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Trees, Deadwood and Tree-Related Microhabitats Explain Patterns of Alpha and Beta Saproxylic Beetle Diversity in Silver Fir-Beech Forests in Central Italy

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Abstract

Forest structure, including trees, deadwood and tree-related microhabitats, is a key determinant of forest biodiversity. Their relative contribution in shaping local (alpha) biodiversity and its variation (beta) between sites remains unclear. We assessed how forest characteristics shape alpha and beta diversity of beetle communities in mixed silver fir–beech forests within the Vallombrosa Nature Reserve (Tuscany, Italy). We sampled 47 circular plots recording single-tree attributes, deadwood volume and decay stage, and the occurrence of tree-related microhabitats. Beetle assemblages were surveyed using window flight traps, yielding over 11,000 individuals belonging to 187 species, 20% of those known from central-southern Italian forests, 58% of which were listed in the Italian Red List of Saproxylic Beetles and 10% of which were threatened. Statistical models (GLMs and GDMs) revealed that alpha diversity was driven by fine-scale features, including tree species composition, microhabitats (cavities, bark, epiphytes) and deadwood diversity. In contrast, beta diversity was shaped by stand structure and inter-stand heterogeneity. Our results highlight the need for conservation strategies that simultaneously maintain tree-level heterogeneity and secure variation across the landscape. Management should therefore combine retention of microhabitats and diverse deadwood substrates with promotion of structurally diverse, mixed stands to sustain beetle diversity at multiple spatial scales.

Keywords: conservation management; habitat heterogeneity; saproxylic beetles; threatened species; tree species composition; vertical stratification; window flight traps

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1. Introduction

Forests represent one of the most complex and functionally relevant ecosystems of the terrestrial biosphere [1–3]. They host a significant share of the global biodiversity and play a crucial role in sustaining both ecological processes and human societies [4,5]. Their structure is not uniform but characterized by high heterogeneity, emerging from the interaction among trees, shrubs and herbaceous layers of different species and ages, vertical stratification of the canopy, the presence of senescent individuals, and the formation of secondary habitats. This heterogeneity, reflected in the architectural complexity of stands, constitutes a key factor shaping forest biodiversity, supporting both composition and functions of species communities [5,6].

Deadwood, in its standing (snags) and downed (coarse woody debris) components, is important in shaping forest heterogeneity in temperate and Mediterranean forests [7,8]. The volume and stage of decomposition of deadwood directly influence resource availability for a wide range of organisms, promoting ecological niche diversification and sustaining ecosystem functionality. Forests characterized by abundant and diverse deadwood exhibit a greater capacity to support species-rich communities. However, the systematic removal of deadwood, typical of intensively managed forests, lead to habitat simplification and the progressive loss of species dependent on specialized resources [9,10].

In addition to deadwood, tree-related microhabitats (TreMs) further magnify forest structural complexity, which increases the diversity of forest-dwelling species [11,12]. Terms, such as cavities, bark fissures, broken branches, fire scars, fungal colonization, or the presence of fruiting bodies represent critical resources for numerous taxa. The richness and variety of tree-related microhabitats within a stand are regarded as integrative indicators of its biodiversity potential: the greater their availability, the broader the spectrum of ecological niches that the forest can sustain [13,14]. Temporal continuity of such microhabitats, often linked to the persistence of habitat trees, is particularly important for the survival of xylophagous and saproxylophagous species.

Within this mosaic of forest structural elements, beetles, and particularly saproxylic species, occupy a central role for forest biodiversity, e.g., [15,16]. This group is extremely diverse from a taxonomic and functional perspective. Beetles account for approximately 30% of all the forest-dwelling taxa in Mediterranean forests and play a functional vital role in ecosystem processes. Beetles participate in decomposition processes, nutrient cycling, and soil formation. They occupy a wide range of trophic niches, including from xylophagous, saprophagous, and mycetophagous to predatory, parasitoid, and phytophagous species, thereby supporting complex food webs [17]. Saproxylic beetles are also widely recognized as sensitive bioindicators of the degree of forest ecological integrity. Their presence reflects both current habitat quality and the historical continuity of structural elements such as large senescent trees and accumulations of decayed wood [18–20]. Many species exhibit a high degree of ecological specialization and depend on substrates that develop exclusively in mature or unmanaged forests, including tree hollows, large-diameter logs in advanced decay, or lignicolous fungi [21,22].

Forest structural elements affect differently patterns of alpha biodiversity, i.e., within-site local biodiversity, and beta diversity, i.e., between-site biodiversity variation across space. Alpha diversity is partitioned into its two components species richness and evenness at the local scale. For saproxylic beetles, alpha diversity is primarily shaped by fine-scale forest attributes such as deadwood volume and decay stage, density of cavities, and variety of microhabitats [23,24]. Beta diversity reflects species turnover across spatial gradients. For saproxylic beetles, this is primarily driven instead by broader-scale factors such as tree species composition, stand age structure, and landscape heterogeneity [25,26]. Evidence from Apennine forests in Italy indicates that, for saproxylic beetles, alpha diversity is positively associated with coarse woody debris and vertical heterogeneity, whereas beta diversity reflects differences in tree dominance and microhabitat availability [27–29].

Recognizing how forest characteristics influence different components of biodiversity can guide management strategies that support local species assemblages while maintaining community heterogeneity across the landscape. An exemplary case is the Vallombrosa Nature Reserve in the central Apennines of Tuscany, one of Italy's largest and most historically significant forest complexes. The long silvicultural tradition in Vallombrosa originated with the management of the Benedictine monks and was later continued by the National Forest

Service [30]. Together they have created a mosaic of conifer and broadleaf stands with even-aged structures. These stands were actively managed until the 1970s. Combined with abundant deadwood and microhabitats [31], these conditions make Vallombrosa an exceptional natural laboratory for exploring the links between forest complexity and biodiversity. The site provides extensive field data on forest structure (living trees, deadwood and microhabitats) and saproxylic beetle assemblages (species abundance from window traps).

Studies that address the holistic effect of forest structural complexity on alpha and beta diversity are still scarce but see [27–29]. To fill this gap of knowledge, our study aims to comparatively evaluate the role of forest complexity in shaping forest dwelling beetle assemblages within and between sites in the Vallombrosa Nature Reserve. We (1) describe key forest characteristics linked with beetle diversity, including living trees, deadwood and microhabitat, (2) characterize the beetle community by taxonomy, trophic role and conservation value and (3) model the effect of these three forest characteristics on the patterns of alpha diversity (local diversity) and beta diversity (species turnover). This study provides a comprehensive understanding of how forest structural complexity sustains beetle diversity and offers insights to guide conservation-oriented management in temperate forests.

2. Materials and Methods

2.1. Study Area

The study was conducted within the Vallombrosa Nature Reserve, situated in the Tuscany region (Central Italy) on the northwestern slope of the Pratomagno Massif (coordinates: 43.745° E, 11.562° N) (Figure 1a). The Reserve encompasses both pure and mixed stands of silver fir (*Abies alba*) and European beech (*Fagus sylvatica*). This plant association is qualified in the EUNIS habitat classification (European Nature Information System) with code 9220 "Apennine beech forests with *Abies alba*". The Reserve is part of the Natura 2000 Network and designated as a Special Area of Conservation (SAC) under the EU Habitats Directive (92/43/EEC), specifically within the site "Vallombrosa e Bosco di S. Antonio" (code IT5140012) [31].

The Reserve covers an area of 1273 hectares, of which 1209 ha (95%) are represented by forest, with altitudinal variation ranging from 470 to 1447 m above sea level. The predominant forest type is composed of even-aged pure stands of silver fir (*Abies alba* Mill.), extending over 664 ha (54.9% of the forest area) (Figure 1c), followed by pure beech (*Fagus sylvatica* L.) stands covering 187 ha (15.5%) (Figure 1d). The rest of the forested area, covering 358 ha (29.6%), is represented by plantations of black pine (*Pinus nigra* J.F. Arnold) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (introduced for experimental trials), as well as mixed deciduous forests (Figure 1d) comprising European chestnut (*Castanea sativa* Mill.), Turkey oak (*Quercus cerris* L.), European hop-hornbeam (*Ostrya carpinifolia* Scop.), and South European flowering ash (*Fraxinus ornus* L.). However, these mixed stands were excluded from the present study.

In the Reserve, conifer stands were planted in the past, while beech stands, which were managed as coppice in the past, now are in conversion to high forest. The cultivation of silver fir in pure stands has a long-standing tradition in Vallombrosa, although recent socio-economic and environmental changes have markedly influenced forest management practices [30].

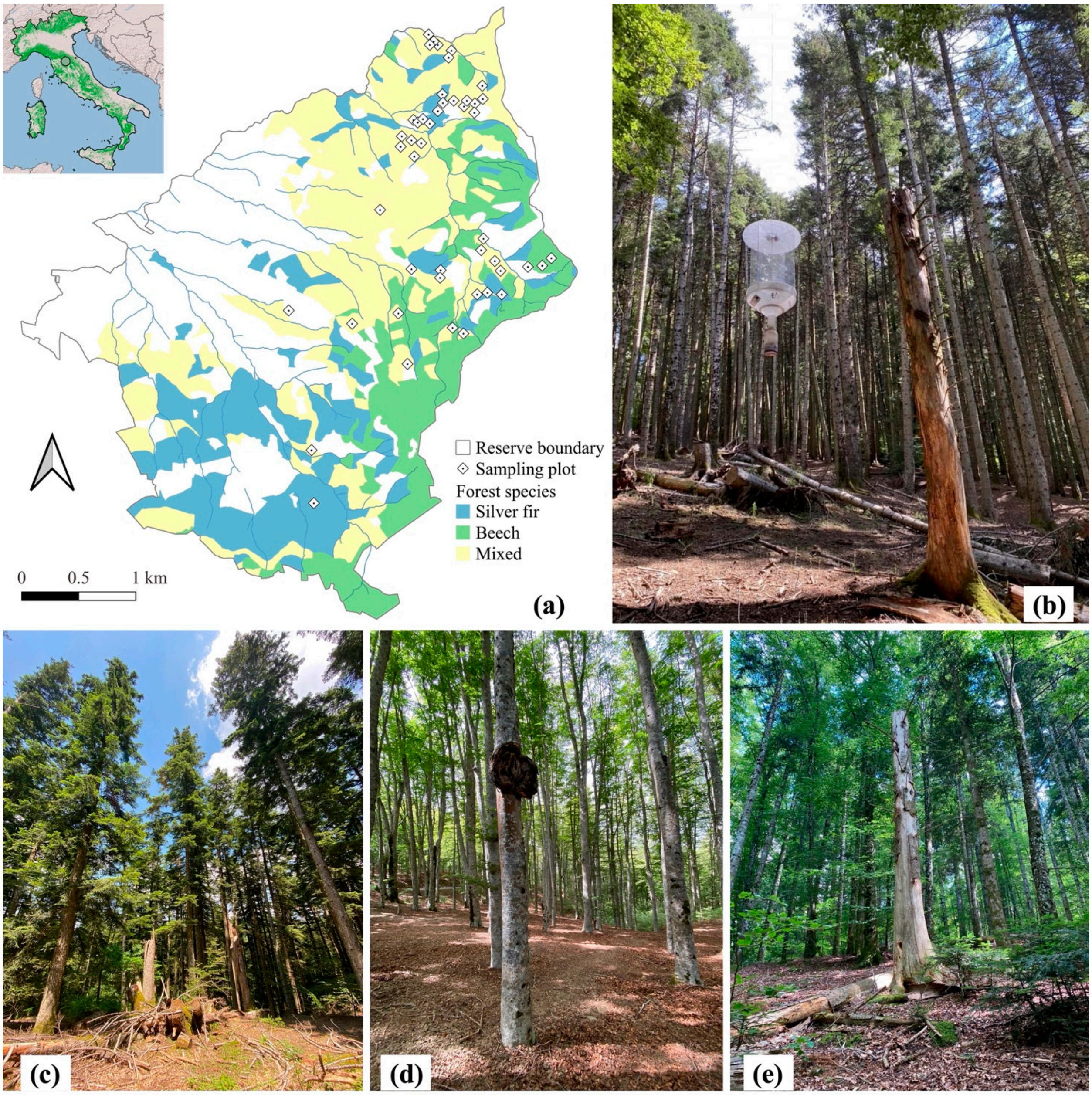

Figure 1. Vallombrosa Nature Reserve and sampling scheme. (**a**) Window flight trap used for beetle monitoring; (**b**) silver fir; (**c**) beech (**d**); and mixed stands (**e**).

The most recent forest regulation plan, dating back to 1970, was never implemented. As a result, forest composition and structure particularly within plantations of silver fir have been undergoing progressive natural change, including an increasing presence of broadleaved species, especially beech. A new Forest Management Plan for the period 2006–2025 [32], based on the silvosystemic approach [32,33], promotes natural regeneration and the development of structurally diversified and mixed stands by silvicultural operations that support natural dynamics. Additionally, recent severe windstorm events have accelerated these ecological dynamics [34].

Site-specific data were obtained from historical and current forest management plans, in particular the 2006–2025 plan [32], which provided detailed information for each management unit (forest stand), including altitude, aspect, slope, site quality, forest type, stand age, and year of the last silvicultural intervention.

2.2. Sampling Scheme

The reference sampling scheme consisted of 47 circular plots with a 13 m radius located within the Reserve in *A. alba* and *F. sylvatica* pure and mixed stands (Figure 1a). The plots were located at elevations between 900 and 1250 m a.s.l., with a minimum slope of 9% and a maximum of 48%. The stand age varied from 50 to 180 years old. Twenty-seven plots were established in mixed stands, while the remaining 20 plots were established in pure stands. We did not apply a fully random sampling because our objective was to focus on specific forest habitats. Instead, we used an opportunistic, pseudo-random approach coverage of the target habitats while retaining some randomness in site selection. This approach may limit the generalization of results across other forest types, it provides a robust basis for detecting biodiversity patterns within the focal habitats. Field surveys were conducted in 2020 to collect in each plot the data needed to quantify forest structure, deadwood, tree-related microhabitats and beetles. More details on these surveys are provided in the following sections. For each sampling plot, UTM datum WGS84 coordinates (Zone 32 T) and altitude (m a.s.l.) were recorded using the Juno SB Global Positioning System (GPS; Trimble, Sunnyvale, CA, USA).

2.3. Living Trees, Deadwood and Tree-Related Microhabitats

Living trees (diameter at breast height, DBH $\geq$ 5 cm) and deadwood (diameter $\geq$ 10 cm) were sampled in each plot. For living trees, we recorded the following variables: tree DBH measured with a calliper, total height with a vertex hypsometer and species. For deadwood, we recorded dead downed trees, snags, coarse woody debris and stumps, measuring their length/height with a vertex, minimum and maximum diameter with a calliper and recording the species, when recognizable. Standing dead trees were characterized by the presence of crown (dead branches and twigs), while snags referred to stems without crown. A snag was defined as any standing dead tree with a minimum height of 1.3 m. The volume of living trees and standing and dead downed trees was calculated by double-entry volume equations [35], while the volume of snags, coarse woody debris and stumps were calculated through the cone trunk formula [36]. The decay stage of each deadwood sample was visually assigned, using the five-grade scale proposed by Hunter [37], in which the morphological characteristics of deadwood are assessed. Details on the applied sampling protocol are reported in Lombardi et al. [36].

We also surveyed tree-related microhabitats on living trees, carefully examining by visual inspection the trunk from the ground to the crown and following the hierarchical classification proposed in the catalogue of tree-related microhabitats by Kraus et al. [38] (Table A1).

All the forest variables measured in the sampling scheme and used as predictors in GLMs and GDMs for alpha and beta diversity are reported in Table 1. Quadratic mean diameter of living trees was computed as the diameter of the mean basal area tree and mean height was computed as the height of the mean basal area tree.

Table 1. Legend of codes of the forest variables included in the sampling scheme and used as predictors in GLMs and GDMs for alpha and beta diversity.

Predictor Type	Predictor Acronym	Predictor Description
Space	ID	Plot identity
Space	Exposure	North or South exposure
Space	X	Longitude in metres
Space	Y	Latitude in metres
Space	PCNM1/Geographic	Principal Coordinates of Neighbour Matrix (alpha models)/ Geographic distance between sites (beta models)

Table 1. *Cont.*

Predictor Type	Predictor Acronym	Predictor Description
Living wood	Species	Tree species (Fagus = 1, mixed = 2, Abies = 3)
Living wood	Age	Stand age
Living wood	Layers	Number of forest layers
Living wood	N	Number of living trees per ha
Living wood	D	Quadratic mean diameter of living trees in cm
Living wood	BA	Basal area of living trees in m^2 per ha
Living wood	V	Volume of living trees in m^3 per ha
Living wood	H	Mean height of living tree in m
Deadwood	Vdead	Volume of deadwood per ha
Deadwood	Vcwd	Volume of coarse woody debris per ha
Deadwood	Vdowned	Volume of dead downed trees per ha
Deadwood	Vstanding	Volume of dead standing trees per ha
Deadwood	Vstumps	Volume of stumps per ha
Deadwood	Vsnags	Volume of snags per ha
Deadwood	Ndead	Number of deadwood pieces per ha
Deadwood	Ncwd	Number of coarse woody debris pieces per ha
Deadwood	Ndowned	Number of dead downed trees per ha
Deadwood	Nstanding	Number of dead standing trees per ha
Deadwood	Nstumps	Number of stumps per ha
Deadwood	Nsnags	Number of snags per ha
Deadwood	Shannon_Vd_tot	Diversity of volume of total deadwood by decay classes
Deadwood	Shannon_Vcwd_tot	Diversity of volume of coarse woody debris by decay classes
Deadwood	Shannon_Vddt	Diversity of volume of dead downed trees by decay classes
Deadwood	Shannon_Vdst	Diversity of volume of dead standing trees by decay classes
Deadwood	Shannon_Vsnags	Diversity of volume of snags by decay classes
Deadwood	Shannon_Vstumps	Diversity of volume of stumps by decay classes
Microhabitat	Nm	Number of microhabitats per ha
Microhabitat	CV1	Number of woodpecker cavities per ha
Microhabitat	CV2	Number of trunk and mould cavities per ha
Microhabitat	CV3	Number of branch holes per ha
Microhabitat	CV4	Number of dendrotelms and water-filled holes per ha
Microhabitat	CV5	Number of insect galleries and bore holes per ha
Microhabitat	IN1	Number of bark loss/exposed sapwood per ha
Microhabitat	IN2	Number of exposed heartwood/trunk and crown breakages per ha
Microhabitat	IN3	Number of cracks and scars per ha
Microhabitat	BA1	Number of bark pockets per ha
Microhabitat	BA2	Number of bark structures per ha
Microhabitat	DE1	Number of dead branches and limbs/crown deadwood per ha
Microhabitat	GR1	Number of root buttress cavities per ha
Microhabitat	GR2	Number of witches broom per ha
Microhabitat	GR3	Number of cankers and burrs per ha
Microhabitat	EP1	Number of fruiting bodies fungi per ha
Microhabitat	EP2	Number of myxomycetes per ha
Microhabitat	EP3	Number of epiphytic crypto- and phanerogams per ha
Microhabitat	NE	Number of nests per ha
Microhabitat	OT1	Number of sap and resin runs per ha
Microhabitat	OT2	Number of microsoil per ha

2.4. Beetles Sampling

In the 47 plots of the sampling scheme both saproxylic and non-saproxylic adult beetles were collected using window flight traps (Figure 1b), as described by Bouget et al. [39] and Campanaro and Parisi [40]. Window traps were installed at a height of 2 m above the ground and applied consistently across all sampling areas. This standardized setup ensures data comparability among sites but may influence the relative capture of species associated with the canopy or ground layers [39,40]. Trap contents were collected monthly from May to October, resulting in four sampling sessions. All monitoring equipment was subsequently removed during the winter months. Taxonomic identification and nomenclature followed the frameworks proposed by Bouchard et al. [41] and Carpaneto et al. [18]. All collected taxa are listed in Table A2, arranged alphabetically. This table also specifies which species are strictly saproxylic, based on the criteria established by Carpaneto et al. [18], and indicates their respective Italian IUCN conservation status.

Species identified in our samples that are recognized as saproxylic by Carpaneto et al. [18] were further classified according to their predominant trophic guild, as outlined in Table A2: (i) xylophagous (organisms feeding primarily or exclusively on wood); (ii) saproxylophagous (organisms feeding mainly on wood colonized by fungi); (iii) mycophagous (organisms feeding predominantly on fungi); (iv) mycetobiontic (species associated with fungal fruiting bodies, particularly those of Polyporales on aged trees and stumps); (v) commensal (species living in association with xylophagous or saproxylophagous insects); (vi) sap-feeding (species exploiting tree sap, typically on trees attacked by xylophagous insects); (vii) predatory (organisms that obtain nutrition by consuming other organisms); (viii) unknown (species with an uncertain or undocumented trophic role). Conversely, for beetle species recorded in our samples but not included in Carpaneto et al. [18], trophic assignments remain undetermined and thus were not specified in Table A2, pending further ecological investigation.

For the conservation status, the classification of saproxylic species in terms of extinction risk followed the Italian Red List of Saproxylic Beetles [18], using the following categories: Critically Endangered (CR), Vulnerable (VU), Near Threatened (NT), Data Deficient (DD), and Least Concern (LC).

2.5. Statistical Analysis

2.5.1. Rarefaction Curves

We assessed the completeness of our beetle sampling using rarefaction curves. The curves were employed to compare the diversity for the 47 sampling plots for the whole species community and separately for the saproxylic and non-saproxylic communities. The curves showed the expected number of species as a function of sampling effort, and were calculated with the iNext4 R package version 1.0.1 [42], for the indices of species richness, Shannon diversity and Simpson diversity (corresponding to the first three Hill numbers [43]: $q = 0$, $q = 1$, and $q = 2$, respectively).

2.5.2. Indices of Alpha and Beta Diversity

For the beetle community we calculated alpha (=site-level) diversity and beta (=between sites) diversity indices employing the 3 Hill numbers (q) as follows:

- We calculated alpha diversity for each sampling site as richness (Hill number = 0) from species presences/absence (1/0) data, and as Shannon index ($q = 1$) and Simpson index ($q = 2$) from abundance data.
- We calculated beta diversity as turnover among sampling sites employing distance indices equivalent for the 3 Hill numbers (q): Jaccard dissimilarity index ($q = 0$) was calculated from presence/absence (1/0) data [44] and corresponds to richness; Horn index ($q = 1$) was calculated from abundance data and corresponds to Shannon diversity; rare and common species influence this index based on their abundance; Morisita index ($q = 2$) was calculated from abundance data and corresponds to Simpson diversity; it is more sensitive to common species [45].

2.5.3. Models for Alpha and Beta Diversity

We fitted Generalized Linear Model (GLMs) [46] and Generalized Dissimilarity Models (GDM) [47,48] to assess how the six indices of alpha and beta diversity (Paragraph 2.5) relate to the forest predictors listed in Table 1. We excluded from model fitting 61 species collected with only one record (=singletons) of the total 187 because they were too rare to reliably estimate their niches [49]. Instead, we retained doubletons to avoid a biased assessment of species richness.

The three indices of alpha diversity were modelled with GLMs, as follows: species richness (Hill number = 0) was modelled with a Poisson distribution for the response variable and a log link function while Shannon (Hill number = 1) and Simpson (Hill number = 2) diversity indices were modelled with a Gaussian distribution for the response variable and an identity link function. GLMs were fitted with the MASS package in R [50]. Importance of the predictors in the models was calculated with the R package vip [51]. The three indices of beta diversity were modelled with GDMs fitted with the R package gdm [52]. Importance of the predictors in the models was calculated with the gdm.varImp function. In the alpha models, negative signs for importance were indicative of the negative signs of the predictors' estimates, while for beta models, as split sums are always positive, importance was also always positive. Predictor importance was rescaled in the range 0%–100% to allow comparisons among all models.

Both for alpha and beta models, highly collinear predictors (Variance Inflation Factor (VIF) > 0.7) were excluded from the GLMs/GDMs with the collinearity-filtering algorithm "vifstep" of the "usdm" R package [53]. For alpha models, a bidirectional selection procedure based on the Akaike Information Criterion (AIC; [54]), balancing model fit and number of predictors, was applied to the GLMs fitted with all normalized (i.e., centred and scaled) predictors retained after the collinearity check with the "stepAIC" function of the "MASS" R package [50], which finally retained only forest predictors significant at $p < 0.05$. For beta models, we first fitted full GDMs with all normalized predictors and afterwards we removed all predictors with importance < 1.0% and the predictors with spline sums = 0. Then we refitted the final GDMs. For all GDMs, each predictor was modelled using 3 I-spline basis functions (i.e., 3 knots).

For all models, the residual spatial autocorrelation was found to be non-significant (For GLMs: $-0.02 <$ Moran's $I < 0.06$; For GDMs: $-0.05 <$ Moran's $I < 0.07$, for all models: $p > 0.1$) (Table A4).

The statistical analyses and graphs were all produced using R version 4.3.2 (https://www.R-project.org/).

3. Results

3.1. Forest Structure and Tree-Related Microhabitats

A total of 1941 trees were measured in the sampling plots, mostly beech (*Fagus sylvatica* L., 1753, 49%), fir (*Abies alba* Mill., 1759, 33%), black pine (*Pinus nigra* J.F. Arnold, 4.3%), holly (*Ilex aquifolium* L., 3.2%), chestnut (*Castanea sativa* Miller, 1768, 2.6%), Norway spruce (*Picea abies* (L.) H. Karst, 1.5%), and Scots pine (*Pinus sylvestris* L., 1.4%). The average standing timber stock was 691 m^3/ha (SD = 285 m^3/ha) (Table 2). Stands had mostly a bistratified (45% of the sample area) or multistratified (38% of the sample area) profile. Basal area was moderately diversified among the plots (51 $\pm$ 20 m^2/ha). Tree diameters were distributed in nine 5 cm diameter classes and most of the plots were in the range 25–35 cm (33 plots). Smaller and larger diameter classes were less frequent, with only 9 plots in the range 10–20 cm, 5 above 40 cm, and a single exceptionally large DBH at 135 cm.

Table 2. Statistics of the numerical forest variables included in the sampling scheme.

Predictor Type	Predictor Acronym	Mean	SD	Range
Space	X	707,337	472.0	706,010–708,310
	Y	4,847,723	995.3	4,845,040–4,849,115
Living wood	age	83	27.6	48–179
	layers	2	0.8	1–4
	N	778	405.4	188–2298
	D	32	17.1	13–135
	BA	51	20.2	15–112
	V	691	285.2	194–1428
	H	19	4.8	7–27
Deadwood	Vdead	182	164.8	6–731
	Vcwd	90	135.6	0–659
	Vdowned	24	38.3	0–159
	Vstanding	16	19.5	0–75
	Vstumps	16	17.4	0–83
	Vsnags	37	55.4	0–219
	Ndead	599	291.7	113–1695
	Ncwd	337	235.0	0–1055
	Ndowned	29	33.7	0–113
	Nstanding	43	48.2	0–188
	Nstumps	163	116.3	0–584
	Nsnags	27	39.6	0–170
	Vdead_class1	45	47.28	0–201
	Vdead_class2	63	99.67	0–606
	Vdead_class3	42	48.87	0–243
	Vdead_class4	32	87.89	0–592
	Vdead_class5	1	3.21	0–20
Tree-related Microhabitats	Nm	1031	470.9	452–2203
	CV1	52	120.5	0–565
	CV2	10	14.6	0–57
	CV3	28	44.4	0–151
	CV4	21	38.2	0–170
	CV5	302	169.1	38–1055
	IN1	21	25.9	0–94
	IN2	7	19.5	0–113
	IN3	34	44.4	0–207
	BA1	7	13.8	0–57
	BA2	36	79.0	0–414
	DE1	211	225.7	0–979
	GR1	70	72.3	0–414
	GR2	28	54.1	0–283
	GR3	3	9.9	0–57
	EP1	136	217.2	0–848
	EP3	55	108.5	0–377
	NE	0	2.7	0–19
	OT1	9	15.1	0–57

We measured 1496 deadwood elements (599/ha), mainly fir (53%) and beech (22%), while 17% could not be identified to species level (Table 2). The average total volume of deadwood was 182 m^3/ha (SD = 165 m^3/ha). The proportion of total deadwood in comparison with living volume was 38.3% (SD = 54.2 m^3/ha). Deadwood was divided into the five components: coarse woody debris on the ground (CWD) was the most represented category (90 m^3/ha, SD = 136 m^3/ha), followed by snags (37 m^3/ha, SD = 55 m^3/ha), dead downed trees on the ground (24 m^3/ha, SD = 38 m^3/ha), stumps (16 m^3/ha, SD = 17 m^3/ha) and standing dead trees (16 m^3/ha, SD = 20 m^3/ha). Deadwood was most frequently in early decay (decay class 2, 63 m^3/ha, SD = 100 m^3/ha), while freshly decayed (decay class 1, 44 m^3/ha, SD = 47 m^3/ha), intermediately decayed (decay class 3, 42 m^3/ha, SD = 49 m^3/ha) and extensively decayed (decay class 4, 32 m^3/ha, SD = 88 m^3/ha) deadwood were also well represented. Instead, nearly completely decomposed deadwood was marginally represented (class 5, 0.95 m^3/ha, SD = 3 m^3/ha).

A total of 2573 Tree-related Microhabitats (TreMs) were recorded in the plot areas, on average 1031 TreMs/ha (Table 2). The detected TreMs belonged to two macrocategories: 1820 (729 per hectare) were saproxylic, originated from biotic or abiotic impacts exposing sub-cortical portions of the plant and 753 (302 per ha) were epixylic, originated from external elements physically connected to the tree, such as fungal fruiting bodies. Three TreM categories dominated: insect exit-hole networks in standing deadwood (754 observations), dead branches or crown deadwood in contact with living wood with active phloem and xylem flows (526), and fungal fruiting bodies on trunks of living or dead trees (340).

3.2. Beetle Communities

A total of 11,072 beetle specimens were collected in the sampling plots, belonging to 38 families and 187 species (Table 3). The most abundant families (at least in the 90th percentile) were: Curculionidae (62.8%), Staphylinidae (11.5%), Laemophloeidae (4.9%) and Elateridae (4.4%) (Table 3). The families with the highest species richness (at least in the 90th percentile) were Staphylinidae (27.8% of the total species), Curculionidae (12.8%), Cerambycidae (9.1%) and Elateridae (7.5%). Three Curculionid species represented more than half (57.5%) of the total abundance: *Xylosandrus germanus* (2804 individuals), *Ernoporicus fagi* (2704 individuals) and *Orchestes fagi* (874 individuals). Notably, 108 species (58% of the total) were included in the Italian Red List of Saproxylic Beetles (Table 4). Among these, 77 species (41% of the total) were of Least Concern (LC), 18 species (10%) Near Threatened (NT), 11 species (10%) threatened (i.e., VU + EN + CR) and 2 species (1%) Data Deficient (DD). Among the 11 threatened species, 8 were Vulnerable (VU), 2 Endangered (EN), and 1 Critically Endangered (CR). With regard to trophic guilds (Table 5), among the 187 sampled beetle species, 105 species (56.1%) were saproxylic *sensu lato*, 35 species (18.7%) were xylophagous, feeding primarily or exclusively on wood, 20 species (10.7%) were predators, primarily consuming other organisms or their tissues, 27 species (14.4%) were mycophagous, feeding on saproxylic fungi or associated yeasts, and 15 species (8.0%) were saproxylophagous, feeding predominantly on wood colonized by fungi.

Table 3. Beetle richness and abundance beetle by family.

Family	N. Species	N. Individuals
Biphyllidae	1	5
Bostrichidae	1	8
Buprestidae	1	1
Cantharidae	5	13
Cerambycidae	17	209
Cerylonidae	1	47
Chrysomelidae	1	2
Cleridae	2	6
Cryptophagidae	2	37
Cucujidae	1	8
Curculionidae	24	6957

Table 3. *Cont.*

Family	N. Species	N. Individuals
Elateridae	14	488
Endomychidae	1	2
Erotylidae	1	1
Eucnemidae	1	5
Laemophloeidae	2	544
Lampyridae	1	8
Latridiidae	4	10
Lucanidae	1	2
Lycidae	2	4
Lymexylidae	2	43
Melandryidae	3	32
Melyridae	7	352
Monotomidae	6	35
Mordellidae	2	3
Mycetophagidae	1	18
Nitidulidae	10	55
Oedemeridae	2	26
Ptinidae	1	5
Pyrochroidae	1	3
Salpingidae	3	326
Scraptiidae	5	224
Silphidae	2	2
Silvanidae	1	1
Staphylinidae	52	1268
Tenebrionidae	2	96
Trogossitidae	1	46
Zopheridae	3	180
Total	187	11,072

Table 4. Number of beetle species by IUCN category.

IUCN Category	N. Species
CR	1
DD	2
EN	2
LC	77
NA	79
NT	18
VU	8
Total	187

Table 5. Number of beetle species by trophic category.

Trophic Category	N. Species
Mycetobiontic	3
Mycophagous	27
Non-saproxylic	79
Predatory	20
Sap-feeding	5
Saproxylophagous	15
Unknown	3
Xylophagous	35
Total	187

3.3. Beetle Diversity

Rarefaction curves plateaued for diversity and dominance but not for species richness (Figure 2), indicating that the sampling effort was sufficient to yield reliable estimates of diversity and dominance, but not to capture the full richness of rare species in either saproxylic and non-saproxylic species groups.

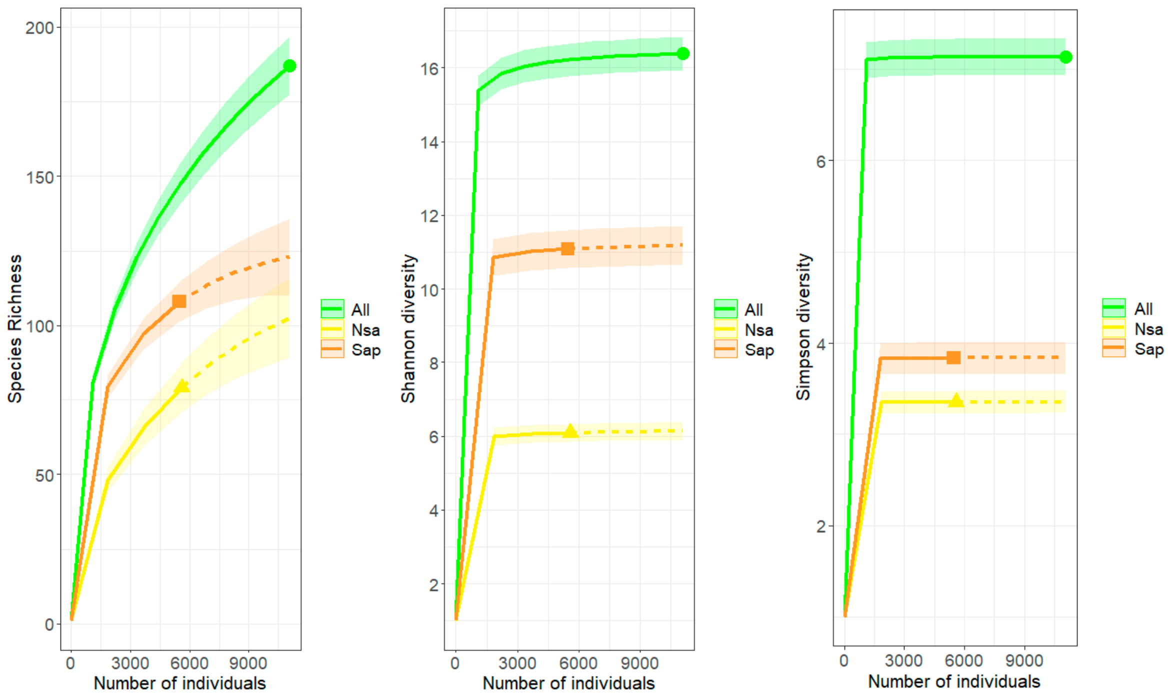

Figure 2. Rarefaction curves with 95% confidence intervals (shaded areas) for the three Hill's numbers (q = 0 species richness, q = 1 Shannon diversity and q = 2 Simpson diversity), considering the whole species assemblage (All) and separately the saproxylic (Sap) and non-saproxylic (Nsa) species. Dashed lines indicate interpolated values to compare the same sample sizes.

3.4. Models for Alpha and Beta Diversity

The deviance explained by the alpha diversity models was consistently higher than that of beta models (Figure 3). This difference likely arises from two factors. First, both model types were fitted with plot-level forest predictors. Second, the structural uniformity of the forest, resulting from homogeneous management, reduced variation among sampling plots and thus lowered the deviance explained in beta models. In alpha models, explanatory power increased with greater weighting of common species, i.e., with stronger dominance effects, whereas in beta models it rose when shifting from species presence/absence (Jaccard index) to abundance metrics (Horn/Morisita indices).

Across alpha diversity models, several predictors stood out as particularly influential (Figure 4): **Tree species composition** was the strongest predictor of Shannon diversity (q = 1; 39.3%) and also contributed notably to Simpson diversity (q = 2; 15.5%) and species richness (q = 0; 15.8%). **Structural heterogeneity**, reflected by the number of trunk and mould cavities (CV2), strongly supported Shannon diversity (23.6%) and also contributed to Simpson diversity (9.1%). **Bark structures** (BA1 and BA2) also enhanced diversity: bark pockets (BA1) influenced Shannon (11.6%) and Simpson (10.0%) diversity, while bark structures (BA2) contributed to richness (11.3%). **Deadwood diversity** played an important role: the diversity of dead downed tree volume by decay class (Shannon_Vddt) strongly supported richness (20.6%), while the volume of coarse woody debris (10.4%) and snags (4.1%) promoted Simpson diversity. In contrast, higher **volumes of downed deadwood** (−17.1%) and more **standing dead trees** (−11.0%) reduced richness, while microhabitats such as **cracks** and **scars** (IN3, −9.9%) also had negative effects. **Other microhabitats** included root buttress cavities (GR1, 7.1%) and epiphytic cryptogams and phanerogams (EP3, 10.7%), both of which enhanced richness and Shannon diversity. By contrast, nests (−5.2%) and sap/resin runs (−4.6%) were negatively associated with Simpson diversity.

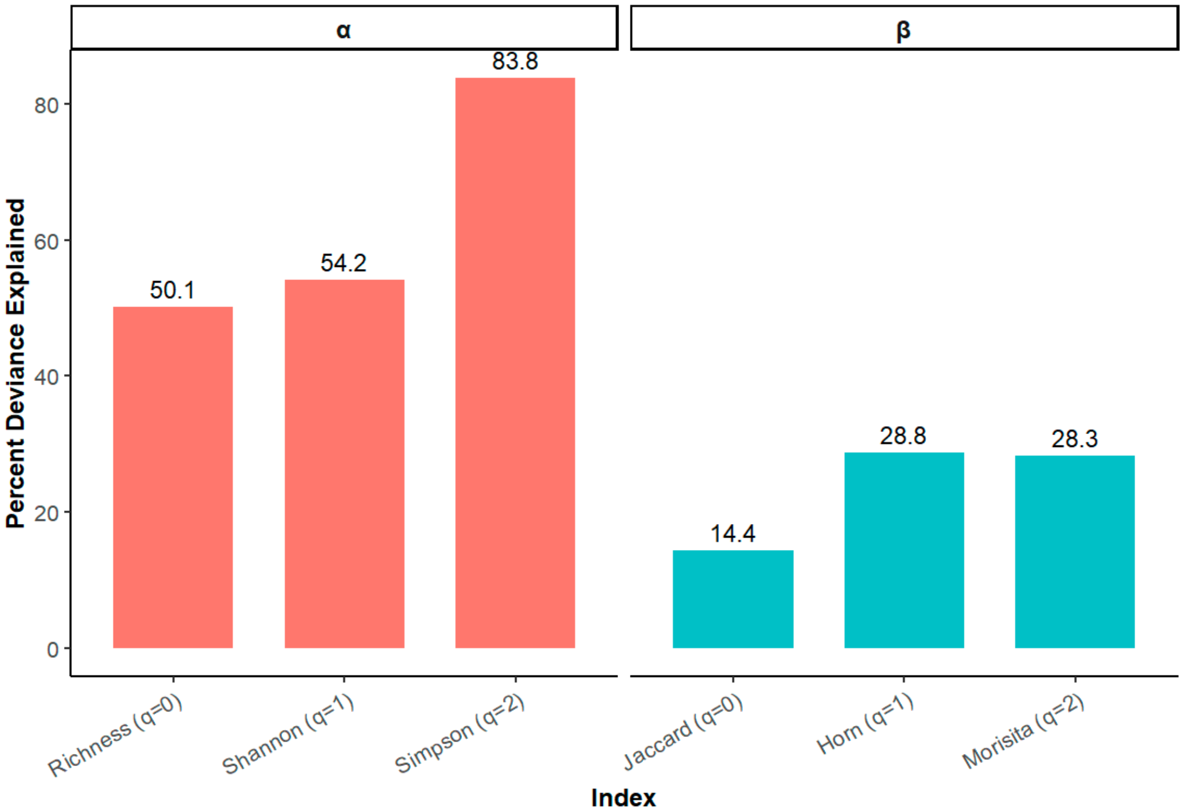

Figure 3. Percent deviance explained by alpha and beta diversity models.

For beta diversity, **basal area of living trees** was the dominant predictor in Jaccard models (27.3%), while also contributing to Horn (9.7%) and Morisita (9.1%) models. Additional consistent predictors included were (Figure 4): **Geographic distance between sites** (PCNM1), which explained 13.8%, 6.2%, and 5.7% of variation in Jaccard, Horn, and Morisita models, respectively. **Number of stumps** had strong effects, particularly in Morisita (20.9%) and Horn (14.4%), with some effect in Jaccard (6.1%). **Forest structure features**, such as stand age (up to 4.8%) and the number of vertical layers (10.5% in Morisita), consistently contributed across models. **Deadwood quantity and diversity** were important: number of coarse woody debris pieces (Ncwd, 17.3% Jaccard), volume of downed deadwood (11.7% Horn; 9.4% Morisita), and volume of standing dead trees (5.2% Horn; 4.2% Morisita) all explained variation. **Microhabitat diversity** also played a role: dendrotelms and water-filled holes (CV4; 11.8% Horn, 11.1% Morisita), cankers and burrs (GR3; 7%–8% across models), and the diversity of standing deadwood volume by decay class (Shannon_Vst, 7.0% Jaccard) added further explanatory power.

Alpha diversity was most strongly linked to tree species composition and microhabitat features (e.g., cavities, bark structures, epiphytes), underscoring the role of fine-scale habitat heterogeneity for within-site diversity (Figure 4). In contrast, beta diversity was driven primarily by stand structural attributes (basal area, stump abundance, deadwood quantities) and geographic distance, highlighting how larger-scale forest structure and spatial turnover shape between-site dissimilarity. Deadwood diversity appeared to have opposite effects in alpha models but consistently explained variation in beta models. This difference arises from the way the models are framed: regression-based alpha models can show positive or negative coefficients, while generalized dissimilarity models only return non-negative contributions. Thus, the substantive conclusion is that alpha and beta diversity respond to different scales of forest features: local composition and microhabitats for alpha, versus broader structural gradients and spatial heterogeneity for beta.

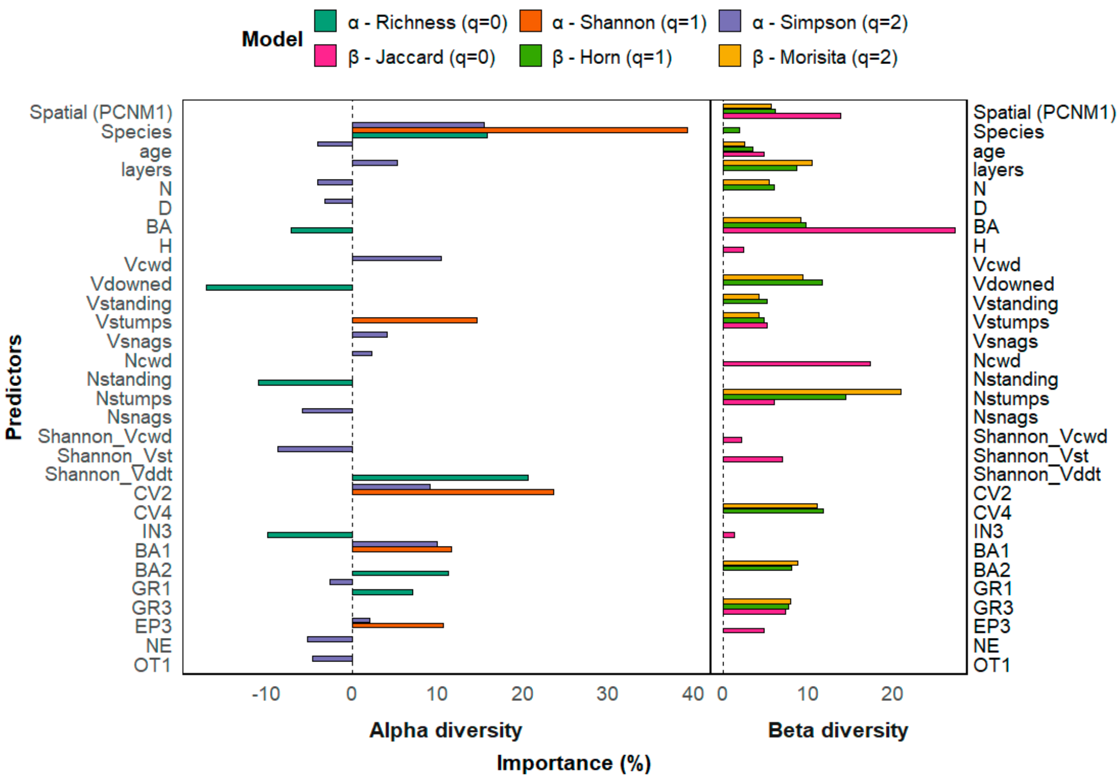

Figure 4. Relative importance (%) of predictors in explaining variation in alpha diversity (**left panels**) and beta diversity (**right panels**) from forest structural variables. Alpha diversity models include richness (q = 0), Shannon diversity (q = 1), and Simpson dominance (q = 2). Beta diversity models include Jaccard (q = 0), Horn (q = 1), and Morisita (q = 2) dissimilarity indices. Bars show importance values, grouped by model type. Spatial effects are represented by the variable Spatial (PCNM1) in alpha models and by geographic distance in beta models. In the alpha models, negative signs for importance are indicative of the negative signs of the predictors' estimates, while for beta models, as split sums are always positive importance is also always positive. See original models in Table A3. All the predictors included in the models have at least 1% importance. A legend for the predictors is shown in Table 1.

When moving from richness/Jaccard (q = 0) to Shannon/Horn (q = 1) and Simpson/Morisita (q = 2), a clear shift in the relative importance of predictors emerged (Figure 4). For richness and Jaccard, diversity of deadwood resources was particularly influential: the diversity of downed deadwood volumes strongly promoted richness (20.6%), while the number of coarse woody debris pieces explained much of the variation in Jaccard (17.3%). At the Shannon/Horn level, predictors became more evenly distributed, with tree species composition dominating Shannon diversity (39.3%) and structural heterogeneity (cavities, bark features) contributing substantially (23.6% for Shannon; 14.4% stumps for Horn), reflecting a balance between rare and common species. At the Simpson/Morisita level, predictors tied to dominant structural features gained greater importance: basal area strongly shaped Morisita dissimilarity (9.1%), stump abundance explained up to 20.9%, and volumes of coarse woody debris and downed deadwood became central to both Simpson diversity and Morisita dissimilarity. This progression illustrates how predictors linked to habitat heterogeneity and rare-resource diversity drive q = 0 metrics, while stand structure and substrates supporting abundant species increasingly dominate at q = 2.

4. Discussion

4.1. Forest Structure in Vallombrosa

Our results indicate that mixed silver fir–beech forests in Vallombrosa are characterized by a high biomass of living trees, high structural complexity, abundant deadwood and a considerable density of tree-related microhabitats (TreMs). Such elements are recognized as essential substrates for saproxylic organisms and indicators of forest naturalness [13,14,31].

In Vallombrosa the average standing living volume (691 m^3/ha) was higher than in other Italian mature forests dominated by silver fir and beech, like Abeti Soprani (451 m^3/ha) and La Verna (653 m^3/ha) forests, but lower than the average values recorded in Camaldoli (930 m^3/ha) and Sasso Fratino (893 m^3/ha) (Refs., [55–57]). The average basal area in Vallombrosa (51 m^2/ha) was higher than Abeti Soprani (44 m^2/ha) and La Verna (45 m^2/ha) but comparable to Camaldoli (59 m^2/ha) and Sasso Fratino (53 m^2/ha) and higher than the control value (29 m^2/ha) proposed by Keddy and Drummond [58] for old-growth forests. These structural patterns are coupled with differences in species dominance: the basal area of silver fir was roughly half of the total basal area for Vallombrosa (55%), Sasso Fratino (≈51%) and La Verna (≈51%) while in Camaldoli (86%) the basal area was higher.

In Vallombrosa, conifer stands were planted in the past and no active management has been carried out in the last 55 years. As a consequence the average amount of total deadwood (182 m^3/ha) was much higher than in Abeti Soprani (41 m^3/ha) [56], Camaldoli (71 m^3/ha), Sasso Fratino (78 m^3/ha), and La Verna (114 m^3/ha), while remaining within the European range reported by Christensen et al. [59]; 73–344 m^3/ha). In Vallombrosa and Abeti Soprani, deadwood consisted almost entirely of coarse woody debris, whereas in the other reserves it was more diversified: in Camaldoli and Sasso Fratino, coarse woody debris still dominated (≈80%) but with smaller contributions from stumps (14% and 3%) and large logs (4% and 11%); in La Verna the deadwood pool was more evenly distributed, with 63% coarse woody debris, 14% snags, and 19% large logs. The deadwood/living wood ratio emphasizes the contrast: Vallombrosa's 38% was over twice that of other reserves with silver fir and beech (La Verna 18%, Abeti Soprani 15%, Sasso Fratino 7%, Camaldoli 6%), indicating an advanced succession toward old-growth features [60]. However, in Vallombrosa the accumulation of deadwood has been fostered by the artificial origin of silver fir stands and by the lack of silvicultural interventions over the past 55 years. The exceptionally high deadwood volume recorded in Vallombrosa (182 m^3 ha^{-1}) likely reflects not only the artificial origin of the silver fir plantations and the prolonged absence of management but also the legacy of severe wind disturbances. Major storms in 2013 and 2015 caused extensive windthrows, with gusts exceeding 160 km h^{-1} and widespread treefall, especially in conifer plantations [34]. These events abruptly increased coarse woody debris inputs and slowed subsequent removal processes. As a result, they amplified the differences with other reserves such as Sasso Fratino (78 m^3 ha^{-1}), where the forest is of natural origin and disturbance intensity and management history diverge.

Vallombrosa, together with the other silver fir and beech Reserves of Abeti Soprani, Camaldoli, Sasso Fratino, and La Verna, presents structural characteristics comparable to those of old-growth forests that differ markedly from those associated with mature managed stands [30]. In all of them, the absence of cutting activities has fostered uneven-aged structures, although the long-lasting effects of past management are still evident, particularly in Abeti Soprani [36], Camaldoli [55] and Vallombrosa. The diameter distributions confirm a high degree of structural heterogeneity: while Vallombrosa spans 9 DBH classes and Abeti Soprani 14, the other reserves extend across 16–18 classes, indicating continuous regeneration and recruitment [55]. These patterns underline that, although management legacies still shape the structure of some stands, the reserves as a whole retain the multi-layered organization typical of old-growth conditions.

The high deadwood volume and diversity in Vallombrosa provide resources and support niche differentiation for saproxylic organisms [17]. Like in the Abeti Soprani Reserve [56], in Vallombrosa we found that deadwood was abundant in early and intermediate decay stages and poorly represented in the most advanced decomposition class, indicating a scarcity of highly senescent substrates. This reflects the intermediate successional stage of the forest [61] and it is likely to reduce the availability of resources for specialized saproxylic species associated with well-decayed deadwood.

The density of TreMs in Vallombrosa (~1000/ha) was markedly higher than in regularly managed forests, usually featuring 50–70 TreMs/ha [62,63], underscoring the role of old trees and forest structural diversity in maintaining fine-scale heterogeneity. The density of TreMs in Vallombrosa was almost ten times higher than the density recorded in Abeti Soprani (~160/ha) [56], with a similar prevalence of saproxylic TreM categories such as insect galleries, crown deadwood, and fungal fruiting bodies. The occurrence of numerous cavities, bark structures, and epiphytes is an indicator for the potential presence of forest-dwelling species associated with functionally diverse resources [13,14].

4.2. Beetle Communities in Vallombrosa

The forest of Vallombrosa featured high species richness, with 187 species recorded, representing 20.4% of the 918 species found in central-southern Italy in managed and unmanaged forests by Campanaro and Parisi [40]. Among them, saproxylic beetles (108 species), represented 12.6%–13.5% of the 800–860 saproxylic species estimated by abundance data for European beech forests [64].

We compared the beetle diversity in Vallombrosa with the diversity in the nearby similar silver fir and beech forests of Abeti Soprani [28] and La Verna [65]. Although Vallombrosa showed higher beetle species richness than Abeti Soprani (187 vs. 156 species), the values can be considered relatively similar considering the sampling effort. The relatively high richness of Abeti Soprani given the much smaller sample size (~4500 individuals) than Vallombrosa (~11,000) indicates that its actual species richness might be comparable to, or potentially higher than Vallombrosa, if richness values would be compared for the same number of individuals.

Vallombrosa and Abeti Soprani differed markedly in beetle family dominance. In Vallombrosa, Curculionidae (63%) prevailed, mostly bark- and wood-boring species such as *X. germanus*, *E. fagi* and *O. fagi*, reflecting the abundance of living wood and woody substrates typical of stands with old-growth traits. In contrast, Abeti Soprani was dominated by Elateridae (60%), mainly *N. parvulus*, associated with deadwood and soil-litter habitats, suggesting a community structured by decompositional processes and finer-scale microhabitats. Although still present, Elateridae (4%) in Vallombrosa and Curculionidae (5%) in Abeti Soprani were secondary components.

In Vallombrosa beetle assemblages were dominated by a few widespread species. This pattern confirms that generalist taxa strongly shape community composition under structurally uniform forest conditions. The occurrence of several threatened species underscores its potential old-growth conditions which confers to the Reserve conservation relevance, with a substantial proportion of the fauna (58%) included in the Italian Red List and 10% of them classified as threatened. This proportion of threatened species is higher than in La Verna (4 species), a similar old-growth unmanaged silver fir–beech forest, and in Abeti Soprani, a silver fir–dominated forest with 6 threatened species.

In Vallombrosa, the high proportion of saproxylic species in the sampled assemblage reflects the abundant deadwood-associated habitats in the Reserve, considered as biodiversity hotspots in temperate forests (Refs., [66,67]). Within this trophic group, the high representation of xylophagous species is notable as they are particularly vulnerable species, depending directly on specific wood resources, and often requiring large-diameter or well-decayed logs increasingly rare in managed forests [68]. By contrast, the robust presence of mycophagous and saproxylophagous beetles highlights the crucial role of fungal colonization in making deadwood resources exploitable, even in forests where substrate diversity is relatively constrained [69]. The high representation of predatory species indicates that, despite the forest's simplified stand structure, trophic networks are still functioning to some extent. Overall, the guild distribution underscores that, in Vallombrosa, increasing deadwood diversity and availability through natural dynamics or targeted management is essential to support functionally diverse beetle communities and safeguard threatened species.

The rarefaction curves for species richness showed that in Vallombrosa, dominant and common species were effectively sampled, whereas rare taxa remained underrepresented. This pattern is similar to the pattern found in Abeti Soprani and in La Verna. This outcome highlights the difficulty of fully documenting richness in saproxylic communities, where many species are naturally scarce or specialized [70,71]. Indeed, several IUCN red-listed species were recorded as single individuals or in very few plots, probably reflecting the low availability of large-diameter deadwood and the scarcity of deadwood in late decay stage [36]. Nevertheless, the observed stabilization of diversity and dominance metrics, as already observed in Parisi et al. [28,65], suggests that the survey provided robust estimates of community structure, supporting reliable interpretation of local diversity patterns.

4.3. Effect of Forest Structure on Beetle Alpha and Beta Diversity

The statistical models showed that forest structure (i.e., living trees, deadwood and TreMs) had a higher explanatory power for beetle alpha diversity than for beetle beta diversity. This lower explanatory power for beta diversity is likely explained by the management applied in the past in Vallombrosa in silver fir forests, clear cut and planting [30], which likely reduced differentiation of beetle species assortments between plots [28,72]. Both for alpha and beta diversity models the explanatory power was higher for diversity and dissimilarity indices weighted by abundance, like Shannon/Horn and Simpson/Morisita, rather than for presence/absence indexes, like richness/Jaccard, indicating the high degree of dominance of few species in structuring the beetle community in Vallombrosa. Local predictors such as tree species composition and TreMs, emerged as the strongest drivers of alpha diversity [73,74], while stand-level structural attributes and spatial heterogeneity more strongly influenced beta diversity. Geographic distance contributed to explain differences in beetle composition and abundance between plots. This can be alternatively explained by two factors: the assumed low dispersal capacity of saproxylic beetles, which brings to a local differentiation in the beetle community in terms of species assortment ([75,76] but see [77]); the spatial variation in the habitats [73]. Importantly, the analysis revealed that resource diversity (e.g., diversity of downed deadwood and stump decay classes) had a positive effect on species richness and incidence-based dissimilarity (Jaccard), while the diversity in the volume of stumps had instead a negative effect on the dominance index (Simpson). This suggests that greater diversity in deadwood structures increases the number of available trophic niches, whereas deadwood homogeneity favours a few dominant species [78].

4.3.1. Effect of Tree Composition and Vertical Structure

Tree species composition was the most influential predictor of beetle diversity (Refs., [79,80]). This reflects the strong role of host tree identity (Ref., [73]), fir and beech, in providing a complementarity of substrates: beech contributes durable wood, hollows, and mould cavities, while silver fir provides resinous runs, stumps, and large volumes of coarse necromass. Together, these substrates supported dominant Curculionids but also a range of mycetophagous and xylophagous taxa. Vertical structure further promoted diversity (Ref., [81]): multistratified stands enhanced beta diversity, likely by buffering microclimatic variation and broadening resource availability (Ref., [74]). These results confirm that both tree diversity and vertical stratification sustain heterogeneous beetle assemblages.

4.3.2. Effect of Deadwood Dynamics

Deadwood quantity and diversity emerged as ambivalent drivers of beetle diversity. Beetle richness was strongly promoted by the diversity of downed deadwood volume across decay classes (Ref., [73]), demonstrating the ecological value of a mosaic of decomposition stages [24,82]. Conversely, higher volumes of uniform substrates such as downed deadwood or standing dead trees were negatively associated with beetle richness, suggesting that resource concentration favours a few dominant species. Simpson beetle diversity was positively affected by coarse woody debris and snag volume, but was negatively associated with microhabitats linked to mechanical injuries. For beta diversity, the number and distribution of coarse woody debris pieces, as well as downed deadwood, contributed significantly to dissimilarity [82]. These results highlight that while substrate heterogeneity sustains beetle richness and turnover, accumulation of litter in uniform deadwood structures tends to reduce evenness of beetle communities.

Deadwood dynamics in Vallombrosa reflects both historical legacies and ecological dynamics. Silver fir plantations and beech stands in conversion to high forest, managed intensively for timber, reduced senescent wood and thus limited substrate diversity for beetles. On the other hand, mixed silver fir–beech forests derived from natural dynamics provided greater variability and supported rare beetle species. Furthermore, broadleaf deadwood decays relatively fast [61], which explains the scarcity of advanced decomposition stages. This condition may limit the presence of highly specialized beetles, although the coexistence of different decay classes still ensures a heterogeneous resource base.

4.3.3. Effect of Tree-Related Microhabitats (TreMs)

TreMs were among the strongest predictors of beetle alpha diversity. Trunk and mould cavities, bark pockets, bark structures, epiphytic cryptogams and phanerogams, and root buttress cavities were all positively associated with beetle diversity indices, confirming their role in increasing stand complexity which contributes to species coexistence and functional diversity [83]. Negative associations were also evident: cracks and scars, nests, and resin flows were linked to lower beetle diversity, likely because they attract opportunists or predators that skew beetle assemblage structure. In beta diversity models, dendrotelms, water-filled holes, cankers, and burrs contributed significantly to explaining species turnover. This demonstrates that TreMs shape both local beetle richness and inter-stand dissimilarity, albeit with variable effects depending on the TreM type and forest type [14,62,84].

In Vallombrosa, TreMs showed not only high abundance but also high variability among plots, contrasting with the homogeneous distribution typical of managed forests [85]. This heterogeneity likely reflects the irregular production of microhabitats due to disturbances and the legacy of old, large trees and snags, which are particularly rich in cavities and decay features [86,87]. Moreover, the prevalence of microhabitats on deadwood components supports the tight functional link between TreMs and saproxylic guilds, especially xylophagous beetles, which benefit from exposed sapwood and heartwood [88,89].

4.4. Conservation and Management Implications

The joint influence of fine-scale predictors (tree species identity, TreMs, deadwood diversity) and stand-scale features (basal area, stump abundance, vertical layers) in shaping beetle alpha and beta diversity patterns underscores the need for multi-scale and landscape level conservation approaches [66,90]. At the stand level, actions should prioritize the preservation of large senescent trees, continuity of cavity- and bark-associated microhabitats, and a balanced representation of deadwood across decay classes [91]. At the landscape level, beta diversity patterns highlight the importance of spatial heterogeneity: promoting mixed stands, age-class diversity, and uneven-aged structures will enhance turnover and buffer against homogenization (Ref., [92]).

Importantly, a considerable share of the beetle fauna recorded in Vallombrosa is included in the Italian Red List, including Threatened and Near Threatened species. This confirms the role of Vallombrosa as a hotspot of saproxylic conservation value in the Apennines. Management should therefore move beyond simple retention of deadwood volumes and aim for structural diversity in both substrates and microhabitats, aligning forest operations with the concept of systemic forestry [33,93] to ensure the continuity of ecological resources over time.

The presence of numerous threatened beetle species reinforces their value as indicators of forest naturalness and highlights the importance of adaptive management strategies to sustain saproxylic diversity under ongoing environmental change [40]. Particularly in Mediterranean mountain forests, where deadwood volumes are often lower than in central European reserves, maintaining substrate variability and microhabitat richness is essential to secure rare and specialized taxa [19,94].

5. Conclusions

This study demonstrates that beetle diversity in the Vallombrosa Nature Reserve is jointly determined by stand-level structure and landscape-scale forest heterogeneity. Field data identified abundant deadwood, diverse tree-related microhabitats (TreMs), and the complementary presence of silver fir and beech as principal resources sustaining saproxylic assemblages. Although communities were numerically dominated by a few generalist species, the occurrence of numerous threatened taxa underscores the high conservation value of these forests.

Model results indicate that alpha diversity is chiefly driven by fine-scale predictors, i.e., tree composition, TreM diversity, and deadwood heterogeneity, whereas beta diversity responds primarily to stand structural attributes, deadwood legacies, and habitat heterogeneity at broader scales. Structurally diverse deadwood and TreMs enhanced species richness. Conversely, when deadwood and microhabitats were concentrated in uniform substrates or repetitive features, assemblages showed increased dominance by a few taxa and reduced community heterogeneity.

Conservation of beetle diversity in Vallombrosa therefore depends on maintaining large senescent trees, a diversity of TreMs, and a mosaic of deadwood types and decay stages. Management should prioritize structurally diverse, mixed stands, retention of legacy trees, and heterogeneity in deadwood size, position, and decay. These actions, together with allowing natural disturbances to contribute to habitat diversification, aim to reconcile silvicultural objectives with biodiversity conservation in Mediterranean montane forests.

Author Contributions: Conceptualization, data curation, methodology, resources, roles/writing—original draft, writing—review and editing A.M.; investigation, methodology, resources, roles/writing—

original draft, writing—review and editing F.P.; supervision, writing—review and editing D.T. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Tree-related microhabitats classified for each tree according to the definition by Kraus et al. (2016) [38].

Tree-Related Microhabitats		
Form	**Head**	**Definition**
CV1- Woodpecker cavities	CV11	Cavity entrance about ø = 4 cm
	CV12	Cavity entrance about ø = 5–6 cm
	CV13	Cavity entrance width is about ø > 10 cm
	CV14	Cavity entrance width is about ø $\geq$ 10 cm
	CV15	At least three in the trunk connected woodpecker breeding cavities
CV2- Trunk and mould cavities	CV21	Mould containing trunk cavity with ground contact about ø $\geq$ 10 cm
	CV22	Mould containing trunk cavity with ground contact about ø $\geq$ 30 cm
	CV23	Mould containing trunk cavity without ground contact about ø $\geq$ 10 cm
	CV24	Mould containing trunk cavity without ground contact about ø; $\geq$, 30; cm,
	CV25	Semi-open trunk cavity with or without mould about ø $\geq$ 30 cm
	CV26	Large trunk cavity with open top and with or without ground contact about ø $\geq$ 30 cm

Table A1. *Cont.*

Tree-Related Microhabitats		
Form	**Head**	**Definition**
CV3- Branch holes	CV31	Rot-holes originating from branch breakage at trunk about ø ≥ 5 cm
	CV32	Rot-holes originating from branch breakage at trunk about ø ≥ 10 cm
	CV33	Hollow more or less horizontal branch about ø ≥ 10 cm
CV4- Dendrotelms and water-filled holes	CV41	Cup-shaped concavities to trunk base with the entrance diameter about ø ≥ 3 cm
	CV42	Cup-shaped concavities to trunk base with the entrance diameter about ø ≥ 15 cm
	CV43	Cup-shaped concavities to crown with the entrance diameter about ø ≥ 5 cm
	CV44	Cup-shaped concavities to crown with the entrance diameter about ø ≥ 15 cm
CV5- Insect galleries and bore holes	CV51	Gallery with single small bore holes
	CV52	Gallery with single large bore hole about ø ≥ 2 cm
IN1- Bark loss/exposed sapwood	IN11	Bark loss 25–600 cm^2 and decay stage < 3
	IN12	Bark loss > 600 cm^2 and decay stage < 3
	IN13	Bark loss 25–600 cm^2 and decay stage = 3
	IN14	Bark loss > 600 cm^2 and decay stage = 3
IN2- Exposed heartwood/trunk and crown breakage	IN21	Broken trunk with the diameter at the end about ø ≥ 20 cm
	IN22	Broken tree crown/fork with exposed wood ≥ 300 cm^2
	IN23	Broken limb with the diameter at the end about ø ≥ 20 cm
	IN24	Splintered stem with the diameter at the end about ø ≥ 20 cm
IN3- Cracks and scars	IN31	Cleft through the bark with length ≥ 30 cm, width > 1 cm, depth > 10 cm
	IN32	Cleft through the bark with length ≥ 100 cm, width > 1 cm, depth > 10 cm
	IN33	Bark loss and crack caused by lightning
	IN34	Fire scars at the lower trunk ≥ 600 cm^2
BA1- Bark pockets	BA11	Bark shelter with width > 1 cm, depth > 10 cm, height > 10 cm
	BA12	Bark pocket with width > 1 cm, depth > 10 cm, height > 10 cm
BA2- Bark structure	BA21	Coarse bark
DE1- Dead branches and limbs/crown deadwood	DE11	Decaying wood ø 10–20 cm, ≥50 cm, sun exposed
	DE12	Decaying wood ø > 20 cm, ≥50 cm, sun exposed
	DE13	Decaying wood ø 10–20 cm, ≥50 cm, not sun exposed
	DE14	Decaying wood ø > 20 cm, ≥50 cm, not sun exposed
	DE15	Decaying wood with dead top ø ≥ 10 cm

Table A1. *Cont.*

Tree-Related Microhabitats		
Form	**Head**	**Definition**
GR1- Root buttress cavities	GR11	Natural cavity formed by the tree roots ø ≥ 5 cm
	GR12	Natural cavity formed by the tree roots ø ≥ 10 cm
	GR13	Trunk cleavage with length ≥ 30 cm
GR2- Witches broom	GR21	Dense agglomeration of twigs ø > 50 cm
	GR22	Dense agglomeration of shoots on the trunk or branches of a tree
GR3- Cankers and burrs	GR31	Cancerous growth ø > 20 cm
	GR32	Decayed canker ø > 20 cm
EP1- Fruiting bodies fungi	EP11	Annual polypores ø > 5 cm
	EP12	Perennial polypores ø > 10 cm
	EP13	Pulpy agaric ø > 5 cm
	EP14	Large ascomycetes ø > 5 cm
EP2- Myxomycetes	EP21	Myxomycetes ø > 5 cm
EP3- Epiphytic crypto- and phanerogams	EP31	Epiphytic bryophytes coverage > 25%
	EP32	Epiphytic foliose and fruticose lichens coverage > 25%
	EP33	Lianas coverage > 25%
	EP34	Epiphytic ferns > 5 fronds
	EP35	Mistletoe
NE1- Nests	NE11	Large vertebrate nest ø > 80 cm
	NE12	Small vertebrate nest ø > 10 cm
	NE21	Invertebrate nest
OT1- Sap and resin run	OT11	Sap flow > 50 cm
	OT12	Resin flow and pockets > 50 cm
OT2- Microsoil	OT21	Crown microsoil
	OT22	Bark microsoil

Table A2. List of the saproxylic and non-saproxylic beetle species sampled in the Nature Reserve of Vallombrosa.

Family	Species	IUCN Category	Trophic Category	Number of Specimens
Biphyllidae	*Diplocoelus fagi* (Chevrolat, 1837)	LC	SX (PR)	5
Bostrichidae	*Xylopertha retusa* (A.G.Olivier, 1790)	VU	XY	8
Buprestidae	*Anthaxia* (*Melanthaxia*) *helvetica* spp. *apennina* Obenberger, 1938	LC	XY	1
Cantharidae	*Cantharis decipiens* Baudi, 1871			6
Cantharidae	*Cantharis monacha* Moscardini, 1862			2
Cantharidae	*Dichelotarsus procerulus* (Kiesenwetter, 1860)			1
Cantharidae	*Malthinus glabellus* Kiesenwetter, 1852			3

Table A2. *Cont.*

Family	Species	IUCN Category	Trophic Category	Number of Specimens
Cantharidae	*Malthodes* sp.			1
Cerambycidae	*Alosterna tabacicolor* (De Geer, 1775)	LC	XY	12
Cerambycidae	*Anaglyptus mysticus* (Linnaeus, 1758)	LC	XY	1
Cerambycidae	*Anastrangalia dubia* (Scopoli, 1763)	LC	XY	17
Cerambycidae	*Clytus arietis* (Linnaeus, 1758)	LC	XY	1
Cerambycidae	*Grammoptera ruficornis* (Fabricius, 1781)	LC	XY	29
Cerambycidae	*Leiopus femoratus* Fairmaire, 1859	NT	XY	30
Cerambycidae	*Mesosa nebulosa* (Fabricius, 1781)	LC	XY	2
Cerambycidae	*Molorchus minor* (Linnaeus, 1758)	LC	XY	1
Cerambycidae	*Obrium cantharinum* (Linnaeus, 1767)	NT	XY	5
Cerambycidae	*Phymatodes testaceus* (Linnaeus, 1758)	LC	XY	3
Cerambycidae	*Rhagium bifasciatum* Fabricius, 1775	LC	XY	6
Cerambycidae	*Rhagium inquisitor* (Linnaeus, 1758)	LC	XY	1
Cerambycidae	*Ropalopus insubricus* (Germar, 1824)	VU	XY	2
Cerambycidae	*Rutpela maculata* (Poda, 1761)	LC	XY	12
Cerambycidae	*Saperda scalaris* (Linnaeus, 1758)	LC	XY	1
Cerambycidae	*Stenurella bifasciata* (O.F.Müller, 1776)	LC	XY	19
Cerambycidae	*Stenurella melanura* (Linnaeus, 1758)	LC	XY	67
Cerylonidae	*Cerylon ferrugineum* Stephen, 1830	LC	MY	47
Cryptophagidae	*Cryptophagus scanicus* (Linneaus, 1758)	LC	MY	17
Cryptophagidae	*Cryptophagus* sp.			20
Chrysomelidae	*Galerucella* (*Neogalerucella*) *lineola* (Fabricius, 1781)			2
Cleridae	*Thanasimus formicarius* (Linneaus, 1758)	LC	PR	4
Cleridae	*Tillus elongatus* (Linneaus, 1758)			2
Cucujidae	*Pediacus dermestoides* (Fabricius, 1792)	NT	PR	8
Curculionidae	*Anisandrus dispar* (Fabricius, 1792)	LC	MY	202
Curculionidae	*Cryphalus piceae* (Ratzeburg, 1837)	LC	XY	4
Curculionidae	*Dryocoetes autographus* (Ratzeburg, 1837)	LC	XY	2
Curculionidae	*Dryocoetes villosus* (Fabricius, 1792)	LC	XY	1
Curculionidae	*Ernoporicus fagi* (Fabricius, 1798)	LC	XY	2704
Curculionidae	*Hylesinus crenatus* (Fabricius, 1787)	LC	XY	32
Curculionidae	*Ips cembrae* (Heer, 1836)	LC	XY	2
Curculionidae	*Lasiorhynchites* (*Coccygorrhynchites*) *sericeus* (Herbst, 1797)			1
Curculionidae	*Orchestes fagi* (Linneaus, 1758)			874
Curculionidae	*Phyllobius etruscus* Desbrochers, 1873			2
Curculionidae	*Pissodes* (*Pissodes*) *piceae* Illiger, 1807	LC	XY	2
Curculionidae	*Pissodes* (*Pissodes*) *pini* (Linnaeus, 1758)	LC	XY	2

Table A2. *Cont.*

Family	Species	IUCN Category	Trophic Category	Number of Specimens
Curculionidae	*Pityokteines curvidens* (Germar, 1824)	LC	XY	33
Curculionidae	*Platypus cylindrus* (Fabricius, 1792)	LC	XY	6
Curculionidae	*Polydrusus* (*Metallites*) *aeratus* (Gravenhorst, 1807)			60
Curculionidae	*Polydrusus impar* Des Gozis, 1882			2
Curculionidae	*Polygraphus poligraphus* (Linnaeus, 1758)	LC	XY	1
Curculionidae	*Scolytus intricatus* (Ratzeburg, 1837)	LC	XY	42
Curculionidae	*Tatianaerhynchites aequatus* (Linnaeus, 1767)			1
Curculionidae	*Trypodendron domesticum* (Linnaeus, 1758)	LC	MY	5
Curculionidae	*Trypodendron signatum* (Fabricius, 1792)	LC	XY	105
Curculionidae	*Xyleborinus saxesenii* (Ratzeburg, 1837)	LC	MY	4
Curculionidae	*Xyleborus monographus* (Fabricius, 1792)	LC	MY	66
Curculionidae	*Xylosandrus germanus* (Blandford, 1894)			2804
Elateridae	*Agriotes* (*Agriotes*) *acuminatus* (Stephens, 1830)			8
Elateridae	Agriotes (*Agriotes*) infuscatus Desbrochers des Loges, 1870			62
Elateridae	*Ampedus coenobita* (Costa, 1882)	NT	PR	5
Elateridae	*Ampedus elegantulus* (Schönherr, 1817)	VU	PR	3
Elateridae	*Ampedus erythrogonus* (O.F. Müller, 1821)	NT	PR	3
Elateridae	*Ampedus nemoralis* Bouwer, 1980	VU	PR	1
Elateridae	*Ampedus nigerrimus* (Boisduval & Lacordaire, 1835)	LC	PR	1
Elateridae	*Athous* (*Haplathous*) *subfuscus* (O.F. Muller,1767)			67
Elateridae	*Athous flavipennis* Candèze, 1860			2
Elateridae	*Athous vittatus* (Fabricius, 1792)			31
Elateridae	*Limonius minutus* (Linnaeus, 1758)			3
Elateridae	*Megathous nigerrimus* (Desbrochers des Loges, 1870)	EN	PR	52
Elateridae	*Nothodes parvulus* (Panzer, 1799)			232
Elateridae	*Stenagostus rhombeus* (A.G.Olivier, 1790)	VU	PR	18
Endomychidae	*Mycetina cruciata* (Schaller, 1783)	LC	MB	2
Eucnemidae	*Melasis buprestoides* (Linnaeus, 1760)	LC	SX	5
Erotylidae	*Triplax lacordairii* Crotch, 1870	NT	MB	1
Laemophloeidae	*Cryptolestes* (*Leptophloeus*) *alternans* (Erichson, 1846)	NT	PR (MY)	520
Laemophloeidae	*Notolaemus unifasciatus* (Latreille, 1804)	NT	MY	2
Lampyridae	*Luciola pedemontana* Motschulsky, 1853			8
Latridiidae	*Enicmus brevicornis* (Mannerheim, 1844)	LC	MY	4
Latridiidae	*Cartodere nodifer* (Westwood, 1839)	LC	MY	1
Latridiidae	*Stephostethus alternans* (Mannerheim, 1844)	LC	MY	1
Latridiidae	*Enicmus testaceus* (Stephens, 1830)	LC	MY	5
Lucanidae	*Sinodendron cylindricum* (Linnaeus, 1758)	LC	SX	2

Table A2. *Cont.*

Family	Species	IUCN Category	Trophic Category	Number of Specimens
Lycidae	*Dictyoptera aurora* (Herbst, 1784)	LC	MY	1
Lycidae	*Pyropterus nigroruber* (DeGeer, 1774)	LC	MY	3
Lymexylidae	*Elateroides dermestoides* (Linnaeus, 1761)	NT	XY (MY)	31
Lymexylidae	*Lymexylon navale* (Linnaeus, 1758)	NT	XY (MY)	12
Melandryidae	*Abdera* (*Abdera*) *biflexuosa* (Curtis, 1829)	NT	MY	2
Melandryidae	*Conopalpus testaceus* (A.G.Olivier, 1790)	NT	MY	1
Melandryidae	*Serropalpus barbatus* (Schaller, 1783)	NT	MY	29
Melyridae	*Aplocnemus* (*Aplocnemus*) *nigricornis* (Fabricius, 1792)	LC	PR	26
Melyridae	*Danacea* (*Danacea*) *ambigua* Mulsant & Rey, 1868			69
Melyridae	*Danacea cusanensis* (Costa, 1847)			7
Melyridae	*Dasytes* (*Mesodasytes*) *nigrocyaneus* Mulsant & Rey, 1868	LC	PR	1
Melyridae	*Dasytes* (*Mesodasytes*) *plumbeus* (O.F. Müller, 1776)	LC	PR	236
Melyridae	*Dasytes* (*Metadasytes*) *caeruleus* (De Geer, 1774)	LC	PR	11
Melyridae	*Trichoceble floralis* (A.G.Olivier, 1790)	VU	PR	2
Monotomidae	*Rhizophagus* (*Rhizophagus*) *bipustulatus* (Fabricius, 1792)	LC	MY (PR)	9
Monotomidae	*Rhizophagus* (*Rhizophagus*) *cribratus* Gyllenhal, 1827	DD	MY (PR)	2
Monotomidae	*Rhizophagus* (*Rhizophagus*) *dispar* (Paykull, 1800)	LC	MY (PR)	2
Monotomidae	*Rhizophagus* (*Rhizophagus*) *ferrugineus* (Paykull, 1800)	LC	MY (PR)	17
Monotomidae	*Rhizophagus* (*Rhizophagus*) *nitidulus* (Fabricius, 1798)	NT	MY (PR)	1
Monotomidae	*Rhizophagus* (*Rhizophagus*) *perforatus* Erichson, 1845	DD	MY (PR)	6
Mordellidae	*Mordellochroa milleri* (Emery, 1876)	CR	SX	1
Mordellidae	*Tomoxia bucephala* (A. Costa, 1854)	LC	SX	2
Mycetophagidae	*Mycetophagus quadripustulatus* (Linneaus, 1761)	LC	MY	18
Nitidulidae	*Cryptarcha strigata* (Fabricius, 1787)	LC	SF	17
Nitidulidae	*Epuraea aestiva* (Linnaeus, 1758)			3
Nitidulidae	*Epuraea fuscicollis* (Stephens, 1835)	LC	SF	5
Nitidulidae	*Epuraea melanocephala* (Marsham, 1802)	LC	MY	2
Nitidulidae	*Epuraea unicolor* (A.G.Olivier, 1790)	LC	SF	1
Nitidulidae	*Glischrochilus quadriguttatus* (Fabricius, 1776)	VU	SF	18
Nitidulidae	*Glischrochilus quadripunctatus* (Linnaeus, 1758)	NT	MY	6
Nitidulidae	*Meligethes fuscus* (Olivier, 1790)			1
Nitidulidae	*Soronia grisea* (Linnaeus, 1758)	LC	SF	1
Nitidulidae	*Teucriogethes obscurus* (Erichson, 1845)			1
Oedemeridae	*Nacerdes* (*Xanthochroa*) *carniolica* (Gistl, 1834)	LC	SX	25
Oedemeridae	*Oedemera flavipes* (Fabricius, 1792)			1
Ptinidae	*Ptinomorphus imperialis* (Linnaeus, 1767)	LC	XY	5

Table A2. *Cont.*

Family	Species	IUCN Category	Trophic Category	Number of Specimens
Pyrochroidae	*Pyrochroa coccinea* (Linnaeus, 1761)	LC	SX	3
Salpingidae	*Salpingus planirostris* (Fabricius, 1787)	LC	SX	187
Salpingidae	*Salpingus ruficollis* (Linnaeus, 1760)	NT	SX	134
Salpingidae	*Vincenzellus ruficollis* (Panzer, 1794)	LC	MY	5
Scraptiidae	*Anaspis lurida* Stephens, 1832	LC	SX	68
Scraptiidae	*Anaspis maculata* (Fourcroy, 1785)			56
Scraptiidae	*Anaspis nigripes* Brisout de Barneville, 1866			9
Scraptiidae	*Anaspis ruficollis* (Fabricius, 1792)	EN	SX	86
Scraptiidae	*Anaspis thoracica* (Linnaeus, 1758)			5
Silphidae	*Nicrophorus humator* (Gleditsch, 1767)			1
Silphidae	*Nicrophorus vespilloides* Herbst, 1783			1
Silvanidae	*Silvanoprus fagi* (Guèrin, 1844)	NT	SX (SF)	1
Staphylinidae	*Aleochara maculata* Brisout de Barneville, 1863			1
Staphylinidae	*Aleochara sparsa* Heer, 1839			273
Staphylinidae	*Amphichroum canaliculatum* (Erichson, 1840)			1
Staphylinidae	*Anthophagus* (*Phaganthus*) *fauveli caprai* Koch, 1933			1
Staphylinidae	*Atheta aeneicollis* (Sharp, 1869)			1
Staphylinidae	*Atheta fungi* (Gravenhorst, 1806)			2
Staphylinidae	*Atheta hybrida* (Sharp, 1869)			3
Staphylinidae	*Atheta* sp.			1
Staphylinidae	*Atheta* sp. pl.			8
Staphylinidae	*Atheta taxiceroides* Münster, 1932			14
Staphylinidae	*Atheta trinotata* (Kraatz, 1856)			2
Staphylinidae	*Atrecus affinis* (Paykull, 1789)	VU	PR	2
Staphylinidae	*Bisnius fimetarius* (Gravenhorst, 1802)			2
Staphylinidae	*Bolitobius cingulatus* Mannerheim, 1830			1
Staphylinidae	*Bryoporus multipunctus* Hampe, 1867			1
Staphylinidae	*Eusphalerum* (*Eusphalerum*) *signatum angulatum* (Luze, 1911)			746
Staphylinidae	*Eusphalerum italicum* (Koch, 1938)			5
Staphylinidae	*Eusphalerum luteum dispar* (Baudi di S, 1889)			1
Staphylinidae	*Eusphalerum montivagum vesubianum* Coiffait, 1959			1
Staphylinidae	*Eusphalerum rectangulum* (Baudi di Selve, 1870)			5
Staphylinidae	*Gabrius* sp.			1
Staphylinidae	*Haploglossa villosula* (Stephens, 1832)			2
Staphylinidae	*Lordithon lunulatus* (Linnaeus, 1760)			1
Staphylinidae	*Nehemitropia lividipennis* Mannerheim, 1830			1
Staphylinidae	*Ocalea* sp.			1

Table A2. *Cont.*

Family	Species	IUCN Category	Trophic Category	Number of Specimens
Staphylinidae	*Othius laeviusculus* Stephens, 1832			2
Staphylinidae	*Oxypoda brevicornis* (Stephens, 1832)			1
Staphylinidae	*Philonthus* (*Philonthus*) *carbonarius* (Gravenhorst, 1802)			1
Staphylinidae	*Philontus* sp.			1
Staphylinidae	*Phloeopora corticalis* (Gravenhorst, 1802)	LC	UN	35
Staphylinidae	*Phloeopora occidentalis* Lohse, 1984			4
Staphylinidae	*Phloeostiba plana* (Paykull, 1792)	LC	SX	23
Staphylinidae	*Placusa atrata* (Mannerheim, 1830)	LC	PR	1
Staphylinidae	*Placusa pumilio* (Gravenhorst, 1802)	LC	PR	10
Staphylinidae	*Placusa* sp.			1
Staphylinidae	*Platystethus nitens* (C.R.Sahlberg, 1832)			1
Staphylinidae	*Platystethus spinosus* Erichson, 1840			1
Staphylinidae	*Pselaphinae* gen. sp			1
Staphylinidae	*Quedius dilatatus* (Fabricius, 1787)			10
Staphylinidae	*Quedius humeralis* Stephens, 1832			3
Staphylinidae	*Quedius latialis* Gridelli, 1924			6
Staphylinidae	*Quedius lucidulus* Erichson, 1839			2
Staphylinidae	*Quedius mesomelinus* (Marsham, 1802)			34
Staphylinidae	*Quedius picipes* (Mannerheim, 1830)			1
Staphylinidae	*Quedius* sp.			1
Staphylinidae	*Rugilus rufipes* Germar, 1836			1
Staphylinidae	*Sepedophilus testaceus* (Fabricius, 1793)	LC	MY	1
Staphylinidae	*Stenus assequens* Rey, 1884			1
Staphylinidae	*Thamiaraea cinnamomea* (Gravenhorst, 1802)	LC	UN	45
Staphylinidae	*Thamiaraea hospita* (Märkel, 1845)	LC	UN	1
Staphylinidae	*Xantholininae*? gen. Sp. 1			1
Staphylinidae	*Zyras* (*Zyras*) *haworthi* (Stephens, 1832)			2
Tenebrionidae	*Diaperis boleti* (Linnaeus, 1758)	LC	MB	1
Tenebrionidae	*Isomira* sp.			95
Trogossitidae	*Nemozoma elongatum* (Linnaeus, 1760)	LC	PR	46
Zopheridae	*Colydium elongatum* (Fabricius, 1787)	LC	PR	32
Zopheridae	*Coxelus pictus* (Sturm, 1807)	LC	SX	147
Zopheridae	*Synchita undata* Guerin-Meneville, 1844	NT	SX	1

In particular, CR = Critically endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient. XY = xylophagous (also on healthy trees), SX = saproxylophagous (on dead wood and woody rotting material, including woodmould), PR = predator (as larvae and/or adults) of Sx/xy or of other saproxylic insects, MY = mycophagous (on hyphae of saproxylic fungi or yeasts, and myxomycetes, mostly under bark), MB = mycetobiontic on carpophora of large Polyporales and other fungi living on old trees and stumps, UN = undefined [18].

Table A3. Effects of predictors in explaining variation in alpha diversity and beta diversity indices from forest structural variables. Alpha diversity models include richness (q = 0), Shannon diversity (q = 1), and Simpson dominance (q = 2). Beta diversity models include Jaccard (q = 0), Horn (q = 1), and Morisita (q = 2) dissimilarity indices. In the alpha models, numeric values are the predictors' estimates, which can be either negative or positive, while for beta models numeric values are split sums and are always positive by definition.

Type of Predictor	Predictor Description	Predictor	α—Richness (q = 0) Model	α—Shannon (q = 1) Model	α—Simpson (q = 2) Model	β—Jaccard (q = 0) Model	β—Horn (q = 1) Model	β—Morisita (q = 2) Model
Intercept	Intercept	Intercept	3.06	2.06	−2.62	0.83	0.04	0.04
Space	Spatial eigenvector (alpha models)/Geographic distance (beta models)	PCNM1/ Geographic	-	-	-	0.09	0.33	0.33
Living wood	Tree species (fagus = 1, mixed = 2, abies = 3)	Species	0.15	3.49	2.60	-	0.08	-
Living wood	Tree age	age	-	-	−0.67	0.06	0.17	0.14
Living wood	Number of forest layers	layers	-	-	1.03	-	0.09	0.10
Living wood	Number of living trees per ha	N	-	-	−0.67	-	0.16	0.15
Living wood	Diameter of living trees per ha	D	-	-	−0.59	-	-	
Living wood	Basal area of living trees in m^2 per ha	BA	−0.06	-	-	0.19	0.22	0.22
Deadwood	Height of living tree in m	H	-	-	-	0.01	-	-
Deadwood	Volume of coarse woody debris per ha	Vcwd	-	-	1.21	-	-	-
Deadwood	Volume of downed deadwood per ha	Vdowned	−0.09	-	-	-	0.15	0.14
Deadwood	Volume of standing deadwood per ha	Vstanding	-	-	-	-	0.13	0.12
Deadwood	Volume of stumps per ha	Vstumps	-	1.21	-	0.10	0.12	0.12
Deadwood	Volume of snags per ha	Vsnags	-	-	0.68	-	-	-
Deadwood	Number of coarse woody debris pieces per ha	Ncwd	-	-	0.50	0.11	-	-
Deadwood	Number of dead standing trees per ha	Nstanding	−0.07	-	-	-	-	-
Deadwood	Number of stumps per ha	Nstumps	-	-	-	0.07	0.26	0.29
Deadwood	Number of snags per ha	Nsnags	-	-	−0.84	-	-	-
Deadwood	Diversity of coarse woody debris volume	Shannon_Vcwd	-	-	-	0.01	-	-
Deadwood	Diversity of stump deadwood volume	Shannon_Vst	-	-	−0.59	0.07	-	-
Deadwood	Diversity of downed deadwood volume	Shannon_Vddt	0.10	-	-	-	-	-
Deadwood	Diversity of stump volume	Shannon_Vst	-	-	−1.08	-	-	-
Microhabitat	Number of trunk and mould cavities per ha	CV2	-	1.60	1.11	-	-	-
Microhabitat	Number of dendrotelms and water-filled holes per ha	CV4	-	-	-	-	0.18	0.18
Microhabitat	Number of cracks and scars per ha	IN3	−0.07	-	-	0.04	-	-
Microhabitat	Number of bark pockets per ha	BA1	-	1.07	1.19	-	-	-
Microhabitat	Number of bark structures per ha	BA2	0.07	-	-	-	0.20	0.21

Table A3. *Cont.*

Type of Predictor	Predictor Description	Predictor	α—Richness (q = 0) Model	α—Shannon (q = 1) Model	α—Simpson (q = 2) Model	β—Jaccard (q = 0) Model	β—Horn (q = 1) Model	β—Morisita (q = 2) Model
Microhabitat	Number of root buttress cavities per ha	GR1	0.05	-	−0.52	-	-	-
Microhabitat	Number of cankers and burrs per ha	GR3	-	-	-	0.06	0.09	0.09
Microhabitat	Number of epiphytic crypto- and phanerogams per ha	EP3	-	1.02	0.47	0.05	-	-
Deadwood	Number of nests per ha	NE	-	-	−0.78	-	-	-
Deadwood	Number of sap and resin runs per ha	OT1	-	-	−0.73	-	-	-

Table A4. Values for the observed (O) and expected (E) Moran's index (I) defining the level of spatial autocorrelation of the residuals of the GLMS and GDMs. The Number of Nearest Neighbours (k) was set at 4 for all the models. The *p*-values correspond to tests of spatial autocorrelation; $p > 0.05$ indicates that spatial autocorrelation is not statistically significant, suggesting that residuals are spatially random and the models adequately account for spatial structure.

	α—Richness (q = 0) Model	α—Shannon (q = 1) Model	α—Simpson (q = 2) Model	β—Jaccard (q = 0) Model	β—Horn (q = 1) Model	β—Morisita (q = 2) Model
Moran's I (O)	0.060	0.042	−0.022	0.074	−0.045	−0.051
Moran's I (E)	−0.022	−0.022	−0.022	−0.022	−0.022	−0.022
p-value	0.182	0.242	0.500	0.142	0.601	0.628

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