblages between hurricane-damaged stands cleared after the hurricane and unaffected managed stands. The rapid accumulation of dead wood resources resulted in an increase in the number of individuals and the concentration of some species on the local scale, although it did not affect the number of species.

Pine coniferous forests were also investigated in areas of high nature value with the aim of finding model patterns. Examples in this respect include the Kampinos Forest [51] and the Białowieża Forest, in which the structure of subcortical beetle assemblages was analysed [11,52] as a tool in the assessment of anthropogenic transformations of primeval forest habitats. In pine coniferous forests of the Białowieża Forest, observations were also made on the impact of fire on alpha and gamma diversity of beetles [53]. In the initial period of habitat regeneration, the diversity indices were higher for the fire-affected stand; however, in the successive years of observations the differences between the stand destroyed by the fire and the control stand were disappearing.

The aim of this study was to identify dependencies between CWD resources and characteristics of assemblages of saproxylic and subcortical beetles in lowland pine stands differing in the management system (unmanaged vs. managed), determining dead wood resources.

2. Materials and Methods

Investigations were conducted in the years 2013–2014 in central-western Poland in terms of its landscape representing the North European Plain (Figure 1).

The objects of the study included stands of similar valuation parameters, such as age and species composition, but differing in intensity of snag removal, based on which it was divided into two categories:

A. unmanaged stands, originally commercial forests, with established protection functions, such as, e.g., landscape, water, or soil protection), in which no logging operations have been conducted for over 30 years and in which tree dieback and self-thinning processes have been undisturbed. They are permanent experimental sites of the Department of Silviculture, PULS, in the Torzym and Gubin Forest Districts [54,55] as well as a stand in the Drawieński National Park subjected to the same principles.

B. managed stands, in which routine tending operations (logging) are performed in accordance with the forest management plan, and naturally dying trees are removed in the course of tending operations and sanitation cuttings.

In these experimental sites, CWD resources were measured, stand dynamics trends were assessed, beetles and saproxylic fungi were inventoried [57,58], and losses of benefits due to the allocation of wood to decompose naturally were estimated [59] (Table 1).

Mean volume in unmanaged stands was 356.7 m³/ha, at the mean volume of dead wood (CWD) of 12.99 m³/ha, the percentage share of dead wood in relation to growing stock was 3.63%. In managed stands the mean volume was higher and amounted to 389 m³/ha, while values of the other parameters were approx. 3-fold lower; the mean volume of dead wood was 4.04 m³/ha and the share of dead wood in relation to growing stock was 1.05%.

Identification of species diversity in Coleoptera. Insects were captured with window flight traps commonly used in inventorying saproxylic beetles in Poland and considered to be highly effective [10,50,60–62]. Two traps of 3800 cm² were hung in each of the experimental sites using for this purpose dying trees, windsnaps as well as broken branches and parts of the crown lying on the ground. Beetle capture operations were conducted from 23 April 2013 to 15 November 2014. Window flight traps were operating for a total of 1692 trap-days (the number of days of trap operation × the number of traps).

The beetles for determination were prepared using techniques recommended for individual families (e.g., with separation of mating apparatus). The available keys and guides for family and species identification as well as taxonomic revisions of selected groups of beetles were used for the determinations. It was used for this, among others: series of keys for determination of beetles in Poland for example [63–65] and Central

Europe [66,67], taxonomic monographs of beetle families [68–70]. The markings were verified using illustrated keys and beetle iconography [71,72]. The specimens are deposited in the authors' collections at the Department of Forest Entomology and Pathology, Poznan University of Life Sciences, Poland.

Figure 1. Locations of experimental sites. Source: Google Earth Pro 7.3.4.8248 (64-bit) Data SIO, NOAA, U.S. Navy, NGA, GEBCO. Image Landsat / Copernicus (2021) [56].

Results of capture operations from individual stands were totalled, distinguishing beetle assemblages, which were assessed based on such parameters as the number of species (S), the number of individuals (n), Margalef's index (d —species richness) [73], Shannon's index (H' —species diversity) [74,75] and the percentage share of trophic forms (zoophagous, mycetophagous, xylophagous, saproxylophagous). Identified species in terms of their trophic levels were divided into five groups: xylophagous, mycetophagous, zoophagous, saproxylic species, and the other trophic groups. Next species richness and the number of individuals in each of the groups were determined. Among the captured insects, also the percentage shares of species were calculated. The species, the share of which exceeded 5%, were considered dominant, while codominant species were those whose share ranged from 2% to 5%.

Similarity between the *Coleoptera* assemblages was assessed using cluster analysis. The analysis used the species dominance index (where the number of individuals $n = 2006$, the number of taxa $S = 244$) in the studied stands. The Euclidean distance was taken as the measure of clustering distances. The analyses were performed using the Statistica13.3 software by StatSoft®. The volume of dead wood, the number of species in an assemblage as well as percentage shares of individual trophic groups were vectors of observations. The Euclidean distance was applied as the metric.

Table 1. Characteristics of experimental sites—unmanaged and managed pine stands in western Poland.

Location and Description/Symbol of the Site	Geographical Coordinates WGS	Area (ha)	Stand Volume Excluding Dead Wood (m ³ /ha)	Volume of Dead Wood (CWD) (m ³ /ha)	Age	Share of Dead Wood/Growing Stock (%)
Unmanaged pine stands						
Gubin Forest District compartment 73j—uneven-aged stand/UG1	N: 51.9817 E: 14.8611	4.03	248 170	8.03	195 62	1.92
Gubin Forest District compartment 57a/UG2	N: 51.9737 E: 14.8195	20.18	317	16.51	92	5.45
Torzym Forest District compartment 264a/UT3	N: 52.2603 E: 15.1254	11.42	481	23.43	85	5.85
Drawieński National Park, compartment 288h/UD4	N: 53.0839 E: 15.9347	6.08	270 35	4.0	145 105	1.31
Managed pine stands						
Drawieński National Park, compartment 15b/MD5	N: 53.1889 E: 16.0235	7.33	310	3.51	125	1.13
Gubin Forest District compartment 56a/MG6	N: 51.9758 E: 14.8229	20.14	303	3.7	113	1.17
Torzym Forest District compartment 263a, c/MT7	N: 52.2625 E: 15.1288	8.04	401	7.52	91	1.56
Jarocin Forest District compartment 200a/MC8	N: 52.1109 E: 17.4994	8.23	449	1.43	63	0.32

Assessment of specificity of Coleoptera assemblages. Characteristics of species and their relationships with the habitat were based on the estimated fidelity classes proposed by A. Szujewski [76,77] and their later modifications taking into consideration the character of the study and the specific nature of beetle groups [78–80] as well as the Catalogue of Polish Fauna and the National Biodiversity Information System website [81].

The following modified estimated fidelity classes were adopted:

F4: obligate characteristic species—strictly (obligately) related, i.e., in terms of their trophic levels and biology, with processes of dieback in coniferous trees, cambio-, xylo-, and endophytophagous (the first stages in the succession chains in the subcortical habitat).

F3: selective characteristic species—found numerously in a given habitat, although also present in other habitats; included predatory, parasitic, and ambrosia beetles as well as mycetophagous species, the occurrence of which is dependent on the presence of host organisms.

F2: auxiliary (accompanying) species—found in the subcortical habitat less numerously than in other habitats or showing no preference to any habitat type; included species facultatively (periodically) appearing in the subcortical habitat, searching for shelter or food.

F1: species alien to a given habitat.

F0: ubiquitous, cosmopolitan species.

R: relic species, of special faunistic value, reported in single localities, related with primeval forests.

Data on the occurrence of clown beetles (Histeridae) was published in a study by Mazur et al. [61].

Saproxylic beetles (understood as species in terms of their ecology associated with dying, dead, and decaying trees, in which the utilisation of wood has led to morphological, anatomical, and metabolic adaptations to the habitat) [82,83] were classified in further analyses to species from fidelity classes R, F4, F3, and F2.

3. Results

A total of 2006 beetles belonging to 244 taxa were captured in the period of the study. Of that number, 1820 individuals were identified to species, which accounts for 90.7% all captured insects. They were classified to 216 species, whereas the other beetles (9.3%) were identified to the level of genus or family (Supplementary Materials). Among them 194 (89.8%) are species permanently or periodically associated with wood, they were represented by 1702 (93.7%) individuals. Characteristics of assemblages in the investigated stands are given in Table 2.

Table 2. Characteristics of Coleoptera assemblages in managed and unmanaged pine stands in western Poland.

Characteristics of Assemblages	Unmanaged					Managed				
	UG1	UG2	UT3	UD4	Mean ($\pm$ SD)	MD5	MG6	MT7	MC8	Mean ($\pm$ SD)
Number of individuals (<i>n</i>)	267	137	126	323	213.25 ($\pm$ 84.2)	531	108	46	282	241.75 ($\pm$ 188.08)
Number of species (<i>S</i>)	64	45	39	84	58 ($\pm$ 17.62)	75	25	18	62	45 ($\pm$ 24.07)
Xylophagous species (%)	14.1	13.3	15.4	22.6	16.3 ($\pm$ 3.7)	28.0	16.0	16.7	22.6	20.8 ($\pm$ 4.9)
Mecytophagous species (%)	15.6	22.2	23.1	14.3	18.8 ($\pm$ 3.9)	16.0	10.7	16.7	27.4	17.7 ($\pm$ 6.1)
Zoophagous species (%)	45.3	51.1	33.3	41.7	42.9 ($\pm$ 6.4)	40.0	46.7	44.4	29.0	40.0 ($\pm$ 6.8)
Saproxylophagous species (%)	9.4	8.9	7.7	6.0	8.0 ($\pm$ 1.3)	8.0	6.7	5.6	9.7	7.5 ($\pm$ 1.5)
Species from other trophic groups (%)	15.6	4.4	20.5	15.5	14.0 ($\pm$ 5.9)	8.0	20.0	16.7	11.3	14.0 ($\pm$ 4.6)
Margalef's index (<i>d</i>)	11.28	8.94	7.86	14.37	10.61 ($\pm$ 2.5)	11.79	5.13	4.44	10.99	8.09 ($\pm$ 3.32)
Shannon's index (<i>H'</i>)	3.49	3.32	2.80	3.92	3.38 ($\pm$ 0.4)	2.56	2.77	2.50	3.35	2.8 ($\pm$ 0.33)

In unmanaged stands, a total of 167 beetle species were reported, which were represented by 936 individuals, whereas in managed stands 153 species were captured, represented by 1067 individuals. On average, in each of the unmanaged stands 55.5 species ($SD = 14.8$) were identified, while in managed stands it was 46.6 species ($SD = 22.6$).

Species captured in unmanaged stands, in the number of minimum 10 specimens, which were not shown in managed stands, included *Phloeonomus pusillus* (Staphylinidae), *Dryophthorus corticalis*, *Orthotomicus longicollis*, *Hylurgops palliatus*, *Hylastes brunneus* (Curculionidae), *Platydema violacea* (Tenebrionidae), and *Latridius hirtus* (Latridiidae). In contrast, *Cardiophorus ruficollis* (Elateridae) and *Xylosandrus germanus* (Curculionidae) were species recorded in managed stands.

Analyses of individual stand showed the highest number of beetle species in the oldest stands (UG1, MD5, UD4), aged over 140 years, which was reflected in the high values of species richness (*d*) and species diversity (*H'*). An exception in this respect was found for the commercial (managed) pine stand established on former farmland (MC8), in which biodiversity indices were relatively high (Table 2). The lowest qualitative and quantitative richness of beetles was recorded in commercial stands in the Gubin and Torzym Forest Districts (MG6, MT7) (Table 2), as it was by 21.2% and 63.5% fewer species compared to unmanaged stands located in their vicinity (UG2, UT3).

Among all the captured beetles *Ampedus balteatus* (Elateridae) was the dominant species ($D = 13.9\%$), while co-dominant species ($2\% < D \leq 5\%$) included *Enicmus rugo-*

sus (Latridiidae), *Tomicus piniperda* (Curculionidae), *Phloeostiba lapponica* (Staphylinidae), *Spondylis buprestoides* (Cerambycidae), *Melanotus villosus* (Elateridae), and *Nicrophorus vespilloides* (Silphidae) (Supplementary Materials). Groups of dominant species in individual stands differed (Table 3). Only *Enicmus rugosus* reached the dominance index above 5% in five stands. Species, which were dominant ($D > 5\%$) in at least three stands included *Phloeostiba lapponica* reported with a very high dominance index in the protected stand in the Torzym Forest District (UT3) and in two managed stands (MT7, MG6); *Spondylis buprestoides* dominant in managed stands as well as *Nicrophorus vespilloides* recorded as dominant only in managed stands. Although *Ampedus balteatus* was the most numerous represented among the captured insects, it was dominant only in one of the analysed stands (MD5).

Table 3. Dominant beetle species ($D > 5\%$) captured in individual stands.

Species	Dominance Index in the Stand							
	UG1	UG2	UT3	UD4	MD5	MG6	MT7	MC8
<i>Enicmus rugosus</i>	16.5	16.1	7.1	-	-	5.6	6.5	-
<i>Dryophthorus corticalis</i>	9.0	-	-	-	-	-	-	-
<i>Placusa tachyporoides</i>	7.5	-	-	-	-	5.6	-	-
<i>Orthotomicus longicollis</i>	5.2	-	-	-	-	-	-	-
<i>Cerylon ferrugineum</i>	-	10.2	-	-	-	-	-	-
<i>Platydemus violacea</i>	-	7.3	-	-	-	-	-	-
<i>Plegaderus caesus</i>	-	5.1	-	-	-	-	-	-
<i>Spondylis buprestoides</i>	-	5.1	-	-	6.4	10.2	-	-
<i>Phloeostiba lapponica</i>	-	-	34.9	-	-	12.1	10.9	-
<i>Paromalus parallelepipedus</i>	-	-	5.5	-	-	-	-	-
<i>Placus atrata</i>	-	-	5.5	-	-	-	-	-
<i>Phloeonomus pusillus</i>	-	-	-	8.4	-	-	-	-
<i>Rhizophagus depressus</i>	-	-	-	7.4	-	-	-	-
<i>Tomicus piniperda</i>	-	-	-	6.8	-	-	-	8.5
<i>Ampedus balteatus</i>	-	-	-	-	49.3	-	-	-
<i>Nicrophorus vespilloides</i>	-	-	-	-	-	13.9	28.2	9.6
<i>Crypturgus hispidulus</i>	-	-	-	-	-	12.9	-	-
<i>Epuraea thoracica</i>	-	-	-	-	-	7.4	8.7	-
<i>Abraeus perpusillus</i>	-	-	-	-	-	-	6.5	-
<i>Salpingus ruficollis</i>	-	-	-	-	-	-	6.5	-
<i>Melanotus villosus</i>	-	-	-	-	-	-	-	17.7
<i>Cerylon impressum</i>	-	-	-	-	-	-	-	5.3

Results of the analyses of Coleoptera assemblages indicate considerable similarity between the stands located the closest geographically (Figure 2). The assemblages form three basic agglomerations: 1. beetles found in unmanaged stands in the Gubin Forest District (UG1, UG2), 2. beetle assemblages in managed stands in the Gubin and Torzym Forest Districts together with the protected stand in the Torzym Forest District (MT7, UT3, MG6), and 3. beetle assemblages in the managed stand in the Jarocin Forest District and assemblages found in the Drawieński National Park (MC8, MD5, UD4). The assemblage of beetles found in stand MD5 is the most distant from all analysed.

Figure 2. Dendrogram of similarity of species dominance in Coleoptera assemblages in managed (MD5, MG6, MT7, MC8) and unmanaged (UG1, UG2, UT3, UD4) pine stands in western Poland.

The percentage shares of individual trophic groups in the beetle assemblages differ in the analysed stands (Table 4).

Table 4. Mean percentage shares of beetle species and individuals captured in managed and unmanaged pine stands in western Poland in terms of trophic groups.

Trophic Group	Unmanaged Stands		Managed Stands	
	Mean Share of Species in the Trophic Group (%)	Mean Frequency of Individuals in the Trophic Group (%)	Mean Share of Species in the Trophic Group (%)	Mean Frequency of Individuals in the Trophic Group (%)
Saproxylophagous	8.0 (± 1.3)	5.7 (± 4.1)	7.5 (± 1.5)	15.5 (± 20.0)
Xylophagous	16.3 (± 3.7)	13.0 (± 5.0)	20.8 (± 4.9)	21.6 (± 8.6)
Mycetophagous	18.8 (± 3.9)	22.2 (± 7.9)	17.7 (± 6.1)	11.4 (± 3.5)
Zoophagous	42.9 (± 6.4)	52.5 (± 6.2)	40.0 (± 6.8)	31.6 (± 9.8)
other	14.0 (± 6.6)	6.6 (± 3.2)	14.0 (± 4.6)	20.0 (± 11.5)

When comparing mean shares of species in the trophic groups in both stand management types, most identified species were zoophages. Species richness of xylophagous and mycetophagous beetles is similar. The lowest share was recorded for saproxylophagous species. In managed stands, a greater share of xylophagous species was reported, while unmanaged stands are generally characterised by a greater share of all trophic groups except for xylophages. The shares of species belonging to the other trophic groups are practically identical.

In unmanaged stands, the highest frequency was recorded for specimens of zoophagous species. The shares of xylophagous and mycetophagous beetles exceeded 10%, while the lowest values were found for saproxylophages and the other trophic groups. In managed stands, the highest number of individuals was also reported in the group of zoophagous specimens; however, their share was much lower than in unmanaged stands. The other trophic groups account for approx. 1/5 of all the individuals, while the frequency of xylophagous and mycetophagous beetles was high, considerably exceeding that in unmanaged stands.

The shares of individuals classified to the adopted fidelity classes varied in the investigated stands (Figure 3). This pertains particularly to the shares of individuals representing alien species in managed stands, which may even exceed 30% (the managed stand in the Torzym Forest District, MT7). Shares of individuals representing obligate characteristic species ranged from 15% to 39%. The highest share of these species was observed in unmanaged stands in the Gubin Forest District (UG1) and the Drawieński National Park (UD4) (Figure 3a).

Figure 3. Percentage shares of species in terms of fidelity classes in analysed managed and unmanaged pine stands in western Poland (a); percentage shares of species depending on fidelity classes in managed and unmanaged pine stands in western Poland (b).

The total number of species belonging to the four fidelity classes most strongly associated with the subcortical habitat (R, F4, F3, F2) is higher in unmanaged stands compared to managed stands (Figure 3b). Occurrence of single relic species (R) was observed in almost all the stands, both unmanaged and managed, with the exception of MT7, where no species from that fidelity class were recorded. Selective characteristic species (F3) and alien species (F1) were more numerous in managed stands, whereas ubiquitous species (F0) had only a slight share in the assemblage (Figure 4).

Indices of species richness (Margalef's index) and species diversity (Shannon's index) in the investigated stands reached higher values in the group of unmanaged stands (Table 2).

Figure 4. Numbers of species depending on fidelity classes in Coleoptera assemblages in managed and unmanaged pine stands in western Poland.

4. Discussion

Information on saproxylic beetles of pine coniferous forests in view of the area covered by these forests and their role in the forest management system in central Europe is not proportional. Data comes mainly from northern and central Europe [40,42,43]. In turn, studies in Poland were conducted primarily in the eastern part of the m which differs significantly in terms of climate from western Poland, which results in different habitats and plant communities [84]. Western Poland is under the influence of the Atlantic climate, and the pine forests form communities in the type of sub-Atlantic fresh forest—*Leucobryo-Pinetum*. Northeast Poland, on the other hand, is under the influence of a subcontinental climate, it is an area of pine forests of the *Peucedano-Pinetum* type [85]. This affects the length of the growing season, which may determine the distribution of some beetle species (including saproxylic beetles) [86].

The use of screen traps as the only trapping method was dictated by utilitarian goals. In managed stands, standing dead trees and broken tree crowns were the most common microhabitats, where saproxylic species may occur. One trapping method, although assessed as very effective, narrows the scale of captured species and does not allow direct comparison of the results. The use of various types of traps (e.g., emergence, screen traps in different colours, etc.), dedicated to specific ecological groups of beetles, results in an increase in the number of species caught [61].

Species richness of saproxylic beetles in the investigated pine stands of western Poland differs from that observed in central and eastern parts of the country [50,52,53,80]. Studies conducted to date were frequently based on many methods of insect capture and observation, which considerably hinders comparability of the obtained results. Nevertheless, in relation to forest ecosystems considered natural, which often are treated as a model, to which research results on species diversity are referred, the number of recorded species was lower. In the Białowieża Forest, a total of 630 species were reported [53], while in mixed coniferous forests of the Kampinos Forest it was 433 species [51]. However, they are one of richest and best preserved forest ecosystems in this part of Europe. On the other hand, studies on the fauna of pine stumps showed 178 species [87], whereas assemblages of saproxylic beetles in boggy pine coniferous forests it was as few as 121 species [50].

As it was shown by the studies conducted in stands affected by hurricane and wild fires, a rapid increase in CWD resources does not cause an equally dynamic increase in species diversity [88,89]. Already in the 5th year after stand damage the diversity indices were more favourable for undamaged unmanaged stands with dead wood resources of 7.8–15 m³/ha. For damaged stands, this index reached a similar value, with a slight advantage of unclear stands (mean CWD resources of 225.5 m³/ha) over cleared stands

(94.5 m³/ha) [50]. These observations show that for the maintenance of species diversity continuous access to dead wood is more important than its abundance. Natural self-thinning processes, which are less dynamic, facilitate full utilisation of microhabitats formed over the years. A broad spectrum of trees at various stages of dieback and wood decomposition distributed as a mosaic in the ecosystem promotes survival of individual species more effectively than a large amount of substrate of similar parameters. This was confirmed by extensive research conducted in France [24,90], showing a significant effect of not only CWD resources, but also the presence of den trees, diversity of arboreal fungi and openness of the habitat providing available light and an advantageous microclimate. Moreover, for saproxylic species developing in dying pine trees a significant role is played by the diameter of the stem or branches, the presence of bark, as well as height above the ground [47].

Presented results show the course of transformation of managed forests into forests with the dominant protection function focused on saproxylic insects. The reported observations confirm that the decision to cease removing dying and dead trees has an advantageous effect on species diversity. Analysis of Coleoptera assemblages showed that sites located closest geographically are most similar (Figure 2), while higher values of diversity and species richness indices within agglomerations were recorded for unmanaged forests (Table 2).

In unmanaged forests, the shares and numbers of obligate characteristic and characteristic species were greater. It is also of interest that the shares of species being strictly saproxylic in both stand categories were comparable. Thus, how can the relatively high share of this trophic group be explained in managed stands, where CWD resources are much smaller?

Such a situation may be explained by the specific character of individual forest ecosystems, determined by their history and intensity of management operations affecting the continuity of natural processes of tree dieback and accumulation of dead wood with all its specific microhabitats. Thus, utilisation of the current abundance of dead wood as an indicator feature of biodiversity may lead to a bias. This parameter does not take into consideration the size and degree of decomposition of dead wood, which determine the occurrence of several specific/stenotopic beetle species [91]. It is obvious that in the case of the accumulation of large CWD amounts a wider spectrum of microhabitats is more probable, although some cases suggest that it is not always the rule [28].

Observed high values of diversity and species richness indices at limited CWD resources in managed stands may be explained as a certain island effect [92]. Dying trees constitute a biotope for several species, while in sterile managed forest they may function as hotspots in a microscale.

Probably a reduced number of dying and dead trees of a given species within a certain range may cause the accumulation of specific fauna, and thus increased species richness on individual trees.

In stands not covered by sanitation regime, in which tree dieback is a common process taking place over larger areas, with an increase in CWD resources the concentration of fauna is observed, which in turn may result in a decrease in the values of diversities and species richness indices.

Posing questions on the volume of dead wood resources as the only factor determining insect assemblages associated with this habitat is an oversimplification of the complex biocenotic associations taking place during tree dieback and wood decomposition between several organisms, among which beetles constitute a considerable group. Assessment and strategies to preserve biodiversity need to take into consideration not only α -diversity, but also β - and γ -diversity [93].

A characteristic differentiating the investigated pine stands in western Poland is connected with the share of species dominant on the local scale. *Ampedus balteatus* (Elateridae) is a superdominant, found at a very high frequency in stand MD5. *Ampedus balteatus* is a zoophagous species developing in pine stumps [80,94], an obligatory saproxylic species [95].

It was captured in traps with retusol and sulcatol in southern Finland [96] and in fermental traps [40], while in studies on subcortical beetles in natural and managed forests with a share of pine and spruce it was recorded only in managed forests [41]. In hurricane-affected stands in the Piska Forest it was co-dominant and found commonly, although its population size did not increase under the influence of the accumulation of hurricane-damaged timber [50]. Its presence in the investigated stands needs thus to be associated with the intensive process of tree dieback and increased presence of organisms constituting its food source.

A list of species dominant in the analysed stands indicates that most identified assemblages have different dominant species. Only *Enicmus rugosus* (Latridiidae) and *Phloeostiba lapponica* (Staphylinidae) were found with the dominant share in three or more assemblages (Table 3). The minute brown scavenger beetle *E. rugosus* is a mycetophagous species, with an extensive distribution in Europe, obligatorily associated with hardwood CWD as well as softwood CWD of larger diameters [95,97]. It does not show a close association to a specific type of forest habitat [95,98], colonising wood dominated by slime mould Eumycetozoa [99]. In many forest habitats it is found as a dominant [79,87,100], colonising tall stumps [87,101], tree hollows [102], and lying boles (trunks) [103] as well as old, solitary oak trees [104].

Another species recorded with high frequency was *Phloeostiba lapponica*, a holarctic species [105]. It is a small, predatory subcortical beetle staying under tree bark, typically in bark beetle galleries on coniferous trees. In eastern Finland it was reported with high frequency on burnt trees, in habitats subjected to controlled burns to renaturalise managed boreal forests [106].

It also needs to be stressed here that groups of dominant species, which are unique rather than common indicate high specificity of each of the assemblages. A comparison of the dominant species systems between the group of managed vs. unmanaged stands identifies dominant species for each category of stands. In unmanaged stands the most numerous were *Enicmus rugosus* and *Phloeostiba lapponica*, while in managed stands it was *Ampedus balteatus*, *Nicrophorus vespilloides*, *Melanotus villosus*, and *Tomicus piniperda*. The presence of large subcortical predators (*Ampedus*, *Melanotus*) accompanying cambiohages (*Tomicus*) may indicate the initiated processes of tree dieback, in which the first succession stages are taken by cambiohages of large body size (part of Scolytinae, Cerambycidae, Buprestidae) [107,108].

When analysing the frequency of families (Supplementary Materials), it is noticed that representatives of families Bothridiidae, Dryophthoridae, Eucnemidae, Trogossitidae, and Zopheridae occur only in unmanaged stands. However, in these stands with a greater frequency than in managed stands, species from the following families occur: Ciidae, Melandryidae, Monotomidae, and Scydmaenidae. They are representatives of typically saproxylic families [6]. Only species of Silvanidae have been found in the managed stands, and bark beetles (Curculionidae) are more numerous than in unmanaged stands.

Research results indicate that the leaving naturally dying trees in pine stands results in a slow accumulation of CWD resources and influences directions of succession for assemblages of subcortical and saproxylic beetles.

This study may illustrate an example of the transition of a stand from the managed type to the unmanaged type as well as changes in fauna with an increase in CWD resources and directions of succession for beetle assemblages associated with processes of dieback and dead wood accumulation.

5. Conclusions

These analyses showed differences between assemblages of saproxylic beetles found in managed and unmanaged stands. These differences are smaller in terms of the number of species, while they are higher in terms of the frequency of individuals in the identified ecological and trophic groups of beetles. However, the number of saproxylic species greater

by eight percentage points recorded in unmanaged stands shows that the management method affects species diversity in this group of insects.

Clustering being the result of analysis of similarity between the analysed stands indicates a significant role of the geographical location of these sites. The closer they were located to one another, the greater the similarity despite their different management methods.

Based on the identified objects, no relationship was confirmed between the species diversity indices and growing CWD resources; however, a trend may be observed for the organisation of *Coleoptera* assemblages towards an increase in the share of zoophagous, saproxylic, mycetobiontic, and relic species. Managed stands with the implemented sanitation cutting regime, in which trees naturally dying are removed, are characterised by lower species diversity indices and a greater share of xylophages.

Simulated dependencies between dead wood resources and species richness and diversity indices in pine coniferous forest with different management regimes may indicate that at a comparable level of biodiversity in managed stands trends are evident towards a grouping (concentration) of fauna dependent on dead trees, while in unmanaged stands with an increase in CWD resources saproxylic beetles are scattered.

Pine coniferous forests of central Europe may serve a considerable role in the system of protection for saproxylic beetles. These forests are habitats transformed by traditional forestry towards monocultures of limited diversity and low dead wood resources, particularly large-sized wood. Nevertheless, this habitat is colonised by numerous saproxylic species, in which numbers of individuals and concentration are directly dependent on the presence of coarse woody debris. Thus, active protection of the forest habitat needs to be focused on increasing this parameter through protection of natural and spontaneous phenomena of tree dieback.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12111558/s1>. The alphabetical list of beetle species caught on dead trees in protected and commercial pine stands of western Poland in 2013–2014.

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References

1. Baycheva-Merger, T.; Wolfslehner, B. Evaluating the implementation of the Pan-European Criteria and indicators for sustainable forest management—A SWOT analysis. *Ecol. Indic.* **2016**, *60*, 1192–1199. [[CrossRef](#)]
2. Rykowski, K. Strategia ochrony różnorodności biologicznej w lasach-zarys koncepcji i propozycje działań. In *Ocena Wpływu Praktyki Leśnej Na Różnorodność Biologiczną W Lasach W Europie Środkowej*; Rykowski, K., Matuszewski, G., Lenart, E., Eds.; Instytut Badawczy Leśnictwa: Warszawa, Poland, 1999; pp. 365–389.

3. Rykowski, K. Gospodarka leśna a różnorodność biologiczna. In *Różnorodność Biologiczna Polski*; Andrzejewski, R., Weigle, A., Eds.; Narodowa Fundacja Ochrona Środowiska: Warszawa, Poland, 2003; pp. 197–202.
4. Weigle, A. Ochrona różnorodności biologicznej. In *Agenda 21 W Polsce-Raport Okresowy 1992–2000*; Podgajnik, T., Ed.; Narodowa Fundacja Ochrony Środowiska: Warszawa, Poland, 2000; pp. 103–110.
5. Gutowski, J.M. Saproksyliczne chrząszcze. *Kosmos* **2006**, *55*, 53–73.
6. Gimmel, M.L.; Ferro, M.L. Chapter 2. General Overview of Saproxylic Coleoptera. In *Saproxylic Insects Diversity, Ecology and Conservation*; Ulyshen, M.D., Ed.; Zoological Monographs 1; Springer: Cham, Switzerland, 2018; pp. 51–128. [[CrossRef](#)]
7. Buchholz, L.; Ossowska, M. Entomofauna martwego drewna—Jej biocenotyczne znaczenie w środowisku leśnym oraz możliwości i problemy ochrony. *Przegląd Przyr.* **1995**, *3–4*, 93–105.
8. Grove, S.J. Saproxylic Insect Ecology and the Sustainable Management of Forests. *Annu. Rev. Ecol. Syst.* **2002**, *33*, 1–23. [[CrossRef](#)]
9. Gutowski, J.M.; Bobiec, A.; Pawlaczyk, P.; Zub, K. *Drugie Życie Drzewa*; WWF Polska: Warszawa, Poland; Hajnówka, Poland, 2004.
10. Gutowski, J.M.; Buchholz, L.; Kubisz, D.; Ossowska, M.; Sućko, K. Chrząszcze saproksyliczne jako wskaźnik odczłuszczeń ekosystemów leśnych borów sosnowych. *Leśne Pr. Badaw.* **2006**, *4*, 101–144.
11. Byk, A.; Mokrzycki, T. Chrząszcze saproksyliczne jako wskaźnik antropogenicznych odczłuszczeń Puszczy Białowieskiej. *Studia I Mater. Cent. Edukac. Przyr.-Leśnej* **2007**, *9*, 475–509.
12. Lachat, T.; Wermelinger, B.; Gossner, M.M.; Bussler, H.; Isacsson, G.; Müller, J. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecol. Indic.* **2012**, *23*, 323–331. [[CrossRef](#)]
13. Seibold, S.; Bässler, C.; Brandl, R.; Gossner, M.M.; Thorn, S.; Ulyshen, M.D.; Müller, J. Experimental studies of dead-wood biodiversity—A review identifying global gaps in knowledge. *Biol. Conserv.* **2015**, *191*, 139–149. [[CrossRef](#)]
14. Eckelt, A.; Müller, J.; Bense, U.; Brustel, H.; Bußler, H.; Chittaro, Y.; Cizek, L.; Frei, A.; Holzer, E.; Kadej, M.; et al. “Primeval forest relict beetles” of Central Europe: A set of 168 umbrella species for the protection of primeval forest remnants. *J. Insect Conserv.* **2017**, *22*, 15–28. [[CrossRef](#)]
15. Parisi, F.; Di Febbraro, M.; Lombardi, F.; Biscaccianti, A.; Campanaro, A.; Tognetti, R.; Marchetti, M. Relationships between stand structural attributes and saproxylic beetle abundance in a Mediterranean broadleaved mixed forest. *For. Ecol. Manag.* **2019**, *432*, 957–966. [[CrossRef](#)]
16. Samuelsson, J.; Gustafsson, L.; Ingelög, T. *Dying and Dead Trees: A Review of Their Importance for Biodiversity*; Swedish Threatened Species Unit: Uppsala, Sweden, 1994.
17. Djupström, L.B.; Weslien, J.; Schroeder, L.M. Dead wood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. *For. Ecol. Manag.* **2008**, *255*, 3340–3350. [[CrossRef](#)]
18. Müller, J.; Büttler, R. A review of habitat thresholds for dead wood: A baseline for management recommendations in European forests. *Eur. J. For. Res.* **2010**, *129*, 981–992. [[CrossRef](#)]
19. Jonsson, B.; Kruys, N.; Ranius, T. Ecology of species living on dead wood—Lessons for dead wood management. *Silva Fenn.* **2005**, *39*, 289–309. [[CrossRef](#)]
20. Schiegg, K. Saproxylic insect diversity of beech: Limbs are richer than trunks. *For. Ecol. Manag.* **2001**, *149*, 295–304. [[CrossRef](#)]
21. Schroeder, L.M.; Sahlin, E.; Paltto, H. Retention of aspen (*Populus tremulae*) at final cuttings—The effect of dead wood characteristics on saproxylic beetles. *For. Ecol. Manag.* **2011**, *262*, 853–862. [[CrossRef](#)]
22. Müller, J.; Wende, B.; Stöbl, C.; Eugster, M.; Gallenberger, I.; Floren, A.; Steffan-Dewenter, I.; Linsenmair, K.E.; Weisser, W.W.; Gossner, M.M. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. *J. Appl. Ecol.* **2015**, *52*, 753–762. [[CrossRef](#)]
23. Parisi, F.; Lombardi, F.; Sciarretta, A.; Tognetti, R.; Campanaro, A.; Marchetti, M.; Trematerra, P. Spatial patterns of saproxylic beetles in a relic silver fir forest (Central Italy), relationships with forest structure and biodiversity indicators. *For. Ecol. Manag.* **2016**, *381*, 217–234. [[CrossRef](#)]
24. Bouget, C.; Larrieu, L.; Brin, A. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecol. Indic.* **2014**, *36*, 656–664. [[CrossRef](#)]
25. Seibold, S.; Bässler, C.; Brandl, R.; Büche, B.; Szallies, A.; Thorn, S.; Ulyshen, M.D.; Müller, J. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *J. Appl. Ecol.* **2016**, *53*, 934–943. [[CrossRef](#)]
26. Janssen, P.; Cateau, E.; Fuhr, M.; Nusillard, B.; Brustel, H.; Bouget, C. Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodivers. Conserv.* **2016**, *25*, 1167–1185. [[CrossRef](#)]
27. Winter, M.-B.; Ammer, C.; Baier, R.; Donato, D.C.; Seibold, S.; Müller, J. Multi-taxon alpha diversity following bark beetle disturbance: Evaluating multi-decade persistence of a diverse early-seral phase. *For. Ecol. Manag.* **2015**, *338*, 32–45. [[CrossRef](#)]
28. Wermelinger, B.; Moretti, M.; Duelli, P.; Lachat, T.; Pezzatti, G.B.; Obrist, M.K. Impact of windthrow and salvage-logging on taxonomic and functional diversity of forest arthropods. *For. Ecol. Manag.* **2017**, *391*, 9–18. [[CrossRef](#)]
29. Boucher, J.; Azeria, E.T.; Ibarzabal, J.; Hébert, C. Saproxylic beetles in disturbed boreal forests: Temporal dynamics, habitat associations, and community structure. *Écoscience* **2012**, *19*, 328–343. [[CrossRef](#)]
30. Hammond, H.J.; Langor, D.W.; Spence, J.R. Changes in saproxylic beetle (Insecta: Coleoptera) assemblages following wildfire and harvest in boreal *Populus* forests. *For. Ecol. Manag.* **2017**, *401*, 319–329. [[CrossRef](#)]
31. Ranius, T.; Jansson, N. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* **2000**, *95*, 85–94. [[CrossRef](#)]

32. Starzyk, J.R.; Grodzki, W.; Kosibowicz, M.; Michalcewicz, J.; Rossa, R. Old and dead trees as the site of occurrence and development of xylobiotic and dendrophilous beetles. *Rocz. Bieszcz.* **2008**, *16*, 325–348.
33. Müller, J.; Noss, R.F.; Bussler, H.; Brandl, R. Learning from a “benign neglect strategy” in a national park: Response of saproxylic beetles to dead wood accumulation. *Biol. Conserv.* **2010**, *143*, 2559–2569. [\[CrossRef\]](#)
34. Rubene, D.; Schroeder, M.; Ranius, T. Effectiveness of local conservation management is affected by landscape properties: Species richness and composition of saproxylic beetles in boreal forest clearcuts. *For. Ecol. Manag.* **2017**, *399*, 54–63. [\[CrossRef\]](#)
35. Statistical Year Book of Forestry. Statistics Poland, Warsaw (2020). Forest Data Bank. Available online: <https://www.bdl.lasy.gov.pl/portal/gus-lesnictwo> (accessed on 29 June 2021).
36. Czerepko, J.; Hilszczański, J.; Jabłoński, T. Martwe drewno—żywy problem. *Studia I Mater. CEPL W Rogowie* **2014**, *41*, 36–45.
37. Czerepko, J.; Boczoń, A.; Cieśla, A.; Forycka, A.; Ksepko, M.; Obidziński, A.; Paluch, R.; Rodziewicz, A.; Różański, W.; Sokołowski, K.; et al. *Stan Różnorodności Biologicznej Lasów W Polsce Na Podstawie Powierzchni Obserwacyjnych Monitoringu*; Czerepko, J., Ed.; Instytut Badawczy Leśnictwa: Sękocin Stary, Poland, 2015.
38. Johansson, T.; Gibb, H.; Hilszczański, J.; Pettersson, R.B.; Hjältén, J.; Atlegrim, O.; Ball, J.P.; Danell, K. Conservation-oriented manipulations of coarse woody debris affect its value as habitat for spruce-infesting bark and ambrosia beetles (Coleoptera: Scolytinae) in northern Sweden. *Can. J. For. Res.* **2006**, *36*, 174–185. [\[CrossRef\]](#)
39. Foit, J. The occurrence of early-arriving saproxylic beetles on Scots pine logging residues generated by thinning. *J. For. Sci.* **2016**, *61*, 332–338. [\[CrossRef\]](#)
40. Väiänen, R.; Biström, O.; Heliövaara, K. Sub-cortical Coleoptera in dead pines and spruces: Is primeval species composition maintained in managed forests? *Biodivers. Conserv.* **1993**, *2*, 95–113. [\[CrossRef\]](#)
41. Siitonen, J. Decaying wood and saproxylic Coleoptera in two old spruce forests: A comparison based on two sampling methods. *Ann. Zool. Fennici.* **1994**, *31*, 89–95.
42. Økland, B.; Bakke, A.; Hågvar, S.; Kvamme, T. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodivers. Conserv.* **1996**, *5*, 75–100. [\[CrossRef\]](#)
43. Similä, M.; Kouki, J.; Martikainen, P.; Uotila, A. Conservation of beetles in boreal pine forests: The effects of forest age and naturalness on species assemblages. *Biol. Conserv.* **2002**, *106*, 19–27. [\[CrossRef\]](#)
44. Similä, M.; Kouki, J.; Martikainen, P. Saproxylic beetles in managed and seminatural Scots pine forests: Quality of dead wood matters. *For. Ecol. Manag.* **2003**, *174*, 365–381. [\[CrossRef\]](#)
45. Jonsell, M.; Weslien, J. Felled or standing retained wood—it makes a difference for saproxylic beetles. *For. Ecol. Manag.* **2003**, *175*, 425–435. [\[CrossRef\]](#)
46. McGeoch, M.A.; Schroeder, M.; Ekbohm, B.; Larsson, S. Saproxylic beetle diversity in a managed boreal forest: Importance of stand characteristics and forestry conservation measures. *Divers. Distrib.* **2007**, *13*, 418–429. [\[CrossRef\]](#)
47. Foit, J. Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. *Agric. For. Entomol.* **2010**, *12*, 133–141. [\[CrossRef\]](#)
48. Work, T.T.; Andersson, J.; Ranius, T.; Hjältén, J. Defining stump harvesting retention targets required to maintain saproxylic beetle biodiversity. *For. Ecol. Manag.* **2016**, *371*, 90–102. [\[CrossRef\]](#)
49. Tylkowski, S. Sosnowe bory bagienne jako refugium występowania chrząszczy (Coleoptera) saproksylicznych. *Studia I Mater. CEPL W Rogowie* **2014**, *16*, 308–321.
50. Gutowski, J.; Kubisz, D.; Sućko, K.; Zub, K. The succession of saproxylic beetles (Coleoptera) on windthrow areas in the Scots pine stands of the Piska Forest. *For. Res. Pap.* **2010**, *71*, 279–298. [\[CrossRef\]](#)
51. Marczak, D. *Chrząszcze Saproksyliczne Głównych Typów Siedliskowych Puszczy Kampinoskiej—Studium Faunistyczno-Ekologiczne*; Instytut Badawczy Leśnictwa: Sękocin Stary, Poland, 2019.
52. Byk, A.; Mokrzycki, T.; Perliński, S.; Rutkiewicz, A. Saproxylic beetles—monitoring of anthropogenic transformations of Białowieża Primeval Forest. In *Zooindication-Based Monitoring of Anthropogenic Transformations in Białowieża Primeval Forest*; Szujewski, A., Ed.; Warsaw Agricultural University Press: Warsaw, Poland, 2006; pp. 325–397.
53. Gutowski, J.M.; Sućko, K.; Borowski, J.; Kubisz, D.; Mazur, M.A.; Melke, A.; Mokrzycki, T.; Plewa, R.; Żmihorski, M. Post-fire beetle succession in a biodiversity hotspot: Białowieża Primeval Forest. *For. Ecol. Manag.* **2020**, *461*, 117893. [\[CrossRef\]](#)
54. Barzdajn, W.; Drogoszewski, B.; Zientarski, J.; Danielewicz, W.; Sienkiewicz, A. Wpływ sposobu zagospodarowania na trwałość i produktywność drzewostanów sosnowych. Cz. I. Założenia metodyczne i charakterystyka obiektu doświadczalnego w Nadleśnictwie Torzym. *Rocz. Akad. Rol. W Pozn.* **1991**, *231*, 3–26.
55. Barzdajn, W.; Drogoszewski, B.; Zientarski, J.; Danielewicz, W.; Sienkiewicz, A. Wpływ sposobu zagospodarowania na trwałość i produktywność drzewostanów sosnowych. Cz. II. Charakterystyka powierzchni doświadczalnej w Nadleśnictwie Gubin. *Rocz. Akad. Rol. W Pozn.* **1993**, *255*, 3–22.
56. Google Earth Pro 7.3.4.8248 (64-Bit) Data SIO, NOAA, U.S. Navy, NGA, GEBCO. Image Landsat/Copernicus. 2021. Available online: <https://www.google.com/earth/> (accessed on 22 October 2021).
57. Kwaśna, H.; Mazur, A.; Łabędzki, A.; Kuźmiński, R.; Łakomy, P. Communities of fungi in decomposed wood of oak and pine. *For. Res. Pap.* **2016**, *77*, 261–275. [\[CrossRef\]](#)
58. Kwaśna, H.; Mazur, A.; Kuźmiński, R.; Jaszczak, R.; Turski, M.; Behnke-Borowczyk, J.; Adamowicz, K.; Łakomy, P. Abundance and diversity of wood-decay fungi in managed and unmanaged stands in a Scots pine forest in western Poland. *For. Ecol. Manag.* **2017**, *400*, 438–446. [\[CrossRef\]](#)

59. Adamowicz, K.; Jaszcak, R.; Kuźmiński, R.; Łabędzki, A.; Łakomy, P.; Mazur, A.; Starosta-Grala, M.; Szramka, H.; Turski, M.; Zientarski, J. An attempt at valuation of wood from dead trees in Polish forests. *Acta Sci. Pol. Silvarum Colendarum Ratio Ind. Lignaria* **2015**, *14*, 5–13. [\[CrossRef\]](#)
60. Bouget, C.; Brustel, H.; Brin, A.; Noblecourt, T. Sampling saproxylic beetles with window flight traps: Methodological insights. *Rev. Écol. (Terre Vie)* **2008**, *63*, 13–24.
61. Mazur, A.; Klejdysz, T.; Dobrowolski, M.; Konwerski, S.; Królik, R.; Łabędzki, A.; Przewoźny, M. Saproxylic beetles of Karkonosze (Giant) Mountains. Part I—Checklist. *Acta Sci. Pol. Silvarum Colendarum Ratio Ind. Lignaria* **2015**, *15*, 269–295. [\[CrossRef\]](#)
62. Mazur, A.; Kuźmiński, R.; Łabędzki, A.; Witkowski, R. Chrząszcze gnilikowe (Coleoptera, Histeridae) jako stały element fauny subkortykalnej lasów sosnowych i dębowych Wielkopolski. *Studia I Mater. CEPL W Rogowie* **2016**, *18*, 132–138.
63. Tarnawski, D.; Buchholz, L. Sprężykowate—Elateridae. Część ogólna oraz podrodziny: Agrypninae, Negastrinae i Dominae. In *Klucze do Oznaczania Owadów Polski, Part XIX 34a*; Polskie Towarzystwo Entomologiczne: Toruń, Poland, 2008; pp. 5–125.
64. Nunberg, M. Korniki—Scolytidae, Wyryniki—Platypodidae. In *Klucze do Oznaczania Owadów Polski, Part XIX 99-100*; Polskie Towarzystwo Entomologiczne: Warszawa, Poland; Wrocław, Poland, 1981; pp. 5–115.
65. Szujewski, A. Kusakowate—Staphylinidae. In *Klucze do Oznaczania Owadów Polski, Part XIX 24a*; Polskie Towarzystwo Entomologiczne: Toruń, Poland, 2008; pp. 5–229.
66. Lohse, G.A. Familie: Staphylinidae. In *Die Käfer Mitteleuropas. Band 4 Staphylinidae I (Micropeplinae Bis Tachyporinae)*; Freude, H., Harde, K.W., Lohse, G.A., Eds.; Goecke & Evers Verlag: Krefeld, Germany, 1964; pp. 5–264.
67. Assing, V.; Schülke, M. *Freude-Harde-Lohse-Klausnitzer—Die Käfer Mitteleuropas. Band Staphylinidae I. Zweite neubearbeitete Auflage*; Spectrum Akademischer Verlag I-XII: Heidelberg, Germany, 2011; pp. 1–560.
68. Bense, U. *Illustrated Key to the Cerambycidae and Vesperidae of Europe*; Margraf Verlag: Weikersheim, Germany, 1995; pp. 1–512.
69. Pfeffer, A. Zentral-und Westpaläarktische Borken-und Kernkäfer (Coleoptera, Scolytidae, Platypodidae). *Entomol. Basileia* **1994**, *17*, 5–310.
70. Mazur, S. *Histeridae Gnilikowe (Insecta: Coleoptera). Fauna Poloniae*; PWN: Warszawa, Poland, 1981; Volume 9, pp. 5–206.
71. Löbl, I. Icones Insectorum Europae Centralis. Coleoptera: Staphylinidae Dasycerinae, Pselaphinae. *Folia Heyrovskyana* **2009**, *10*, 1–26.
72. Jelínek, J. Icones Insectorum Europae Centralis. Coleoptera Sphindidae, Kateretidae, Nitidulidae. *Folia Heyrovskyana* **2014**, *21*, 1–29.
73. Sienkiewicz, J. Concepts of biodiversity—Their dimensions and measures in the light of literature. *Ochr. Sr. I Zasobów Nat.* **2010**, *45*, 7–29.
74. Shannon, C.A. A Mathematical Theory of Communication. *Bell Syst. Tech. J.* **1948**, *27*, 623–656. [\[CrossRef\]](#)
75. Morris, E.K.; Caruso, T.; Buscot, F.; Fischer, M.; Hancock, C.; Maier, T.S.; Meiners, T.; Müller, C.; Obermaier, E.; Prati, D.; et al. Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. *Ecol. Evol.* **2014**, *4*, 3514–3524. [\[CrossRef\]](#)
76. Szujewski, A. Wpływ rębni zupełnej na zgrupowania ściółkowych kusakowatych (Col.; Staphylinidae) borów sosnowych świeżych. *Folia For. Pol.* **1971**, *18*, 5–45.
77. Szujewski, A. *Ekologia Owadów Leśnych*; PWN: Warszawa, Poland, 1980.
78. Pawłowski, J. Reliktowe chrząszcze Coleoptera “Puszczy Karpackiej”. *Rocz. Bieszcz.* **2008**, *16*, 317–324.
79. Byk, A.; Borowski, J.; Mazur, S.; Mokrzycki, T.; Rutkiewicz, A. Waloryzacja lasów Leśnego Kompleksu Promocyjnego “Lasy Spalsko-Rogowskie” na podstawie struktury zgrupowań chrząszczy saproksylicznych. *Studia I Mater. CEPL W Rogowie* **2013**, *2*, 82–128.
80. Mokrzycki, T.; Borowski, J.; Byk, A.; Rutkiewicz, A. Waloryzacja ekosystemów Leśnego Kompleksu Promocyjnego “Lasy Spalsko-Rogowskie” na podstawie struktury zgrupowań chrząszczy (Coleoptera) zasiedlających pniaki. *Studia I Mater. CEPL W Rogowie* **2013**, *2*, 48–79.
81. Biodiversity Map. Available online: <https://baza.biomap.pl/pl/db> (accessed on 29 June 2021).
82. Alexander, K.N.A. Tree biology and saproxylic Coleoptera: Issues of definitions and conservation language. *Rev. Écol. (Terre Vie)* **2008**, *63*, 9–13.
83. Nieto, A.; Alexander, K.N.A. *European Red List of Saproxylic Beetles*; Publications Office of the European Union: Luxembourg, 2010.
84. Kliczkowska, A.; Zielony, R. *Regionalizacja Przyrodniczo-Leśna Polski*; Generalna Dyrekcja Lasów Państwowych: Warszawa, Poland, 2012.
85. Matuszkiewicz, W.; Sikorski, P.; Szwed, W.; Wierzba, M. (Eds.) *Lasy I Zarośla. Zbiorowiska Roślinne Polski*; Wydawnictwo Naukowe PWN: Warszawa, Poland, 2012; p. 520.
86. Kuźmiński, R.; Chrzanowski, A.; Mazur, A.; Rutkowski, P.; Gwiazdowicz, D.J. Distribution and habitat preferences of the stag beetle *Lucanus cervus* (L.) in forested areas of Poland. *Sci. Rep.* **2020**, *10*, 1043. [\[CrossRef\]](#)
87. Mokrzycki, T. *Saproxylic Beetle Assemblages (Coleoptera) of Stumps of Chosen Tree Species—Comparative Study*; Treatises and Monographs; Publications of Warsaw University of Life Sciences—SGGW: Warsaw, Poland, 2011.
88. Butenko, K.O.; Gongalsky, K.B.; Korobushkin, D.I.; Ekschmitt, K.; Zaitsev, A.S. Forest fires alter the trophic structure of soil nematode communities. *Soil Biol. Biochem.* **2017**, *109*, 107–117. [\[CrossRef\]](#)
89. Koltz, A.M.; Burkle, L.A.; Pressler, Y.; Dell, J.E.; Vidal, M.C.; Richards, L.A.; Murphy, S.M. Global change and the importance of fire for the ecology and evolution of insects. *Curr. Opin. Insect Sci.* **2018**, *29*, 110–116. [\[CrossRef\]](#) [\[PubMed\]](#)

90. Bouget, C.; Larrieu, L.; Nusillard, B.; Parmain, G. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodivers. Conserv.* **2013**, *22*, 2111–2130. [[CrossRef](#)]
91. Floren, A.; Müller, T.; Dittrich, M.; Weiss, M.; Linsenmair, K.E. The influence of tree species, stratum and forest management on beetle assemblages responding to deadwood enrichment. *For. Ecol. Manag.* **2014**, *323*, 57–64. [[CrossRef](#)]
92. As, S. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography* **1993**, *16*, 219–228. [[CrossRef](#)]
93. Müller, J.; Goßner, M.M. Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. *Biol. Conserv.* **2010**, *143*, 625–633. [[CrossRef](#)]
94. Knížek, M.; Zahradník, P. Bark and Wood Boring Beetles in the Pine Stands. In *Methodology of Forest Insect and Disease Survey in Central Europe, Proceedings of the Second Workshop of the IUFRO WP 7.03.10, Sion-Chateauneuf, Switzerland, 20–23 April 1999*; Forster, B., Knížek, M., Grodzki, W., Eds.; Swiss Federal Institute for Forest, Snow and Landscape Research (WSL): Birmensdorf, Switzerland, 1999; pp. 54–59.
95. Martikainen, P.; Viiri, H.; Rätty, M. Beetles (Coleoptera) caught with pheromones of *Gnathotrichus retusus* and *G. sulcatus* (Col., Scolytidae) in southern Finland. *Anz. Fur. Schdlingskunde* **2001**, *74*, 7–10. [[CrossRef](#)]
96. Ruchin, A.; Egorov, L.; Khapugin, A. Usage of Fermental Traps for the Study of the Species Diversity of Coleoptera. *Insects* **2021**, *12*, 407. [[CrossRef](#)] [[PubMed](#)]
97. Hjältén, J.; Stenbacka, F.; Andersson, J. Saproxylic beetle assemblages on low stumps, high stumps and logs: Implications for environmental effects of stump harvesting. *For. Ecol. Manag.* **2010**, *260*, 1149–1155. [[CrossRef](#)]
98. Plewa, R.; Jaworski, T.; Hilszczański, J. Dead wood and community structure of saproxylic beetles (Coleoptera) in oak stands. *Studia i Materiały CEPL w Rogowie* **2014**, *16*, 279–299.
99. Vodka, Š.; Cizek, L. The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. *For. Ecol. Manag.* **2013**, *304*, 33–41. [[CrossRef](#)]
100. Horák, J.; Kout, J.; Vodka, Š.; Donato, D.C. Dead wood dependent organisms in one of the oldest protected forests of Europe: Investigating the contrasting effects of within-stand variation in a highly diversified environment. *For. Ecol. Manag.* **2016**, *363*, 229–236. [[CrossRef](#)]
101. Lindhe, A.; Lindelöw, Å. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *For. Ecol. Manag.* **2004**, *203*, 1–20. [[CrossRef](#)]
102. Peuhu, E.; Thomssen, P.-M.; Siitonen, J. Comparison of three trap types in sampling saproxylic beetles living in hollow urban trees. *J. Insect Conserv.* **2018**, *23*, 75–87. [[CrossRef](#)]
103. Wikars, L.-O.; Sahlin, E.; Ranius, T. A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *Can. Entomol.* **2005**, *137*, 304–324. [[CrossRef](#)]
104. Parmain, G.; Bouget, C. Large solitary oaks as keystone structures for saproxylic beetles in European agricultural landscapes. *Insect Conserv. Divers.* **2018**, *11*, 100–115. [[CrossRef](#)]
105. Shavrin, A. Contribution to the knowledge of the fauna of the tribe Omaliini McLeay, 1825 (Coleoptera: Staphylinidae: Omaliinae) of the Baikal region and adjacent territories. *Balt. J. Coleopterol.* **2010**, *10*, 27–44.
106. Hyvärinen, E.; Kouki, J.; Martikainen, P.; Lappalainen, H. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *For. Ecol. Manag.* **2005**, *212*, 315–332. [[CrossRef](#)]
107. Wermelinger, B.; Duelli, P.; Obrist, M.K. Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. *For. Snow Landsc. Res.* **2002**, *77*, 133–148.
108. Nițu, E.; Olenici, N.; Popa, I.; Nae, A.; Biriș, I.A. Soil and saproxylic species (Coleoptera, Collembola, Araneae) in primeval forests from the northern part of South-Eastern Carpathians. *Ann. For. Res.* **2009**, *52*, 27–53.