



ELSEVIER

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Forest stand structure and coarse woody debris determine the biodiversity of beetle communities in Mediterranean mountain beech forests



Francesco Parisi^{a,b,*}, Michele Innangi^c, Roberto Tognetti^{b,d}, Fabio Lombardi^e, Gherardo Chirici^a, Marco Marchetti^f

^a GeoLAB - Laboratorio di Geomatica Forestale, Dipartimento di Scienze e Tecnologie Agrarie, Alimentari, Ambientali e Forestali, Università degli Studi di Firenze, Via San Bonaventura 13, 50145 Firenze, Italy

^b Dipartimento Agricoltura, Ambiente e Alimenti, Università degli Studi del Molise, Via De Sanctis, I-86100 Campobasso, Italy

^c Dipartimento di Scienze e Tecnologie Ambientali Biologiche e Farmaceutiche, Università della Campania "Luigi Vanvitelli", Via Vivaldi 43, 81100 Caserta, Italy

^d Project Centre on Mountain Forests (MOUNTFOR), Edmund Mach Foundation, Via E. Mach 1, 38010 San Michele all'Adige, Trento, Italy

^e Dipartimento di Agraria, Università Mediterranea di Reggio Calabria, Località Feo di Vito, 89122 Reggio Calabria, Italy

^f Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, 86090 Pesche, Isernia, Italy

ARTICLE INFO

Article history:

Received 30 January 2021

Received in revised form 27 April 2021

Accepted 13 May 2021

Available online xxx

Keywords:

Apennines

α -diversity

Coarse woody debris

Old-growth forests

Saproxyllic species

ABSTRACT

The relationships between structural complexity, deadwood abundance, microhabitat type and species-diversity indicators are excellent tools to monitor biodiversity in forest ecosystems.

In spite of their importance, correlations between structural traits and Coleoptera communities in Mediterranean mountain forests have only rarely been investigated. Consequently, the magnitude and direction of the relationships between forest traits and biodiversity indicators remain poorly understood. In this study, we analyzed whether biodiversity indices of saproxyllic and non-saproxyllic beetle communities could be influenced by stand structure, microhabitat type, and deadwood abundance in two protected beech forests located in the central and southern Apennines (namely Gran Sasso e Monti della Laga National Park, GSML, and Cilento, Vallo di Diano e Alburni National Park, CVDA). Standard measurements of forest structural traits and quantitative assessment of tree microhabitats and deadwood were carried out. Adult beetles were collected using window flight traps and emergence traps on decaying deadwood. The two beech forests were different in terms of both beetle communities and structural traits. A two-block partial least squares analysis 2B-PLS highlighted differences in biodiversity indices and structural traits between the two forest ecosystems. In GSML, we observed that biodiversity indices were positively correlated with the volume of coarse woody debris and the presence fungal infections, clefts into the sapwood, and woodpecker cavities, while more dominant beetle communities were found under denser canopy cover. In CVDA, Coleoptera abundance was positively correlated with the basal area and crown broken microhabitats. Our results point toward the relevance of ecological attributes in tracking changes in beetle biodiversity in specific forest contexts. In these protected Mediterranean mountain beech stands, in which the main forest management strategies have the primary objective of biodiversity conservation, we suggest to

* Corresponding author at: GeoLAB - Laboratorio di Geomatica Forestale, Dipartimento di Scienze e Tecnologie Agrarie, Alimentari, Ambientali e Forestali, Università degli Studi di Firenze, Via San Bonaventura 13, 50145 Firenze, Italy.

E-mail address: francesco.parisi@unifi.it (F. Parisi).

progressively increase the structural diversity and canopy dynamics, as well as the volume of coarse woody debris.

© 2021 The Authors. Published by Elsevier B.V.
CC_BY_4.0

1. Introduction

Forest biodiversity is currently under threat from climate and land-use changes, with negative impacts on adaptation and mitigation potentials (Hisano et al., 2018). Thus, the conservation of biological diversity is an important goal of sustainable forest management (Lindenmayer et al., 2000; Brunet et al., 2010), which represents a relevant factor influencing species richness and forest productivity. Accordingly, in relation to the applied measures, there can be either positive or negative effects on forest biodiversity (Kutnar et al., 2015), as different approaches to forest management could be applied for preserving ecological functions and providing ecosystem services. Insects are a key component in the provision, regulation and dynamics of many ecosystem services (Schowalter, 2013) and are involved in the four broad types of services defined by the Millennium Ecosystem Assessment (2003): (i) supply services; (ii) support services; (iii) regulatory services; and (iv) cultural services (Prather et al., 2013). There is a general lack of knowledge on the functional roles played by most species in nature (Hortal et al., 2015). Despite their enormous diversity, insects are often underrepresented in ecosystem studies, so their contribution to ecosystem functioning has been relatively less studied than other organisms such as plants (Schowalter, 2016). As a result, we often lack a complete understanding of the role of insects in many ecosystem processes that underlie ecosystem services (Boerema et al., 2017).

However, monitoring and testing the effectiveness of alternative management approaches to preserve forest biodiversity is challenging (Paillet et al., 2010). Determining status and tracking changes of forest biodiversity require the use of indicators, which help to measure and to monitor the threats to species occurrence and richness (e.g., saproxylic organisms), as well as the dynamics of stand and habitat structures (e.g., deadwood characteristics). Structural elements of forest stands are linked with habitat requirements of forest species (tree microhabitats) and can be used to assess the status of biodiversity in forest ecosystems (Michel and Winter, 2009; Winter and Möller, 2008; Ekström et al., 2021).

The loss of microhabitats is among the various factors that threaten biodiversity in forest ecosystems (Larrieu et al., 2018). These ecological niches include different structural characteristics of trees, which are habitats for several species, or guilds, to carry out their biological cycles, or exploit food resources (Winter and Möller, 2008). Usually, microhabitats are associated with a decrease in tree vitality caused by a combination of fungi, viruses, and bacteria (Larrieu and Cabanettes, 2012). However, microhabitats are useful in describing the level of forest naturalness, integrating structural complexity and diversity of deadwood (Michel and Winter, 2009).

Deadwood represents a typical structural key-component of forest ecosystems and species diversity (Müller and Büttler, 2010; Thorn et al., 2020a). Deadwood is a source of food for invertebrates (Siitonen, 2001) and a supporting substrate for bryophytes (Odor and Standovár, 2001) and lichens (Humphrey et al., 2002). It is pivotal in organic matter decomposition operated by a large community of bacteria and fungi (Sanderman and Amundson, 2003). The progression of deadwood decay provides nutrients and moisture that benefits many organisms (Bani et al., 2018; Parisi et al., 2018). In addition, a large variety of animals use deadwood substrates as a refuge, such as amphibians (Herbeck and Larsen, 1999) and small mammals (Williams-Guillén et al., 2016) or exploit it also for foraging, as in birds (Mikusinski and Angelstam, 1997; Innangi et al., 2019). Deadwood amount depends on numerous factors, including the intensity and type of silvicultural practices (Guby and Dobbertin, 1996). Managed stands are usually poor in deadwood amounts when compared to unmanaged forests (Paillet et al., 2015). However, deadwood amounts are also influenced by the frequency, intensity and type of natural disturbances (Thorn et al., 2020b).

In the mountainous areas of the northern Mediterranean basin, land-use abandonment led to the expansion of forest cover and the increase in the structural complexity of these forests. Nevertheless, deadwood amounts in these forest ecosystems, mainly dominated by *Fagus sylvatica* L. (beech), are still low, ranging between 5 and 40 m³ ha⁻¹, with percentages varying between 5% and 30% of the standing biomass (Forest Europe, 2015). By contrast, in some protected areas, where mature beech stands are dominant, the total amount of deadwood can even reach 150 m³ ha⁻¹ (Lombardi et al., 2012). Further investigations are needed to better understand the ecological relationships between the abundance and diversity of target species (e.g., saproxylic fauna) related to deadwood decomposition, the structural characteristics of the forest stand, and the habitat requirements of decomposers (Paillet et al., 2018).

The link between the complexity of forest stands and the abundance and diversity of saproxylic species has been recently highlighted in Mediterranean forests, confirming the effectiveness of the heterogeneity in these types of microhabitats for monitoring biodiversity (Parisi et al., 2020a; Pioli et al., 2018). It is also true that about 30% of the total biodiversity of a forest environment is linked to deadwood, reaching 50% in some taxonomic groups, such as beetles. In Europe, 4000 species of beetles are dependent on deadwood (Stokland et al., 2012) and they have a pivotal ecological role in assisting fungi and bacteria in the decomposition processes of organic matter and nutrient cycles (Parisi et al., 2018). However, many saproxylic organisms are under threat and the continuous availability of deadwood at a given site is essential for the survival of these species (Nieto and Alexander, 2010). Parisi et al. (2016) highlighted that the spatial distribution of deadwood with large diameters is particularly important for saproxylic species with limited dispersion capacities and with long biological cycles. The complex interactions in

the food network suggest that the loss of basic decomposers can influence the key processes of the whole forest ecosystem (Parisi et al., 2018).

Surveying sites of high conservation value rely on species lists (Rondinini and Chiozza, 2010). However, the assessment of the conservation value of forest areas based on species richness is challenging (Lachat et al., 2012), particularly for the complex communities of Mediterranean mountains. Beetles, especially saproxylic species, are considered promising indicators for assessing the proximity of European forests to near-natural conditions (Gossner et al., 2016; Lelli et al., 2019).

In this contribution we investigated the associations between the abundance and diversity of Coleoptera and the indicators of forest naturalness (i.e. stand structure, microhabitat type, and deadwood abundance) in mountain beech forests of two important national parks of Italy: Gran Sasso e Monti della Laga (GSML), and Cilento, Vallo di Diano e Alburni (CVDA). We expected that patterns of covariation could be found between beetle communities richer in species or higher in dominance and specific microhabitats. By evaluating patterns of abundance and richness of preferential microhabitats and cooccurring Coleoptera in unmanaged forests, we aimed at assessing whether and how the abundance and richness of specific microhabitats may influence the diversity of beetle communities, and if we might consider these relationships as ecological references in terms of biodiversity indicators in mountain beech forests. We believe that protected areas may help counteract species loss and habitat degradation, occurring in more-degraded Mediterranean environments.

2. Materials and methods

2.1. Study area

The study was conducted in two mountain areas located in the central and southern Apennines (Italy) (Fig. 1). The two sites are representative of montane beech and coniferous forests of the Mediterranean, Anatolian and Macaronesian regions (European Environment Agency, 2006), both located within the temperate bioclimatic region, humid-meso-temperate type.

The Gran Sasso e Monti della Laga National Park (GSML) covers approximately 149,000 ha in the central Apennines, between the Marche, Lazio and Abruzzo regions. Forests cover over 60% (about 87,000 ha) of the total protected area. The most widespread forest types are stands dominated by beech, sometimes with the occurrence of *Abies alba* Mill., *Ilex aquifolium* L. and *Taxus baccata* L. They extend mainly on the northern and eastern slopes of the Gran Sasso and the Monti della Laga mountains. Portions of old-growth forest also occur (Calamini et al., 2011).

The Cilento, Vallo di Diano e Alburni National Park (CVDA) is one of the largest protected areas in south-eastern Europe. It extends for over 181,000 ha, in the Campania region. It spreads from the Tyrrhenian sea level to 1899 m a.s.l. of the Cervati mountains, thus showing exceptional ecological interest due to its wide range of habitats and high levels of biodiversity (Marchetti et al., 2010). In fact, more than 1800 plant species are present, and the area is covered mainly by deciduous forests,

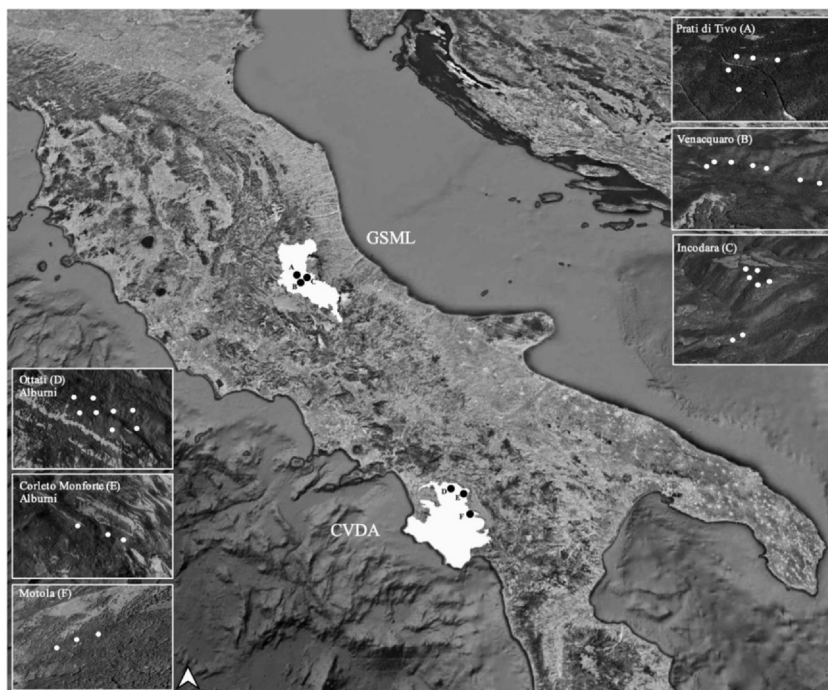


Fig. 1. The two national parks in central and southern Italy; black dots are the study sites selected in each park, while the white dots represent the location of the sampling plots realized for each investigated area.

Table 1
Main characteristics of the study areas (from Sabatini et al., 2016).

| National Park | Municipality (study area) | Coordinates (degrees) | Elevation (m a.s.l.) | Mean Annual Precipitation (mm) | Mean Annual Temperature (°C) | Extension of the area (ha) | Number of sampling plots |
|---------------|------------------------------|-----------------------|----------------------|--------------------------------|------------------------------|----------------------------|--------------------------|
| GSML | Pietracamela (Prati di Tivo) | 42.5096N 13.5679 E | 1500 | 1062 | 10.6 | 7.86 | 5 |
| | Pietracamela (Venacquaro) | 42.4988N 13.5139 E | 1250 | 1097 | 10.0 | 17.45 | 7 |
| | Crognaleto (Incodara) | 42.5123N 13.4735 E | 1400 | 1097 | 10.0 | 11.23 | 7 |
| | Corleto Monforte (Alburni) | 40.4705N 15.4317 E | 1300 | 1250 | 10.0 | 20.21 | 3 |
| CVDA | Ottati (Alburni) | 40.5136N 15.3292 E | 1350 | 718 | 13.6 | 11.82 | 8 |
| | Teggiano (Motola) | 40.3761N 15.4694 E | 1200 | 716 | 13.5 | 1.3 | 3 |

dominated by *Quercus cerris* L., *Q. pubescens* Willd., *Acer* sp. pl., *Ostrya carpinifolia* Scop., *Carpinus* sp. pl., *Fraxinus ornus* L. and *Castanea sativa* Mill. At higher elevations, over 1000 m a.s.l., beech forests are prevalent.

Two priority habitats of European interest according to the EU Habitats Directive (92/43/EEC) are in these areas: the habitat 9210* "Apennine beech forests with *Taxus* and *Ilex*" and the habitat 9220* "Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*". These beech forests are relatively species-rich both in the tree, in the shrub and herb layers. In each national park, three different beech forest stands were investigated (Table 1).

2.2. Living trees, deadwood and microhabitats survey

Three study sites were selected in each investigated national park, for a total of about 70 ha. We sampled 33 plots, 19 in GSML and 14 in CVDA (Table 1).

Two study sites located in the Cilento CVDA (i.e., 'Ottati' and 'Corleto Monforte'), belonging to the same Habitat type (habitat 9210*), were analysed together as "Alburni".

Each plot extended 530 m²; the sampling protocol followed Lombardi et al. (2015). In detail, UTM-WGS84 coordinates (Zone 32T) and elevation (m a.s.l.) were recorded in each plot using a Juno SB Global Positioning System (GPS) (Trimble, Sunnyvale, California). All living trees (minimum diameter at breast height ≥ 10 cm) were sampled, recording stem diameter at breast height (DBH), height, and species of each tree, and canopy cover. Deadwood was also surveyed. In detail, dead downed trees, snags, coarse woody debris (CWD) and stumps were sampled, measuring their length/height, minimum (≥ 5 cm) and maximum diameter and recording the species, when possible (Table 2).

The volume of living trees and standing and dead downed trees was calculated by double-entry volume equations (Tabacchi et al., 2011), while the volume of snags, CWD and stumps were calculated through the cone trunk formula (Lombardi et al., 2012). We also surveyed a set of 15 tree-related microhabitats that were present in the same sample plots (Table 3). These microhabitats are linked to the forest components on which they were found (living trees or deadwood components, e.g., dead branches, stem cavities, cracked and loose bark, fruiting bodies, crown substitute or secondary, mold pockets) and were classified according to Winter and Möller (2008).

2.3. Beetle trapping

In the same 33 plots where the structural characteristics of the forest were measured, the capture of both saproxylic and non-saproxylic adult beetles was carried out. Sampling of beetle fauna was carried out using two methods: window flight traps for flying beetles and emergence traps for beetles moving on the surface of dead trunks/branches or emerging from deadwood at different stages of decay. Traps were checked approximately every 30 days, for a total of four surveys in 2016 (from June to

Table 2
Tree variables used for the statistical analysis.

| Variable | Unit of measurement | Acronym |
|----------------------------|---------------------------------|---------|
| Living trees volume | m ³ ha ⁻¹ | VOL/ha |
| Basal area | m ² ha ⁻¹ | G/ha |
| Canopy cover | % | Canopy |
| Coarse woody debris volume | m ³ ha ⁻¹ | CWD |
| Volume of stumps | m ³ ha ⁻¹ | Stumps |

Table 3

Definition and description of the type of microhabitat used for statistical analysis following Winter and Möller (2008).

| Microhabitat type | Definition |
|-------------------|---|
| M1 | Living trees with fruiting bodies of <i>Fomes fomentarius</i> (L. ex Fr.) Fr. |
| M2 | Living trees with fruiting bodies of <i>Fomitopsis pinicola</i> (Swartz ex Fr.) Karst. |
| M3 | Other fungal infections: living trees with fruiting bodies (for instance <i>Pleurotus ostreatus</i> (Jacq. ex Fr.) Kummer, obvious infections like <i>Inonotus obliquus</i> (Bolton: Fries) Pilát). Fruiting bodies were > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies |
| M4 | < 50% of the crown broken: significant loss of a part or parts of the crown. One or more main branches are lost. The remaining crown seems to be ≥50% of the former crown |
| M5 | ≥50% of the crown broken: several main branches are broken. The remaining crown seems to be < 50% of the former crown |
| M7 | Broken stem: the crown is totally absent. Underneath the fracture, some very small living twigs have remained. This microhabitat type can develop into a substitute crown (M8) |
| M9 | Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood |
| M10 | Crack: cleft into the sapwood > 50 cm long along the stem and at least 2 cm deep in the sapwood |
| M12 | Cavities with > 5 cm aperture: (A) entrance of a Black Woodpecker <i>Dryocopus martius</i> cavity, (B) entrance of a Green Woodpecker <i>Picus viridis</i> cavity and (C) entrance at hollowed branch forms cavity in stem |
| M16 | Mould pockets: space between loose bark and the sapwood with a minimum extension of 5 cm × 5 cm × 2 cm |
| M18 | Canker: proliferation of cell growth; irregular cellular growth on stems or branches, which is caused by bark inhabiting fungi, viruses and bacteria. The healing of the bark by wound callus (Grunwald et al., 2002) fails as the pathogen colonizes the callus tissue of the bark. We recorded areas of canker ≥10 cm in diameter |
| M19 | Bark loss: patches with bark loss of at least 5 cm × 5 cm mainly caused by felling or natural falling of trees. At the stem base, bark losses are caused by moving logs. Bark losses are easily colonized by fungi and later by insects, which results in a loss of vitality of the whole tree within only a few years |
| M21 | System of galleries on deadwood (Scolytid activities) |
| M22 | Woody debris and/or stumps with saproxylic insect holes |
| M23 | Water-filled rot hole on stumps |

October). Emergence traps were emptied only once, at the end of the sampling period. All the monitoring systems were then removed during winter.

Systematics and nomenclature followed Bouchard et al. (2011) and Audisio et al. (2015). All the taxa collected during the field activities are alphabetically listed in Table A. Species strictly considered as saproxylic (*sensu*, Carpaneto et al., 2015) are also reported in Tables A, together with their risk category at the Italian level (see Audisio et al., 2015; Carpaneto et al., 2015).

2.4. Biodiversity and statistical analyses

Several diversity indices were computed, including the overall number of taxa (Taxa), the overall number of individuals (Individuals), Simpson's dominance index (Dominance), Shannon-Wiener entropy index (Shannon), Margalef richness index (Margalef), Pielou's evenness (Equitability), and Fisher's alpha diversity index. These indices are commonly used for investigating alpha diversity within biological communities (Harper, 1999). For a more synthetic description of the beetle community, the most representative 12 species among all sites were selected. We set a threshold of 2% for a Grand Weighted Mean (GWM) based on the percentage abundance of each taxon per sample (Ferraro et al., 2020). Given the total number of samples (33), a taxon *i*, the number of samples *j* where such taxon has at least one individual, the number of individuals *n* for each taxon and the overall number of individual N for each sample; then, the GWM was computed as follow:

$$GWM_i = \frac{\sum_j \left(\frac{n_{ij}}{N_j} \times 100 \right)}{33}$$

When needed, the overall statistical difference between GSML and CVDA was tested by means of a two-samples *t*-test (assuming unequal variances) or a Mann-Whitney *U*-test for normally distributed and count variables, respectively.

In order to assess the patterns of the co-variation between biodiversity indices and forest covariates (including microhabitats), we performed a two-block partial least squares analysis (2B-PLS). The two blocks were plots × biodiversity indexes and plots × forest structure and microhabitat type, respectively, and the analysis was done independently for GSML and CVDA. This statistical approach is well-suited for matrixes with comparatively low sample size and with highly correlated variables (Barker and Rayens, 2003; Carrascal et al., 2009). This statistical technique has been recently applied to several ecological studies, including forest ecosystems (Battipaglia et al., 2020; Innangi et al., 2019). 2B-PLS analysis finds latent variables that explain most of the covariance between two multivariate matrixes, returning variables that account as much as possible for the covariation between two sets of variables (Rohlf and Corti, 2000). The patterns of covariance between the two matrixes can be represented by a scatterplot for the first axis of the 2B-PLS, where the x-axis and the y-axis represent the two multivariate matrixes, respectively. These patterns of covariance can be interpreted using correlations, asserting patterns of positive or inverse correlation both within and between matrixes. All analyses were done in R 3.6.1 (R Core Team, 2019), using packages 'plsdepot' (Sanchez, 2012) and 'ggplot2' (Wickham, 2016).

3. Results

3.1. Forest structure and microhabitats

Measurements related to forest structure and microhabitat type are reported in [Table 4](#).

While both GSML and CVDA showed similar values of canopy cover and CWD volume (64.7 ± 3.4 vs. $61.4 \pm 4.2\%$ and 0.01 ± 0.004 vs. $0.01 \pm 0.008 \text{ m}^3 \text{ ha}^{-1}$, respectively), living tree volume in GSML was more than double than in Cilento (688.3 ± 48.6 vs. $331.1 \text{ m}^3 \text{ ha}^{-1}$, respectively). Additionally, GSML also showed higher basal area (61.8 ± 4.2 vs. $33.5 \pm 3.1 \text{ m}^2 \text{ ha}^{-1}$, respectively) and volume of stumps (0.35 ± 0.09 vs. $0.26 \pm 0.09 \text{ m}^3 \text{ ha}^{-1}$, respectively) than CVDA. In both areas, we found a large number of tree-related microhabitats on living trees (ca. 2002 vs. 1894 per ha, for GSML and CVDA, respectively). In detail, the most representative microhabitats were M21 (i.e., system of galleries on deadwood) and M22 (i.e., woody debris and/or stumps with saproxylic insect holes) for both the national parks, corresponding to the system of galleries on deadwood and woody debris and/or stumps with saproxylic insect holes, respectively.

For the remaining microhabitats, M3 (i.e., other fungal infections), M10 (i.e., cracks), and M12 (i.e., cavities with > 5 cm aperture) were generally more abundant in GSML, while M2 (i.e., living trees with fruiting bodies of *Fomitopsis pinicola*), M5 ($\geq 50\%$ of the crown broken), and M19 (i.e., bark loss) were more represented in CVDA.

3.2. Coleoptera communities

A total of 257 taxa were identified, namely 159 in GSML and 152 in CVDA. Among these taxa, 84 were shared between locations, while 75 and 98 taxa were found exclusively in GSML and CVDA, respectively. We found a fairly high contingent of saproxylic species included in the main IUCN risk categories: 22 species out of 72 in GSML; 22 species out of 52 in CVDA ([Table A](#)).

A list of 12 taxa that were all above the GWM threshold of 2% is reported in [Table 5](#).

All of these taxa occurred both in GSML and CVDA. Among these more abundant species, 50% were Elateridae, followed by Cerambycidae (17%). In general, the most abundant species was *Nothodes parvulus* (Elateridae), which accounted for 11% of the GWM.

In total, the communities of GSML were characterized by a relatively larger number of individuals when compared to CVDA (109 ± 14 vs. 97 ± 12 , respectively, Mann-Whitney U 91.5, $z = 1.5$, $p = 0.135$). The Simpson's dominance was significantly higher in GSML than in CVDA (0.14 ± 0.03 vs. 0.08 ± 0.01 , respectively, $t = 2.27$, $p = 0.034$). By contrast, all the other biodiversity indices were marginally higher in CVDA than in GSML, including the Pielou's evenness (0.86 ± 0.01 vs. 0.79 vs. 0.03 , respectively, $t = 2.09$, $p = 0.047$) ([Table 6](#)).

3.3. 2B-PLS analyses

The analyses put forward a separation between some locations in the upper-right quadrant (with Inc 4 & 5 at the extremes) compared to those in the lower-left quadrant (noticeably Ven 3 & 5) ([Fig. 2](#) and [Table 7](#)). The correlation within and between blocks showed that those locations with higher biodiversity indices (noticeably Shannon-Wiener, Margalef and Fisher's alpha indices) were positively correlated with higher volumes of CWD and the presence of M4 (i.e., $< 50\%$ of the crown broken). On the contrary, communities with higher Simpson's dominance were correlated with a higher canopy cover and the presence of M1 & M12 (i.e., Living trees with fruiting bodies of *Fomes fomentarius* and Cavities with > 5 cm aperture, respectively), albeit the correlations between the Forest Structure and Microhabitat type block were weaker if compared to the Biodiversity Indices block. As for CVDA ([Fig. 3](#) and [Table 7](#)), in GSML, the locations that segregated in the upper-left quadrant were led by all those from Motola plus Alb 100, while in the lower-right quadrant Alb 68 and 69 were found.

Once again, the driving variables from the Biodiversity Indices block were all measures of diversity, yet the most important ones, in this case, were the Margalef biodiversity index and the number of taxa. Noticeably, in CVDA, the number of individuals was also on the positive side of the correlation axis, while in GSML it was on the negative side. M5 (i.e., $\geq 50\%$ of the crown broken) was clearly positively correlated with the aforementioned biodiversity indices, followed again by M4, while CWD was less important. Again, Simpson's dominance was the most important indicator on the opposite site of the correlations yet with a weaker effect compared to GSML. Remarkably, M2 (i.e., Living trees with fruiting bodies of *Fomitopsis pinicola*) was the leading variable in covariation with communities with lower diversity and higher dominance. Most of the other Forest Structure and Microhabitat Type variables did not show a remarkable effect in explaining patterns of covariance neither within nor between locations.

Table 4
Forest structure and microhabitat type in GSML and CVDA.

| | GSML | | | | | | | | | | | | | | | CVDA | | | | | | | | | | | | | | | | | | | |
|------------------|----------|-------|-------|-------|-------|---------------|-------|-------|-------|-------|-----------|-------|-------|-------|-------|---------|-------|-------|-------|-------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| | Incodera | | | | | Prati di Tivo | | | | | Venacuaro | | | | | Alburni | | | | | Molida | | | | | | | | | | | | | | |
| | In_1 | In_2 | In_3 | In_4 | In_5 | In_6 | In_7 | In_8 | In_9 | In_10 | In_11 | In_12 | In_13 | In_14 | In_15 | In_16 | In_17 | In_18 | In_19 | In_20 | In_21 | In_22 | In_23 | In_24 | In_25 | In_26 | In_27 | In_28 | In_29 | In_30 | In_31 | In_32 | In_33 | In_34 | In_35 |
| Forest Structure | 617 | 400 | 778 | 434 | 770 | 1086 | 659 | 770 | 748 | 840 | 590 | 451 | 1007 | 900 | 562 | 624 | 882 | 694 | 266 | 140 | 427 | 659 | 553 | 240 | 234 | 194 | 183 | 756 | 222 | 133 | 245 | 243 | 316 | | |
| YOL_ba | 56 | 37 | 73 | 42 | 71 | 102 | 68 | 61 | 65 | 72 | 50 | 37 | 76 | 78 | 54 | 56 | 84 | 65 | 29 | 21 | 45 | 42 | 37 | 19 | 31 | 23 | 27 | 58 | 27 | 20 | 32 | 43 | 44 | | |
| Clba | 80 | 70 | 40 | 45 | 70 | 75 | 40 | 65 | 55 | 50 | 80 | 70 | 75 | 85 | 80 | 75 | 60 | 45 | 70 | 60 | 55 | 80 | 50 | 60 | 35 | 80 | 85 | 50 | 50 | 70 | 40 | 75 | | | |
| CVD | 0.014 | 0.027 | 0.005 | 0.064 | 0.030 | 0.002 | 0.064 | 0.005 | 0.007 | 0.002 | 0.003 | 0.006 | 0.006 | 0.004 | 0.001 | 0.000 | 0.009 | 0.001 | 0.002 | 0.002 | 0.006 | 0.002 | 0.001 | 0.001 | 0.014 | 0.003 | 0.001 | 0.001 | 0.000 | 0.001 | 0.024 | 0.119 | 0.005 | | |
| Stamps | 0.014 | 0.016 | 0.044 | 0.306 | 0.562 | 0.126 | 0.090 | 1.629 | 0.537 | 0.245 | 0.165 | 0.011 | 0.614 | 0.211 | 0.260 | 0.142 | 0.445 | 0.447 | 0.747 | 0.424 | 0.072 | 0.000 | 0.000 | 0.766 | 0.117 | 0.071 | 0.070 | 0.589 | 0.317 | 0.074 | 0.000 | 1.160 | 0.005 | | |
| Microhabitats | M1 | - | 1 | - | 1 | - | 1 | - | - | - | - | - | - | 1 | - | - | 1 | - | 1 | 1 | - | - | - | - | - | 1 | - | 2 | - | 1 | - | - | - | - | |
| M2 | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | 3 | 4 | 2 | 1 | - | 1 | - | - | - | | |
| M3 | 2 | 4 | 1 | 1 | - | 1 | - | 2 | - | 1 | - | 3 | 2 | 1 | 1 | - | 2 | 3 | - | - | - | - | 2 | - | - | - | - | - | - | 1 | - | - | 1 | 2 | |
| M4 | 1 | 1 | - | - | 2 | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 2 | - | - | - | - | - | - | - | 1 | - | 2 | - | 1 | 2 | 1 | |
| M5 | - | - | 1 | 2 | 1 | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | 1 | 1 | 2 | - | - | - | - | - | - | - | 1 | - | 1 | 2 | 3 | |
| M7 | - | - | 1 | - | 1 | - | 1 | - | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | 1 | - | 2 | - | - | |
| M9 | 2 | 1 | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | 2 | 1 | - | |
| M10 | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | 1 | - | 1 | - | 2 | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | |
| M12 | - | - | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| M16 | 3 | 1 | - | - | 1 | - | 2 | 3 | 1 | - | 2 | 1 | 2 | - | 1 | - | 1 | 3 | 2 | 2 | 1 | 1 | 4 | - | 2 | 1 | - | 1 | - | 1 | - | 3 | 4 | 2 | 3 |
| M18 | 2 | 1 | 1 | - | 3 | 2 | 1 | 3 | 1 | 4 | 2 | - | 2 | 4 | - | 1 | 4 | 1 | - | - | 1 | - | - | - | - | 1 | - | 2 | 1 | 2 | 1 | - | 2 | - | 1 |
| M19 | - | - | - | - | 2 | - | 2 | - | - | 1 | - | 1 | 1 | - | 1 | 2 | - | 1 | - | 3 | 1 | - | 2 | 1 | - | 3 | - | 2 | - | 1 | 3 | - | 2 | - | |
| M21 | 9 | 11 | 8 | 4 | 9 | 15 | 13 | 6 | 9 | 6 | 11 | 4 | 7 | 7 | 6 | 4 | 9 | 11 | 13 | 8 | 6 | 5 | 9 | 15 | 7 | 5 | 8 | 9 | 19 | 6 | 9 | 13 | 9 | | |
| M22 | 7 | 12 | 10 | 7 | 18 | 11 | 10 | 4 | 12 | 15 | 13 | 9 | 14 | 11 | 4 | 6 | 6 | 8 | 13 | 11 | 8 | 7 | 2 | 4 | 9 | 13 | 7 | 8 | 12 | 5 | 12 | 9 | 2 | | |
| M23 | 2 | - | - | 1 | - | - | - | 1 | - | 1 | - | 1 | 1 | - | 1 | - | 1 | 2 | - | 1 | 1 | - | - | - | - | 1 | - | 1 | - | 1 | - | 1 | 1 | - | |

Table 5
Absolute abundance for the 12 beetle species that were above the 2% threshold of the GWM, in GSML and CVDA.

| Family | Species | Gran Sasso | | | | | | | | | | | | Cilentò | | | | | | | | | | | | | | | | | | | | | |
|----------------|------------------------------|------------|-------|-------|-------|-------|-------|---------------|--------|--------|--------|--------|--------|-------------|-------|-------|-------|-------|-------|---------|-------|-------|-------|-------|-------|--------|-------|----|----|----|----|----|-----|-----|---|
| | | Incodara | | | | | | Prati di Tivo | | | | | | Venoscquaro | | | | | | Alburni | | | | | | Mofola | | | | | | | | | |
| | | Inc.1 | Inc.2 | Inc.3 | Inc.4 | Inc.5 | Inc.6 | Prat.1 | Prat.2 | Prat.3 | Prat.4 | Prat.5 | Prat.6 | Ven.1 | Ven.2 | Ven.3 | Ven.4 | Ven.5 | Ven.6 | Alb.1 | Alb.2 | Alb.3 | Alb.4 | Alb.5 | Alb.6 | Mof.1 | Mof.2 | | | | | | | | |
| Elaeteridae | <i>Neohodes porvulus</i> | 1 | 4 | 2 | - | 1 | 1 | 1 | 2 | 8 | 4 | 5 | - | 24 | 32 | 106 | 54 | 120 | 31 | 76 | 14 | 47 | - | 2 | - | - | - | 1 | 3 | 2 | - | 4 | 2 | 4 | |
| Melyridae | <i>Dasytes plumbeus</i> | - | 4 | 5 | 8 | 1 | 6 | 6 | 35 | 6 | 16 | 8 | 7 | 12 | 14 | 11 | 15 | 28 | 8 | 3 | 3 | 3 | 2 | 2 | 8 | 6 | 7 | 2 | 3 | 2 | - | 56 | 13 | 18 | |
| Trogosinidae | <i>Nemocoma elongatum</i> | - | 19 | 7 | 28 | 6 | 6 | 13 | - | 2 | 1 | 1 | 3 | 16 | 21 | 40 | 1 | - | 3 | 14 | 4 | 2 | 1 | - | - | - | 1 | 6 | 6 | 1 | 2 | - | - | 2 | |
| Elaeteridae | <i>Dalopius marginatus</i> | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 13 | 10 | 12 | 13 | 10 | 17 | 10 | 18 | 3 | 7 | 10 | 5 | 8 | |
| Cerambycidae | <i>Semaneilla melanoza</i> | 1 | 13 | 8 | 16 | 1 | 2 | 65 | - | - | - | - | - | 9 | 47 | 10 | 12 | 5 | 37 | 17 | - | - | - | - | - | - | - | - | - | - | - | 5 | 2 | 1 | |
| Cerambycidae | <i>Phyllobius argentatus</i> | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 8 | 6 | 4 | 3 | 7 | 9 | 8 | 3 | 13 | 8 | 1 | 5 | 7 | |
| Elaeteridae | <i>Abonus komarzhinskii</i> | - | 4 | 2 | 3 | 6 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 4 | 6 | 2 | 2 | 4 | 1 | 1 | 3 | 1 | - | 4 | 2 | 1 | 1 | 2 | 3 | 1 | 1 | 5 | 1 | 7 | 5 |
| Tenebrionidae | <i>Isometis muricata</i> | - | 1 | - | 2 | 1 | 1 | 2 | - | 8 | 4 | 2 | 1 | 1 | - | - | - | 1 | 1 | - | 3 | - | 1 | 7 | 3 | 3 | 3 | 4 | 1 | 2 | 4 | 10 | 4 | 5 | |
| Elaeteridae | <i>Agonius affinis</i> | 1 | 1 | 6 | 9 | 2 | 3 | 2 | 1 | 1 | 1 | - | - | 4 | 3 | 2 | 1 | - | 3 | - | 2 | 9 | 1 | 1 | - | - | 5 | 5 | 4 | 3 | 4 | 1 | 1 | 1 | |
| Elaeteridae | <i>Abonus subfuscus</i> | 4 | 8 | 1 | 4 | 3 | 2 | - | 2 | 1 | 3 | - | - | - | 3 | - | 4 | - | 2 | 4 | - | 4 | 3 | 1 | - | 1 | - | 2 | 10 | - | 1 | - | 5 | 3 | |
| Cerambycidae | <i>Semaneilla senilis</i> | - | 2 | 3 | 3 | - | - | 16 | - | - | - | - | - | 6 | 25 | 3 | 11 | 8 | 14 | 14 | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | |
| Elaeteridae | <i>Melampus villosus</i> | 6 | - | - | 2 | 2 | - | 1 | 2 | - | - | 5 | - | 2 | 2 | 1 | - | 1 | - | 1 | 2 | 2 | - | 3 | 2 | 2 | 2 | 1 | - | - | 3 | 3 | 7 | 2 | |
| All other taxa | | 46 | 20 | 40 | 60 | 34 | 46 | 30 | 23 | 24 | 12 | 30 | 16 | 67 | 65 | 23 | 47 | 16 | 53 | 37 | 58 | 49 | 48 | 36 | 54 | 22 | 18 | 30 | 17 | 23 | 20 | 99 | 106 | 109 | |

Table 6
Biodiversity indices for the beetle communities in GSML and CVDA.

| Diversity Index | Gran Sasso | | | | | | | | | | | | | | | Cilento | | | | | | | | | | | | | | | | | | | |
|-----------------|------------|--------|--------|--------|--------|---------------|--------|--------|--------|---------|------------|---------|---------|---------|---------|---------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|---------|--------|--------|--------|--------|--------|
| | Incodara | | | | | Prati di Tivo | | | | | Venacquaro | | | | | Alburni | | | | | Motola | | | | | | | | | | | | | | |
| | Inc. 1 | Inc. 2 | Inc. 3 | Inc. 4 | Inc. 5 | Inc. 6 | Inc. 7 | Inc. 8 | Inc. 9 | Inc. 10 | Prat. 1 | Prat. 2 | Prat. 3 | Prat. 4 | Prat. 5 | Ven. 1 | Ven. 2 | Ven. 3 | Ven. 4 | Ven. 5 | Alb. 1 | Alb. 2 | Alb. 3 | Alb. 4 | Alb. 5 | Alb. 6 | Alb. 7 | Alb. 8 | Alb. 9 | Alb. 10 | Mot. 1 | Mot. 2 | Mot. 3 | Mot. 4 | Mot. 5 |
| Taxa | 36 | 28 | 30 | 47 | 53 | 30 | 27 | 22 | 24 | 16 | 22 | 16 | 39 | 40 | 24 | 36 | 17 | 33 | 32 | 49 | 49 | 35 | 34 | 28 | 38 | 22 | 20 | 31 | 56 | 26 | 24 | 54 | 50 | 58 | 58 |
| Individuals | 60 | 76 | 75 | 136 | 57 | 69 | 143 | 37 | 82 | 32 | 61 | 33 | 142 | 210 | 201 | 146 | 167 | 174 | 175 | 94 | 137 | 76 | 70 | 84 | 84 | 53 | 69 | 72 | 81 | 51 | 52 | 191 | 158 | 165 | 165 |
| Dominance | 0.05 | 0.12 | 0.06 | 0.07 | 0.05 | 0.05 | 0.24 | 0.07 | 0.21 | 0.10 | 0.11 | 0.11 | 0.08 | 0.11 | 0.33 | 0.16 | 0.53 | 0.12 | 0.22 | 0.05 | 0.15 | 0.07 | 0.09 | 0.06 | 0.06 | 0.09 | 0.11 | 0.06 | 0.08 | 0.09 | 0.08 | 0.11 | 0.07 | 0.04 | 0.04 |
| Shannon | 3.3 | 2.7 | 3.0 | 3.2 | 3.2 | 3.2 | 2.2 | 2.9 | 2.3 | 2.6 | 2.6 | 2.5 | 3.0 | 2.7 | 1.7 | 2.6 | 1.2 | 2.6 | 2.3 | 3.6 | 2.6 | 3.1 | 2.8 | 3.2 | 3.2 | 2.7 | 2.5 | 3.1 | 3.1 | 2.9 | 2.9 | 3.1 | 3.3 | 3.3 | 3.6 |
| Margalef | 8.5 | 6.2 | 6.7 | 9.4 | 7.9 | 6.8 | 5.2 | 5.8 | 5.2 | 4.3 | 5.1 | 4.3 | 7.7 | 7.3 | 4.3 | 7.0 | 3.1 | 6.2 | 6.0 | 10.6 | 6.9 | 7.6 | 6.4 | 8.4 | 8.4 | 5.3 | 4.5 | 7.0 | 8.0 | 6.4 | 5.8 | 10.1 | 9.7 | 11.2 | 11.2 |
| Evenness | 0.92 | 0.80 | 0.90 | 0.84 | 0.93 | 0.94 | 0.67 | 0.93 | 0.71 | 0.92 | 0.85 | 0.89 | 0.81 | 0.73 | 0.54 | 0.72 | 0.43 | 0.75 | 0.66 | 0.91 | 0.74 | 0.87 | 0.85 | 0.89 | 0.88 | 0.85 | 0.90 | 0.85 | 0.86 | 0.89 | 0.90 | 0.77 | 0.84 | 0.89 | 0.89 |
| Fisher's alpha | 38 | 16 | 19 | 25 | 33 | 20 | 10 | 23 | 11 | 13 | 12 | 12 | 18 | 15 | 7 | 15 | 5 | 12 | 11 | 41 | 15 | 24 | 17 | 27 | 27 | 14 | 9 | 21 | 25 | 21 | 17 | 25 | 25 | 25 | 32 |

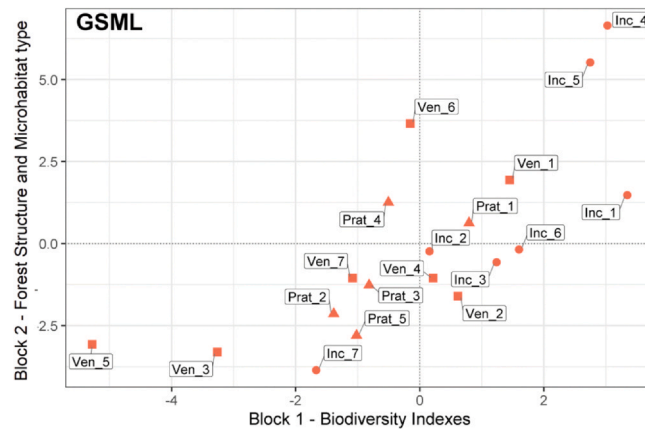


Fig. 2. Scatterplot of the first axis of the 2B-PLS for GSML. The x-axis represents biodiversity indices, while the y-axis represents forest structure and microhabitat type. The correlation within and between blocks is shown in Table 7.

Table 7

Correlations within and between blocks for the first axis of the 2B-PLS, with Block 1 corresponding to the x-axis in Figs. 3 and 4 (i.e., biodiversity indices), and Block 2 corresponding to the y-axis in Figs. 3 and 4 (i.e., forest structure and microhabitat type).

| GSML | | | CVDA | | |
|---------------------------|---------|----------------------------------|------------------------------|---------|--------------------------------------|
| | Block 1 | Block 2 | | Block 1 | Block 2 |
| Shannon | 1.0 | | Margalef & Taxa | 1.0 | |
| Fisher alpha's & Margalef | 0.9 | | Shannon | 0.9 | |
| Equitability | 0.8 | | Individuals & Fisher's alpha | 0.8 | |
| Taxa | 0.7 | | | 0.7 | M5 |
| | 0.6 | | | 0.6 | |
| | 0.5 | CWD | | 0.5 | M4 |
| | 0.4 | M4 | | 0.4 | CWD, M7 & M9 |
| | 0.3 | M7, M5 & M10 | | 0.3 | G/HA, Stumps, Canopy, M16, M19 & M23 |
| | 0.2 | M22 & M23 | | 0.2 | M3, M12 & M21 |
| | 0.1 | VOL/HA & M9 | | 0.1 | M18 |
| | 0.0 | G/HA, Stumps, M3, M16, M18 & M19 | | 0.0 | |
| | -0.1 | M2 & M21 | Equitability | -0.1 | M22 |
| | -0.2 | M1 & M12 | | -0.2 | M1 |
| | -0.3 | Canopy | | -0.3 | M10 |
| Individuals | -0.4 | | Dominance | -0.4 | |
| | -0.5 | | | -0.5 | |
| | -0.6 | | | -0.6 | |
| | -0.7 | | | -0.7 | M2 |
| | -0.8 | | | -0.8 | |
| Dominance | -0.9 | | | -0.9 | |
| | -1.0 | | | -1.0 | |

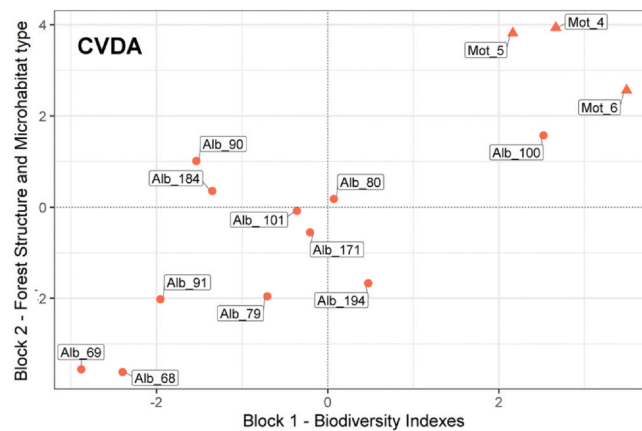


Fig. 3. Scatterplot of the first axis of the 2B-PLS for CVDA stand. The x-axis represents biodiversity indices, while the y-axis represents forest structure and microhabitat type. The correlations within and between blocks is shown in Table 7.

4. Discussion

In this study, the importance of forest biodiversity indicators was studied by analyzing the covariation between beetle communities and forest characteristics in two national parks. The beech forests here investigated have an old legacy of forest management, which has induced a reduction of the structural complexity, but also a simplification of the overall forest ecosystem, with negative effects on the abundance of the saproxylic communities (Bani et al., 2018; Parisi et al., 2018). The biodiversity indices (Dominance, Shannon, Margalef, Equitability and Fisher's alpha) were mainly related to the structural complexity of these forests and microhabitat abundance, although with differences between stands in the two protected areas.

Diversity indices showed quite similar and homogeneous diversity and specific richness values in GSML and CVDA. In particular, this was confirmed by nonsignificant differences in Shannon and Margalef indices, indicating a lack of similarity in the distribution of dominant species. However, the alpha diversity suggested differences in specific composition between the two protected areas. Regardless of the low diversity, a significant fraction of diversity was fully recovered in the different trophic categories found. Nevertheless, the covariance analysis indicated that beetle communities included both abundant and rare species. Therefore, the structure of the beetle community was not determined by the type of habitat, as the beech forests were similar in terms of fauna and vegetation.

From a quantitative point of view, the Elateridae family dominated for both areas, although with two different species that led the statistical analyses (*Nothodes parvulus* and *Dalopius marginatus*, for GSML and CVDA, respectively). *N. parvulus* species was the most abundant (22%). The abundance of the two taxa influenced the diversity analyses, as total individuals.

The main habitats related to beetle fauna did not show significant differences in terms of deadwood volume (m^3 , CWD and stumps) and abundance of microhabitats (see Table 4). CVDA showed a more even distribution in the number of species than GSML. This could be due to more stable environmental conditions, as confirmed by the biodiversity indices (Margalef and Taxa indices, Table 6). These features might guarantee the availability of bio-habitats over time and space for saproxylic fauna, promoting stability of the insect community.

In CVDA, the weak positive correlation between the abundance of beetles and the basal area was likely due to the absence of cutting activities, which created an un-even aged structure. Indeed, the value of the basal area (61.8 vs. $33.5 \text{ m}^2 \text{ ha}^{-1}$, for GSML and CVDA, respectively), is consistent with the control category (basal area greater than $29 \text{ m}^2 \text{ ha}^{-1}$) proposed by Keddy and Drummond (1996) for old-growth forests. Nevertheless, the long-lasting effects of past management still influence the actual forest structure (Lombardi et al., 2012). The relative structural homogeneity of these forests gave rise to a poor association of forest structure with beetle diversity (Parisi et al., 2016; Sabatini et al., 2016). We hypothesize that the absence of forest gaps and the forest continuity, resulting from the past forest management, but also the absence of differentiated forest development stages, induced an homogenization of microclimatic conditions. In fact, over 98% of the beetles sampled in this study belong to the same families (35 vs. 36 families, for GSML and CVDA, respectively). By contrast, spatial differentiation and vertical heterogeneity could be more easily observed in complex forest structures, such as in old-growth forests (Paillet et al., 2018), affecting light, moisture, and temperature, as well as other habitat characteristics required by beetle communities.

Several authors reported that forest management might affect saproxylic richness and distribution (Brin et al., 2009; Buse et al., 2010; Gibb et al., 2006; Lassaue et al., 2011; Siitonen, 2001; Parisi et al. 2019, 2020a). Studies on saproxylic beetles in European forests revealed that many species, often at high risk of extinction (Seibold et al., 2015), which are active on deadwood of large diameters and exposed to the sun, could be strongly influenced by forest management (Gossner et al., 2013; Parisi et al., 2020b). Yet, their abundance could be negatively affected by the increase of continuous canopy cover (Schall et al., 2017), but also by the loss of large veteran trees (Bauhus et al., 2009). In several protected beech forests in Central and Southern Italy,

saproxylic beetles ranged from 25% to 55% of the whole beetle fauna, typical of unmanaged forests in the Apennine mountain (Cocciufa et al., 2014; Parisi et al., 2020a).

The amount of CWD, the density of microhabitats occurring on living trees and canopy cover (visually estimated as %) significantly influenced the beetle communities in these beech forest stands. We observed variations between the beetle species that grow on deadwood in comparison with those occurring on the ground, on dead branches, or on fruiting bodies. Similar results were found in silver fir and beech forests of central Italy (Parisi et al., 2020a), where the volume of deadwood and the abundance of microhabitats were used as a predictive factor for beetles included in the IUCN red list.

In GSML, the most abundant microhabitats were those related to deadwood (i.e., fungal infections, clefts into the sapwood and woodpecker cavities). Whereas, in CVDA, microhabitats linked to living trees prevailed (i.e., living trees with fruiting bodies, crown broken and bark loss). However, some microhabitats M4 (i.e., < 50% of the crown broken) and M5 (i.e., ≥50% of the crown broken) positively influenced the diversity of beetles in both the study sites, suggesting a differentiation of ecological niches where specialized organisms occur which live in large trees with broken crown. We also observed how the most abundant microhabitats (i.e., system of galleries on deadwood, woody debris and/or stumps with saproxylic insect holes) were linked to the trophic activity of many saproxylic species. The abundance of tree-related microhabitats is, in general, strictly correlated to trees of large diameters and veteran trees (Regnery et al., 2013).

Results showed that the presence of large dead trees, but also specific types of microhabitats (e.g., M1 and M2 - living trees with fruiting bodies of *Fomes fomentarius* or *Fomitopsis pinicola*) largely influenced the diversity of Coleoptera communities, suggesting a high variability among the species that feed on dead substrates and associated fungi (see Table 7). These ecological niches represent the optimal substrate for the oviposition of primary saproxylic beetles on living trees (i.e., Cerambycidae, Lucanidae, Curculionidae, Bostrichidae, Tenebrionidae and Throscidae), fundamental for the correct functioning of the forest ecosystem (Lassauce et al., 2011).

Many sampled species were related to living trees and deadwood components of the forest, providing a representative matrix of the beetle community. From a quantitative point of view, the number of saproxylic species would depend on the volume of CWD, while the decay stage of CWD should influence highly specialized taxa, often found in Red Lists (Lonsdale et al., 2008; Dodelin, 2010). Furthermore, the different species depending on deadwood do not colonize it directly by feeding at the expense of other decomposers (secondary saproxylic). In fact, many species of beetles may feed on the fungal mycelium (Esseen et al., 1997).

The activity and abundance of keystone species would determine “the integrity of the community” and its unaltered persistence over time (Paine, 1969), as evidenced by the dominance index, resulting in the maintenance of species diversity (Parisi et al., 2020c). This condition is frequent in ecosystems with a high degree of naturalness, and where the biotic components are in equilibrium (Thorn et al., 2020a). Indeed, we observed rather high variability of all the trophic categories (see Table A).

Several studies have empirically established the dependence of species and groups on specific microhabitats (Bouget et al., 2014; Larrieu et al., 2018; Percel et al., 2019; Siitonen, 2012), though correlations between species richness or diversity with microhabitat metrics generally show moderate association (Paillet et al., 2018). Here, a positive correlation between the occurrence of microhabitats with the presence of fungi and the richness of beetle species was observed. This correlation and those between biodiversity indices and forest components (Table 7) were relevant for both the structural characteristics of the forests and for the abundance of deadwood in relation to the diversity of beetle species. The highest correlations between structural attributes, microhabitat types and beetle richness emerged when the community was considered as a whole and separated for the two protected areas. The clear separation between locations in GSML (Inc 4 & 5 and Ven 3 & 5) could be attributable to differences in forest structure and deadwood abundance (data not shown) compared to the other plots, affecting the beetle communities; similar observations were made in other locations (Motola, Alb 100, Alb 68 and 69) in CVDA (Figs. 2 and 3). Therefore, we may conclude that the response of species richness to deadwood availability was relatively good (cf. Sabatini et al., 2016).

Our results are in line with the findings of Vanderwel et al. (2006), regarding the correlation between beetle diversity and CWD volume, but not with those regarding the composition of the insect community. The correlations highlighted in Table 7 further highlighted the complexity of the interrelationships, emphasizing the importance of the availability of resources in both qualitative and quantitative terms. Similar results were obtained in other studies concerning CWD (e.g., Heilmann-Clausen and Christensen, 2005).

The canopy cover did not have a clear influence on biodiversity indices. This could be attributable to the early stage of old-growth forest structure in these forest stands (Lombardi et al., 2010; Sabatini et al., 2016). From the analysis of the canopy cover, in both GSML and CVDA forests, we might infer a rather open structure. In conditions of relatively high irradiance reaching the ground, a high density and diversity of understory vegetation (Sabatini et al., 2014) and lichens (Aragon et al., 2010) can be expected. Forest gaps are generally characterized by a greater abundance of understory plants that may represent a key resource for many saproxylic beetles (Bouget et al., 2014). Lachat et al. (2016) showed that the abundance and composition of the beetles were greater in the sunny areas inside and outside the forest, but these authors did not find differences in species richness.

To improve our understanding of trade-offs and synergies between forest management and biodiversity conservation, long-term monitoring of forest ecosystems strategies should be implemented (Durak, 2012). Long-term monitoring of these habitats provides important information on their resilience to disturbance. Sustainable forest management strategies adopted in protected areas may also contribute to maintain a certain degree of biodiversity, although appropriate biodiversity indices and conservation status indicators need to be defined first at the habitat level. Nevertheless, a high level of diversity is known to be an important indicator of the conservation status of both managed and unmanaged forest ecosystems (Kutnar et al., 2015).

4.1. Implications for conservation

Saproxylic species represent an important percentage of forest biodiversity, which in some groups can reach 60%. Overall, about 25% of all forest species are saproxylic (Paillet et al., 2010) and these organisms are known to be highly threatened (Davies et al., 2008). Intensive utilization and deadwood removal had major impacts on forest ecosystems and associated species in Mediterranean mountain systems (e.g., Motta et al., 2006), which caused a decrease in biodiversity (Cálix et al., 2018). Based on the present results, conservation measures, such as the retention habitat trees, snags or lying deadwood, were confirmed of key elements for saproxylic species (Kraus and Krumm, 2013).

We recommend to promote deadwood retention, habitat heterogeneity, and canopy openness in these protected beech forests. In these forests, long-term monitoring plots should be established for elucidating the role of species composition, habitat availability, and microclimatic conditions on biodiversity at different spatial scales (from the single plot to the whole park), as well as to explore the effects of linking mixed management systems with large conservation areas to preserve biodiversity from a landscape perspective (Heikkala et al., 2017).

5. Conclusions

Overall, our results indicate that forest structure and tree-related microhabitats were the most important variables for determining the biodiversity of beetle communities in these Mediterranean mountain beech forests. In particular, the amount of deadwood positively influenced saproxylic beetle communities. Forest structure, deadwood abundance, canopy cover, and microhabitat type were important indicators for monitoring biodiversity, including threatened species, in line with the objectives of the EU Biodiversity Strategy for 2030 (EU Biodiversity Strategy for 2030). This information is particularly important for implementing the objectives of sustainable forest management and for planning strategies aimed at the conservation of biodiversity in protected mountain environments (Burrascano et al., 2008; Pohjanmies et al., 2019).

Indicator species should be used to determine conservation areas with high ecological value, having a more limited distribution and being more vulnerable to disturbances than generalist species (Schouten et al., 2010). Although we found as many as 7 species included in the IUCN red list, rare and threatened taxa were collected only in some sites and with few individuals and could hardly be used as indicators (whole saproxylic vs. threatened species, Table A). Traits characterizing the biology of saproxylic and non-saproxylic beetles and the links to the forest components make it possible to connect the extinction risk to human pressure or the conservation response. This is useful for drawing implications for conservation strategies at the landscape scale and for increasing the resilience of these mountain ecosystems threatened by climate and land-use changes.

Funding sources

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Competing Interest

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

Acknowledgments

The authors thank the specialists of the various taxonomic groups: Paolo Audisio (Nitidulidae), Alessandro Bruno Biscaccianti (Alexiidae, Biphylidae, Cerylonidae, Dascillidae, Dermestidae, Erotylidae, Eucemidae, Laemophloeidae, Lathridiidae, Lucanidae, Mycetophagidae, Salpingidae, Scirtidae, Sphindidae, Tenebrionidae, Trogossitidae), Enzo Colonnelli (Anthribidae, Attelebidae, Brentidae, Curculionidae), Gianluca Magnani (Buprestidae), Massimo Faccoli (Curculionidae Scolytinae), Fabrizio Fanti (Cantharidae, Lampyridae), Emanuele Piattella (Scarabaeidae), Giuseppe Platia (Elateridae), Roberto Poggi (Staphylinidae Pselaphinae), Pierpaolo Rapuzzi (Cerambycidae (pars)), Enrico Ruzzier (Mordellidae, Scaptiidae), Adriano Zanetti (Staphylinidae (pars)). We are grateful to Bruno Lasserre (Università degli Studi del Molise, Italy) for technical support.

Appendix

See Appendix Table A1.

Table A1

List of species of Coleoptera and number of specimens collected from GSML and CVDA national parks.

| Families | Species | IUCN | CT | GSML | CVDA |
|----------------|--|------|----|------|------|
| Anthribidae | Platyrhinus resinosus (Scopoli, 1763) | LC | XY | 1 | |
| Anthribidae | Platystomos albinus (Linnaeus, 1758) | LC | XY | 1 | 2 |
| Attelabidae | Neocoenorrhinus interpunctatus (Stephens, 1831) | | | | 1 |
| Biphylidae | Diplocoelus fagi (Chevrolat, 1837) | LC | SX | | 2 |
| Brentidae | Holotrichapion pisi (Fabricius, 1801) | | | | 2 |
| Buprestidae | Agrilus angustulus (Illiger, 1803) | LC | XY | | 1 |
| Buprestidae | Agrilus graminis Gory & Laporte de Castelnau, 1837 | LC | XY | 1 | |
| Buprestidae | Agrilus olivicolor Kiesenwetter, 1857 | LC | XY | | 2 |
| Byturidae | Byturus tomentosus (De Geer, 1774) | | | 1 | 1 |
| Cantharidae | Cantharis decipiens Baudi, 1871 | | | | 7 |
| Cantharidae | Malthinus deceptor Baudi, 1983 | | | 1 | 1 |
| Cantharidae | Rhagonycha lignosa (Müller, 1764) | | | 1 | |
| Cantharidae | Rhagonycha lutea (Müller, 1764) | | | | 1 |
| Cantharidae | Rhagonycha nigriceps (Waltl, 1838) | | | 1 | |
| Cantharidae | Rhagonycha nigrosuta Fiori, 1900 | | | | 2 |
| Cerambycidae | Acanthocinus xanthoneurus (Mulsant & Rey, 1852) | NT | XY | | 1 |
| Cerambycidae | Alosterna tabacicolor (De Geer, 1775) | LC | XY | 3 | |
| Cerambycidae | Leopus nebulosus (Linnaeus, 1758) | LC | XY | | 1 |
| Cerambycidae | Oxymirus cursor (Linnaeus, 1758) | LC | XY | 1 | |
| Cerambycidae | Paracorymbia fulva (De Geer, 1775) | LC | XY | 1 | |
| Cerambycidae | Phymatodes testaceus (Linnaeus, 1758) | LC | XY | | 1 |
| Cerambycidae | Pseudovadonia livida (Fabricius, 1777) | LC | XY | 1 | 22 |
| Cerambycidae | Pyrrhidium sanguineum (Linnaeus, 1758) | LC | XY | 1 | |
| Cerambycidae | Rhagium mordax (De Geer, 1775) | LC | XY | | 1 |
| Cerambycidae | Rutpela maculata (Poda, 1761) | LC | XY | 4 | |
| Cerambycidae | Saphanus piceus (Laicharting, 1784) | NT | XY | 3 | |
| Cerambycidae | Stenurella melanura (Linnaeus, 1758) | LC | XY | 244 | 8 |
| Cerambycidae | Stenurella sennii Sama, 2002 | DD | XY | 98 | 2 |
| Cerambycidae | Stictoleptura rubra (Linnaeus, 1758) | LC | XY | 1 | |
| Cerambycidae | Tetrops praeustus (Linnaeus, 1758) | LC | XY | | 1 |
| Cerambycidae | Xylotrechus arvicola (Olivier, 1795) | LC | XY | | 3 |
| Chrysomelidae | Aphthona euphorbiae (Schrank, 1781) | | | | 1 |
| Chrysomelidae | Aphthona venustula (Kutschera, 1861) | | | | 10 |
| Chrysomelidae | Galerucella lineola (Fabricius, 1781) | | | | 7 |
| Cerylonidae | Cerylon ferrugineum Stephens, 1830 | LC | MY | 5 | 1 |
| Ciidae | Cis boleti (Scopoli, 1763) | LC | MB | 3 | |
| Ciidae | Rhopalodontus perforatus (Gyllenhal, 1813) | LC | MB | | 1 |
| Cleridae | Opilo mollis (Linnaeus 1758) | LC | PR | 1 | 2 |
| Cleridae | Tillus elongatus (Linnaeus 1758) | NT | PR | 6 | 9 |
| Cleridae | Thanasimus formicarius (Linnaeus, 1758) | LC | PR | | 1 |
| Coccinellidae | Subcoccinella vigintiquatuorpuntata (Linnaeus, 1758) | | | | 1 |
| Corylophidae | Arthrolips nana (Mulsant & Rey, 1861) | DD | MY | 1 | 1 |
| Cryptophagidae | Cryptophagus sp. A | | | 2 | |
| Cryptophagidae | Cryptophagus sp. B | | | 1 | 1 |
| Curculionidae | Acalles parvulus Boheman, 1837 | LC | SX | | 1 |
| Curculionidae | Anisandrus dispar (Fabricius, 1793) | LC | MY | 1 | |
| Curculionidae | Ceutorhynchus picitarsis Gyllenhal, 1837 | | | | 1 |
| Curculionidae | Dichotrachelus bensai Solari & Solari, 1903 | | | 1 | |
| Curculionidae | Ernoporicus fagi (Fabricius, 1798) | LC | XY | | 3 |
| Curculionidae | Gymnetron veronicae (Germar, 1821) | | | | 1 |
| Curculionidae | Hylastinus obscurus (Marsham, 1802) | LC | XY | 2 | |
| Curculionidae | Hylesinus toranio (Danthoine, 1788) | LC | XY | | 6 |
| Curculionidae | Lymantror coryli (Perris, 1853) | VU | XY | | 1 |
| Curculionidae | Orchestes fagi (Linnaeus, 1758) | | | 4 | 15 |
| Curculionidae | Phyllobius argentatus (Linnaeus, 1758) | | | 11 | 64 |
| Curculionidae | Phyllobius longipilis Boheman, 1843 | | | 20 | |
| Curculionidae | Phyllobius romanus Faust, 1890 | | | 11 | 41 |
| Curculionidae | Polydrusus aeratus (Gravenhorst, 1807) | | | 2 | |
| Curculionidae | Polydrusus cervinus (Linnaeus, 1758) | | | 2 | |
| Curculionidae | Polydrusus impar Gozis, 1882 | | | | 1 |
| Curculionidae | Polydrusus neapolitanus Desbrochers des Loges, 1871 | | | | 1 |
| Curculionidae | Polydrusus pterygomalis Boheman, 1840 | | | 2 | |
| Curculionidae | Polydrusus sericeus Goeze, 1777 | | | | 2 |
| Curculionidae | Polydrusus transalpinus Daniel & Daniel, 1906 | | | 12 | |
| Curculionidae | Polydrusus raverae Solari & Solari, 1904 | | | | 1 |
| Curculionidae | Rhynchaenus fagi (Linnaeus, 1758) | | | 10 | 2 |
| Curculionidae | Rhyncolus elongatus (Gyllenhal, 1827) | LC | SX | | 1 |
| Curculionidae | Scolytus intricatus (Ratzeburg, 1837) | LC | XY | 2 | 8 |
| Curculionidae | Scolytus multistriatus (Marsham, 1802) | LC | XY | | 3 |

(continued on next page)

Table A1 (continued)

| Families | Species | IUCN | CT | GSML | CVDA |
|----------------|--|------|----|------|------|
| Curculionidae | <i>Taphrorhynchus bicolor</i> (Herbst, 1793) | LC | XY | 1 | 1 |
| Curculionidae | <i>Taphrorhynchus villifrons</i> (Dufour, 1843) | LC | XY | 1 | |
| Curculionidae | <i>Trypodendron domesticum</i> (Linnaeus, 1758) | LC | MY | 1 | 2 |
| Curculionidae | <i>Tychius meliloti</i> Stephens, 1831 | | | | 1 |
| Curculionidae | <i>Xyleborinus saxesenii</i> (Ratzeburg, 1837) | LC | MY | 4 | |
| Curculionidae | <i>Xylosandrus germanus</i> (Blandford, 1894) | | | 5 | |
| Dascillidae | <i>Dascillus cervinus</i> (Linnaeus, 1758) | | | 2 | 3 |
| Dermestidae | <i>Anthrenus fuscus</i> Olivier, 1789 | | | 1 | |
| Dermestidae | <i>Globicornis emarginata</i> (Gyllenhal, 1808) | LC | NI | 1 | |
| Dermestidae | <i>Globicornis luckowi</i> Herrmann, Háva & Kadej, 2011 | NT | NI | 3 | 1 |
| Elateridae | <i>Agriotes infuscatus</i> Desbrochers des Loges, 1870 | | | 21 | 24 |
| Elateridae | <i>Agrypnus murinus</i> (Linnaeus, 1758) | | | | 1 |
| Elateridae | <i>Ampedus quercicola</i> (Buysson, 1887) | LC | PR | | 1 |
| Elateridae | <i>Athous haemorrhoidalis</i> (Fabricius, 1801) | | | 27 | 29 |
| Elateridae | <i>Athous puncticollis</i> Kiesenwetter, 1858 | | | 1 | 6 |
| Elateridae | <i>Athous subfuscus</i> (Müller, 1764) | | | 22 | 13 |
| Elateridae | <i>Athous vittatus</i> (Fabricius, 1793) | | | 7 | 8 |
| Elateridae | <i>Cardiophorus vestigialis</i> Erichson, 1840 | | | | 1 |
| Elateridae | <i>Dalopius marginatus</i> (Linnaeus, 1758) | | | | 134 |
| Elateridae | <i>Denticollis linearis</i> (Linnaeus, 1758) | CR | PR | 1 | 1 |
| Elateridae | <i>Dicronychus cinereus</i> (Herbst, 1784) | | | | 9 |
| Elateridae | <i>Drilus flavescens</i> Olivier, 1790 | | | | 1 |
| Elateridae | <i>Hemicrepidius hirtus</i> (Herbst, 1784) | | | 1 | 2 |
| Elateridae | <i>Hypoganus inunctus</i> (Panzer, 1795) | EN | PR | | 1 |
| Elateridae | <i>Idolus picipennis</i> (Bach, 1852) | | | | 2 |
| Elateridae | <i>Limonius minutus</i> (Linnaeus, 1758) | | | | 7 |
| Elateridae | <i>Melanotus villosus</i> (Geoffroy in Fourcroy, 1785) | LC | PR | 11 | 15 |
| Elateridae | <i>Nothodes parvulus</i> (Panzer, 1799) | | | 397 | 79 |
| Elateridae | <i>Pheletes quercus</i> (Olivier, 1790) | | | | 1 |
| Elateridae | <i>Stenagostus rhombeus</i> (Olivier, 1790) | VU | PR | 12 | 3 |
| Erotylidae | <i>Triplax elongata</i> Lacordaire, 1842 | NT | MB | 1 | 1 |
| Erotylidae | <i>Triplax lacordairii</i> Crotch, 1870 | NT | MB | 3 | 1 |
| Erotylidae | <i>Triplax lepida</i> (Faldermann, 1837) | NT | MB | 4 | |
| Erotylidae | <i>Triplax marseuli</i> Bedel, 1864 | NT | MB | | 1 |
| Erotylidae | <i>Triplax russica</i> (Linnaeus, 1758) | LC | MB | | 2 |
| Eucnemidae | <i>Eucnemis capucina</i> Ahrens, 1812 | NT | SX | | 1 |
| Eucnemidae | <i>Hylis cariniceps</i> (Reitter, 1902) | NT | SX | 1 | 14 |
| Eucnemidae | <i>Hylis simonae</i> (Olexa, 1970) | NT | SX | 8 | 14 |
| Eucnemidae | <i>Isorhipis melasoides</i> (Laporte de Castelnau, 1835) | LC | SX | | 8 |
| Eucnemidae | <i>Melasis buprestoides</i> (Linnaeus, 1760) | LC | SX | 3 | 3 |
| Eucnemidae | <i>Microrrhagus pygmaeus</i> (Fabricius, 1793) | NT | SX | | 2 |
| Kateretidae | <i>Brachypterolus linariae</i> (Stephens, 1830) | | | | 2 |
| Histeridae | <i>Atholus duodecimstriatus</i> (Schrank, 1781) | | | | 1 |
| Histeridae | <i>Paromalus flavicornis</i> (Herbst, 1792) | LC | PR | 1 | |
| Laemophloeidae | <i>Laemophloeus monilis</i> (Fabricius, 1787) | | | 7 | 6 |
| Lampyridae | <i>Lampyrus vesuvius vesuvius</i> (Geisthardt, 2007) | | | 1 | 5 |
| Lampyridae | <i>Luciola lusitanica</i> (Charpentier, 1825) | | | 3 | 2 |
| Latridiidae | <i>Cartodere nodifer</i> (Westwood, 1839) | LC | MY | 1 | 1 |
| Latridiidae | <i>Enicmus atriceps</i> Hansen, 1962 | DD | MY | 4 | 4 |
| Latridiidae | <i>Enicmus brevicornis</i> (Mannerheim, 1844) | LC | MY | 5 | 15 |
| Latridiidae | <i>Enicmus fungicola</i> Thomson, 1868 | LC | MY | | 1 |
| Latridiidae | <i>Enicmus testaceus</i> (Stephens, 1830) | LC | MY | 1 | 2 |
| Leiodidae | <i>Agathidium varians</i> Beck, 1817 | LC | MY | 3 | 2 |
| Leiodidae | <i>Leiodes</i> sp. A | | | | 3 |
| Leiodidae | <i>Leiodes</i> sp. B | | | | 1 |
| Lucanidae | <i>Platycerus caprea</i> (De Geer, 1774) | LC | SX | 1 | |
| Lucanidae | <i>Platycerus caraboides</i> (Linnaeus, 1758) | LC | SX | | 4 |
| Lucanidae | <i>Sinodendron cylindricum</i> (Linnaeus, 1758) | LC | SX | 2 | 9 |
| Melandryidae | <i>Abdera quadrifasciata</i> (Curtis, 1829) | NT | MY | 3 | |
| Melandryidae | <i>Conopalpus testaceus</i> (Olivier, 1790) | NT | MY | 9 | 5 |
| Melandryidae | <i>Melandrya caraboides</i> (Linnaeus, 1760) | NT | MY | | 2 |
| Melandryidae | <i>Phloiolytra tenuis</i> (Hampe, 1850) | NT | MY | 1 | |
| Melyridae | <i>Aplocnemus nigricornis</i> (Fabricius, 1793) | LC | PR | 16 | |
| Melyridae | <i>Danacea ambigua</i> (Mulsant & Rey, 1868) | | | 17 | 7 |
| Melyridae | <i>Dasytes caeruleus</i> (De Geer, 1774) | LC | PR | 3 | |
| Melyridae | <i>Dasytes plumbeus</i> (Müller, 1776) | LC | PR | 191 | 122 |
| Monotomidae | <i>Rhizophagus nitidulus</i> (Fabricius, 1798) | NT | MY | 1 | |
| Mordellidae | <i>Mordellistena pumila</i> (Gyllenhal, 1810) | | | | 2 |
| Mordellidae | <i>Mordellochroa milleri</i> (Emery, 1878) | | | 3 | 1 |

(continued on next page)

Table A1 (continued)

| Families | Species | IUCN | CT | GSML | CVDA |
|----------------|---|------|----|------|------|
| Mycetophagidae | Litargus connexus (Geoffroy, 1785) | LC | MY | | 1 |
| Mycetophagidae | Mycetophagus atomarius (Fabricius, 1787) | LC | MY | 2 | |
| Mycetophagidae | Triphyllus bicolor (Fabricius, 1777) | LC | MY | 3 | 2 |
| Nitidulidae | Acanthogethes brevis (Sturm, 1845) | | | | 1 |
| Nitidulidae | Brassicogethes aeneus (Fabricius, 1775) | | | | 1 |
| Nitidulidae | Brassicogethes viridescens (Fabricius, 1787) | | | 1 | 30 |
| Nitidulidae | Carpophilus nepos Murray, 1854 | | | 1 | |
| Nitidulidae | Eपुरaea melanocephala (Marsham, 1802) | LC | MY | | 1 |
| Nitidulidae | Eपुरaea unicolor (Olivier, 1790) | LC | SF | | 1 |
| Nitidulidae | Eपुरaea fuscicollis (Stephens, 1835) | LC | SF | 4 | |
| Nitidulidae | Genistogethes erichsoni (Brisout de Barneville, 1863) | | | | 1 |
| Nitidulidae | Lamiogethes brunnicornis (Sturm, 1845) | | | | 1 |
| Nitidulidae | Lamiogethes bidens (Brisout de Barneville, 1863) | | | | 1 |
| Nitidulidae | Meligethes atratus (Olivier, 1790) | | | 1 | |
| Nitidulidae | Sagittogethes distinctus (Sturm, 1845) | | | 1 | |
| Nitidulidae | Soronia oblonga Brisout de Barneville, 1863 | LC | SF | | 5 |
| Nitidulidae | Thalycra fervida (Olivier, 1790) | | | | 3 |
| Oedemeridae | Oedemera podagrariae (Linnaeus 1767) | | | | 2 |
| Ptinidae | Dorcatoma punctulata Mulsant & Rey, 1864 | VU | XY | | 1 |
| Ptinidae | Grynobius planus (Fabricius, 1787) | LC | XY | 3 | |
| Ptinidae | Hedobia pubescens (Olivier, 1790) | LC | XY | 1 | 1 |
| Ptinidae | Hemicoelus costatus Aragona, 1830 | LC | XY | 23 | 20 |
| Ptinidae | Ochina latreilli (Bonelli, 1812) | NT | XY | | 2 |
| Ptinidae | Ptilinus pectinicornis (Linnaeus, 1758) | LC | XY | 39 | 9 |
| Ptinidae | Ptinomorphus imperialis (Linnaeus, 1767) | LC | XY | 20 | |
| Ptinidae | Ptinomorphus regalis (Duftschmid, 1825) | LC | XY | | 4 |
| Ptinidae | Stegobium paniceum (Linnaeus, 1758) | | | 1 | |
| Salpingidae | Salpingus planirostris (Fabricius, 1787) | LC | SX | 10 | 5 |
| Salpingidae | Vincenzellus ruficollis (Panzer, 1794) | LC | MY | | 1 |
| Scarabaeidae | Anoplotrupes stercorosus (Hartmann in Scriba, 1791) | | | 4 | 1 |
| Scarabaeidae | Aphodius borealis Gyllenhal, 1827 | | | 1 | 2 |
| Scarabaeidae | Aphodius niger (Illiger, 1798) | | | 1 | |
| Scarabaeidae | Aphodius rufa (Moll, 1782) | | | | 4 |
| Scarabaeidae | Aphodius rufipes (Linnaeus, 1758) | | | 5 | 6 |
| Scarabaeidae | Aphodius sticticus (Panzer, 1798) | | | 2 | 6 |
| Scarabaeidae | Aphodius zenkeri Germar, 1813 | | | 2 | |
| Scarabaeidae | Geotrupes stercorarius (Linnaeus, 1758) | | | 1 | |
| Scarabaeidae | Gnorimus nobilis (Linnaeus, 1758) | NT | SX | 1 | 2 |
| Scarabaeidae | Rizothrogus sp. | | | | 1 |
| Scarabaeidae | Serica brunnea (Linnaeus, 1758) | | | | 3 |
| Scirtidae | Prionocyphon serricornis (Müller, 1821) | NT | HW | 2 | 1 |
| Scirtidae | Elodes cf. gredleri Kiesenwetter, 1863 | | | 1 | |
| Scirtidae | Elodes cf. marginata Fabricius, 1798 | | | 1 | |
| Scraptiidae | Anaspis costai Emery, 1876 | VU | SX | 1 | |
| Scraptiidae | Anaspis nigripes Brisout de Barneville 1866 | | | 2 | 6 |
| Scraptiidae | Anaspis rufilabris (Gyllenhal, 1827) | EN | SX | 5 | |
| Silphidae | Nicrophorus interruptus Stephens, 1830 | | | 5 | |
| Silphidae | Nicrophorus vespilloides (Herbst, 1783) | | | | 1 |
| Staphylinidae | Aleochara intricata Mannerheim, 1830 | | | | 1 |
| Staphylinidae | Aleochara sparsa Heer, 1839 | | | 1 | 1 |
| Staphylinidae | Anthophagus fauveli caprai Koch, 1933 | | | 9 | 3 |
| Staphylinidae | Anthophagus torretassoi torretassoi Koch, 1933 | | | 1 | |
| Staphylinidae | Atheta crassicornis (Fabricius, 1793) | | | | 3 |
| Staphylinidae | Atheta taxiceroides Munster, 1932 | | | 1 | 4 |
| Staphylinidae | Atrecus affinis (Paykull, 1789) | LC | PR | 2 | 1 |
| Staphylinidae | Bisnius fimetarius (Gravenhorst, 1802) | | | | 1 |
| Staphylinidae | Dinothenarus flavocephalus (Goeze, 1777) | | | | 1 |
| Staphylinidae | Eusphalerum bargagli (Luze, 1910) | | | 1 | |
| Staphylinidae | Eusphalerum baudii (Fiori, 1894) | | | | 14 |
| Staphylinidae | Eusphalerum clavipes (Scriba, 1868) | | | 2 | |
| Staphylinidae | Eusphalerum italicum italicum (Koch, 1938) | | | 2 | |
| Staphylinidae | Eusphalerum martinae (Zanetti, 2004) | | | | 4 |
| Staphylinidae | Eusphalerum signatum angulatum (Luze, 1911) | | | 18 | 4 |
| Staphylinidae | Gyrohypus fracticornis (Müller, 1776) | | | | 1 |
| Staphylinidae | Habrocerus capillaricornis (Gravenhorst, 1806) | | | 1 | |
| Staphylinidae | Haploglossa cf. picipennis (Gyllenhal, 1827) | | | | 1 |
| Staphylinidae | Lordithon lunulatus (Linnaeus, 1760) | | | 2 | 3 |
| Staphylinidae | Neuraphes sp. | | | | 1 |
| Staphylinidae | Ocypus italicus (Aragona, 1830) | | | 3 | 2 |

(continued on next page)

Table A1 (continued)

| Families | Species | IUCN | CT | GSML | CVDA |
|---------------|---|------|----|------|------|
| Staphylinidae | <i>Ontholestes murinus</i> (Linnaeus, 1758) | | | | 1 |
| Staphylinidae | <i>Paraphloeostiba gayndahensis</i> (MacLeay, 1873) | | | 1 | |
| Staphylinidae | <i>Philonthus carbonarius</i> (Gravenhorst, 1802) | | | | 1 |
| Staphylinidae | <i>Philonthus cognatus</i> (Stephens, 1832) | | | | 1 |
| Staphylinidae | <i>Philonthus concinnus</i> (Gravenhorst, 1822) | | | | 1 |
| Staphylinidae | <i>Philonthus decorus</i> (Gravenhorst, 1802) | | | 1 | 1 |
| Staphylinidae | <i>Philonthus laminatus</i> (Creutzer, 1799) | | | 1 | |
| Staphylinidae | <i>Philonthus succicola</i> (Thomson, 1860) | | | | 1 |
| Staphylinidae | <i>Phloeopora corticalis</i> (Gravenhorst, 1802) | LC | UN | 1 | |
| Staphylinidae | <i>Phloeostiba plana</i> (Paykull, 1792) | LC | SX | 1 | |
| Staphylinidae | <i>Platystethus nitens</i> (Sahlberg, 1832) | | | | 1 |
| Staphylinidae | <i>Quedius cinctus</i> (Paykull, 1790) | | | 1 | 3 |
| Staphylinidae | <i>Quedius collaris italicus</i> Gridelli, 1925 | | | | |
| Staphylinidae | <i>Quedius humeralis</i> (Stephens, 1832) | | | | 2 |
| Staphylinidae | <i>Quedius laticollis</i> Gridelli, 1924 | | | 2 | |
| Staphylinidae | <i>Quedius levicollis</i> (Brullé, 1832) | | | | 1 |
| Staphylinidae | <i>Quedius nigrocaeruleus</i> (Fauvel, 1876) | | | | 1 |
| Staphylinidae | <i>Quedius picipes</i> (Mannerheim, 1830) | | | | 1 |
| Staphylinidae | <i>Tachinus humeralis</i> Gravenhorst, 1802 | | | 1 | |
| Staphylinidae | <i>Tachyporus nitidulus</i> (Fabricius, 1781) | | | | 5 |
| Tenebrionidae | <i>Accanthopus velikensis</i> (Piller & Mitterpacher, 1783) | LC | SX | 9 | 5 |
| Tenebrionidae | <i>Cteniopus sulphureus</i> (Linnaeus, 1758) | | | | 1 |
| Tenebrionidae | <i>Gonodera luperus</i> (Herbst, 1783) | | | 5 | 22 |
| Tenebrionidae | <i>Gonodera metallica</i> (Küster, 1850) | | | 1 | 8 |
| Tenebrionidae | <i>Helops coeruleus</i> (Linnaeus, 1758) | LC | SX | 1 | |
| Tenebrionidae | <i>Isomira marcida</i> (Kiesenwetter, 1863) | | | 25 | 50 |
| Tenebrionidae | <i>Mycetochara linearis</i> (Illiger, 1794) | LC | SX | 2 | 7 |
| Tenebrionidae | <i>Omophlus lepturoides</i> (Fabricius, 1787) | | | | 1 |
| Tenebrionidae | <i>Pseudocistela ceramboides</i> (Linnaeus, 1760) | NT | SX | 1 | |
| Tenebrionidae | <i>Stenomax aeneus</i> (Scopoli, 1763) | LC | SX | | 1 |
| Trogossitidae | <i>Nemozoma elongatum</i> (Linnaeus, 1760) | LC | PR | 71 | 24 |
| Trogossitidae | <i>Thymalus limbatus</i> (Fabricius, 1787) | | | 2 | |
| Zopheridae | <i>Corticus celtis</i> Dejean, 1821 | LC | SX | | 2 |
| Zopheridae | <i>Coxelus pictus</i> (Sturm, 1807) | LC | SX | 3 | 3 |

IUCN = Red List Categories (Audisio et al. 2015). CR = Critically endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient.

CT = Trophic Categories. 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, NI (CO) = inhabiting birds' and small mammals' nests in hollow trees, CO = commensal of Sx/xy or of other saproxylic insects, SF = sap-feeder on trees attacked by xy, SP = saprophytophagous (on dead vegetal rotting material associated with dead wood debris) (Audisio et al., 2015).

References

- Aragon, G., Martínez, I., Izquierdo, P., Belinchón, R., Escudero, A., 2010. Effects of forest management on epiphytic lichen diversity in Mediterranean forests. *Appl. Veg. Sci.* 13, 183–194. <https://doi.org/10.1111/j.1654-109X.2009.01060.x>
- Audisio, P., Alonso-Zarazaga, M., Slipinski, A., Nilsson, A., Jelínek, J., Vigna Taglianti, A., Turco, F., Otero, C., Canepari, C., Kral, D., Liberti, G., Sama, G., Nardi, G., Löbl, I., Horák, J., Kolibac, J., Háva, J., Sapiejewski, M., Jäch, M., Bologna, M., Biondi, M., Nikitsky, N., Mazzoldi, P., Zahradnik, P., Węgrzynowicz, P., Constantin, R., Gerstmeier, R., Zhantiev, R., Fattorini, S., Tomaszewska, W., Rücker, W., Vazquez-Albalade, X., Cassola, F., Angelini, F., Johnson, C., Schawaller, W., Regalin, R., Baviera, C., Rocchi, S., Cianferoni, F., Beenen, R., Schmitt, M., Sassi, D., Kippenberg, H., Zampetti, M., Trizzino, M., Chiari, S., Carpaneto, G.M., Sabatelli, S., De Jong, Y., 2015. Fauna Europaea: coleoptera 2 (excl. series Elateriformia, Scarabaeiformia, Staphyliniformia and superfamily Curculionoidea). *Biodivers. Data J.* 3, 4750. <https://doi.org/10.3897/BDJ.3.e4750>
- Bani, A., Pioli, S., Ventura, M., Panzacchi, P., Borruso, L., Tognetti, R., Tonon, G., Brusetti, L., 2018. The role of microbial community in the decomposition of leaf litter and deadwood. *Appl. Soil Ecol.* 126, 75–84. <https://doi.org/10.1016/j.apsoil.2018.02.017>
- Barker, M., Rayens, W., 2003. Partial least squares for discrimination. *J. Chemom.* 17, 166–173. <https://doi.org/10.1002/cem.785>
- Battipaglia, G., Awada, T., Aus Der Au, R., Innangi, M., Saurer, M., Cherubini, P., 2020. Increasing atmospheric CO₂ concentrations outweighs effects of stand density in determining growth and water use efficiency in *Pinus ponderosa* of the semi-arid grasslands of Nebraska (U.S.A.). *Glob. Ecol. Conserv.* 24, e01274. <https://doi.org/10.1016/j.gecco.2020.e01274>
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manag.* 258, 525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Boerema, A., Rebelo, A.J., Bodi, M.B., Esler, K.J., Meire, P., 2017. Are ecosystem services adequately quantified? *J. Appl. Ecol.* 54, 358–370. <https://doi.org/10.1111/1365-2664.12696>
- Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Slipinski, S.A., Smith, A.B.T., 2011. Family-group names in Coleoptera (Insecta). *ZooKeys* 88, 1–972. <https://doi.org/10.3897/zookeys.88.807>
- Bouget, C., Larrieu, L., Brin, A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecol. Indic.* 36, 656–664. <https://doi.org/10.1016/j.ecolind.2013.09.031>
- Brin, A., Brustel, H., Jactel, H., 2009. Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in Maritime pine plantations. *Ann. For. Sci.* 66, 306. <https://doi.org/10.1051/forest/20090>
- Brunet, J., Fritz, O., Richnau, G., 2010. Biodiversity in European beech forests – A review with recommendations for sustainable forest management. *Ecol. Bullet.* 53, 77–94. <https://doi.org/10.1046/j.1365-294X.1996.00094.x>
- Burrascano, S., Lombardi, F., Marchetti, M., 2008. Old-growth forest structure and deadwood: are they indicators of plant species composition? A case study from central Italy. *Plant Biosyst.* 142, 313–323. <https://doi.org/10.1080/11263500802150613>

- Buse, J., Levanony, T., Timm, A., Dayan, T., Assmann, T., 2010. Saproxylic beetle assemblages in the Mediterranean region: impact of forest management on richness and structure. *For. Ecol. Manag.* 259, 1376–1384. <https://doi.org/10.1016/j.foreco.2010.01.004>
- Calamini, G., Maltoni, A., Travaglini, D., Iovino, F., Nicolaci, A., Menguzzato, G., Corona, P., Ferrari, B., Di Santo, D., Chirici, G., Lombardi, F., 2011. Stand structure attributes in potential old-growth forests in the Apennines. *Italy Ital. For. Mt.* 66, 365–381.
- Cálix, M., Alexander, K.N.A., Nieto, A., Dodelin, B., Soldati, F., Telnov, D., Vazquez-Albalade, X., Aleksandrowicz, O., Audisio, P., Istrate, P., Jansson, N., Legakis, A., Liberto, A., Makris, C., Merkl, O., Mugerwa, Pettersson, R., Schlaghamersky, J., Bologna, M.A., Brustel, H., Buse, J., Novák, V., Purchart, L., 2018. European Red List of Saproxylic Beetles. IUCN., Brussels, Belgium.
- Carpaneto, G.M., Baviera, C., Biscaccianti, A.B., Brandmayr, P., Mazzei, A., Mason, F., Battistoni, A., Teofili, C., Rondinini, C., Fattorini, S., Audisio, P., 2015. A Red List of Italian Saproxylic Beetles: taxonomic overview, ecological features and conservation issues (Coleoptera). *Fragm. Entomol.* 47, 53–126. <https://doi.org/10.4081/fe.2015.138>
- Carrascal, L.M., Galván, I., Gordo, O., 2009. Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos* 118, 681–690. <https://doi.org/10.1111/j.1600-0706.2008.16881.x>
- Cocciufa, C., Gerth, W., Luiselli, L., Redolfi de Zan, L., Cerretti, P., Carpaneto, G.M., 2014. Survey of saproxylic beetle assemblages at different forest plots in central Italy. *Bull. Insectol.* 67, 295–306. <https://doi.org/10.1093/jisesa/jiew030>
- Davies, Z.G., Tyler, C., Stewart, G.B., Pullin, A.S., 2008. Are current management recommendations for saproxylic invertebrates effective?: a systematic review. *Biodivers. Conserv.* 17, 209–234. <https://doi.org/10.1007/s10531-007-9242-y>
- Dodelin, B., 2010. Saproxylic beetles biodiversity in old-growth forest in the South-East of France. *Plant Biosyst.* 144, 262–270. <https://doi.org/10.1080/11263500903561155>
- Durak, T., 2012. Changes in diversity of the moun- tain beech forest herb layer as a function of the forest management method. *For. Ecol. Manag.* 276, 154–164. <https://doi.org/10.1016/j.foreco.2012.03.027>
- Ekström, A.L., Bergmark, P., Hekkala, A.M., 2021. Can multifunctional forest landscapes sustain a high diversity of saproxylic beetles? *For. Ecol. Manag.* 490, 119107. <https://doi.org/10.1016/j.foreco.2021.119107>
- Esseen, P.A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. *Ecol. Bull.* 46, 16–47.
- EU Biodiversity Strategy for 2030 Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. COM 2020, 380. Brussels. (https://ec.europa.eu/info/sites/info/files/communication-annex-eu-biodiversity-strategy-2030_en.pdf) (accessed 17 January 2021).
- Ferraro, L., Innangi, S., Di Martino, G., Russo, B., Tonielli, R., Innangi, M., 2020. Seafloor features and benthic foraminifera off Linosa Island (Sicily Channel, southern Mediterranean). *J. Mar. Syst.* 211, 103421. <https://doi.org/10.1016/j.jmarsys.2020.103421>
- Forest Europe 2015. State of Europe's forests. Ministerial Conference on the Protection of Forests in Europe, FAO/UNECE/ Forest Europe Liaison Unit, Madrid, Spain.
- Gibb, H., Hjältén, J.P., Ball, J., Atlegrim, O., Pettersson, R.B., Hilszczanski, J., Johansson, T., Danell, K., 2006. Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography* 29, 191–204. <https://doi.org/10.1111/j.2006.0906-7590.04372.x>
- Gossner, M.M., Lachat, T., Brunet, J., Gunnar, I., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W., Müller, J., 2013. Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conserv. Biol.* 27, 605–614. <https://doi.org/10.1111/cobi.12023>
- Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan- Dewenter, I., Schulze, E.-D., Weisser, W.W., 2016. Deadwood enrichment in European forests – which tree species should be used to promote saproxylic beetle diversity? *Biol. Conserv.* 201, 92–102. <https://doi.org/10.1016/j.biocon.2016.06.032>
- Grunwald, C., Stobbe, H., Schmitt, U., 2002. Developmental stages of callus formation on wound edges of broad-leaved trees. *Forstwiss. Cent.* 121, 50–58.
- Guby, N.B., Dobberrin, M., 1996. Quantitative estimates of coarse woody debris and standing dead trees in selected Swiss forests. *Glob. Ecol. Biogeogr. Lett.* 5, 327–341. <https://doi.org/10.2307/2997588>
- Harper, D.A.T., 1999. *Numerical Palaeobiology: Computer-based Modelling and Analysis of Fossils and Their Distributions*. John Wiley & Sons, Chichester, pp. 468.
- Heikkala, O., Kouki, J., Martikainen, P., 2017. Prescribed burning is an effective and quick method to conserve rare pyrophilous forest-dwelling flat bugs. *Insect Conserv. Divers.* 10, 32–41. <https://doi.org/10.1111/icad.12195>
- Heilmann-Clausen, J., Christensen, M., 2005. Wood-inhabiting macrofungi in Danish beech-forests: conflicting diversity patterns and their implications in a conservation perspective. *Biol. Conserv.* 122, 633–642. <https://doi.org/10.1016/j.biocon.2004.10.001>
- Herbeck, L.A., Larsen, D.R., 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. *Conserv. Biol.* 13, 623–632. <https://doi.org/10.1046/j.1523-1739.1999.98097.x>
- Hisano, M., Searle, E.B., Chen, H.Y.H., 2018. Biodiversity as a solution to mitigate climate change affects the functioning of forest ecosystems. *Biol. Rev.* 93, 439–456. <https://doi.org/10.1111/brv.12351>
- Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Syst.* 46, 523–549. <https://doi.org/10.1146/annurev-ecolsys-112414-054400>
- Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., Harding, K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biol. Conserv.* 107, 165–180. [https://doi.org/10.1016/S0006-3207\(02\)00057-5](https://doi.org/10.1016/S0006-3207(02)00057-5)
- Innangi, M., Balestrieri, R., Danise, T., d'Alessandro, F., Fioretto, A., 2019. From soil to bird community: a partial least squares approach to investigate a natural wooded area surrounded by urban patchwork (Astroni crater, southern Italy). *Ecol. Modell.* 394, 1–10. <https://doi.org/10.1016/j.ecolmodel.2019.01.002>
- Keddy, P.A., Drummond, C.G., 1996. *Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems*. *Ecol. Appl.* 6, 748–762.
- Kraus, D., Krumm, F. (Eds.), 2013. *Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity*. European Forest Institute, pp. 284.
- Kutnar, L., Eler, K., Marinšek, A., 2015. Effects of different silvicultural measures on plant diversity –the case of the Illyrian *Fagus sylvatica* habitat type (Natura 2000). *iForest* 9, 318–324. <https://doi.org/10.3832/ifor1587-008>
- Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacson, G., Müller, J., 2012. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecol. Indic.* 23, 323–331. <https://doi.org/10.1016/j.ecolind.2012.04.013>
- Lachat, T., Chumak, M., Chumak, V., Jakoby, O., Müller, J., Tanadini, M., Wermelinger, B., 2016. Influence of canopy gaps on saproxylic beetles in primeval beech forests: a case study from the Uholka Shyroky Luh forest, Ukraine. *Insect Conserv. Divers.* 9, 559–573. <https://doi.org/10.1111/icad.12188>
- Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. *Can. J. For. Res.* 42, 1433–1445. <https://doi.org/10.1139/x2012-077>
- Larrieu, L., Paillet, Y., Winter, S., Büttler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B., Vandekerckhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecol. Indic.* 84, 194–207. <https://doi.org/10.1016/j.ecolind.2017.08.051>
- Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* 11, 1027–1039. <https://doi.org/10.1016/j.ecolind.2011.02.004>
- Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, Ö., Goldberg, I., Nascimbene, J., Tøttrup, A.P., Rahbek, C., Heilmann-Clausen, J., 2019. Biodiversity response to forest structure and management: comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. *For. Ecol. Manag.* 432, 707–717. <https://doi.org/10.1016/j.foreco.2018.09.057>
- Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conserv. Biol.* 14, 941–950. <https://doi.org/10.1046/j.1523-1739.2000.98533.x>

- Lombardi, F., Chirici, G., Marchetti, M., Tognetti, R., Lasserre, B., Corona, P., Barbati, A., Ferrari, B., Di Paolo, S., Giuliarelli, D., Mason, F., Iovino, F., Nicolaci, A., Bianchi, L., Maltoni, A., Travaglini, D., 2010. Deadwood in forest stands close to old-growthness under Mediterranean conditions in the Italian peninsula. *Ital. J. For. Mt. Environ.* 65, 481–504. <https://doi.org/10.4129/ijfm.2010.5.02>
- Lombardi, F., Lasserre, B., Chirici, G., Tognetti, R., Marchetti, M., 2012. Deadwood occurrence and forest structure as indicators of old-growth forest conditions in Mediterranean mountainous ecosystems. *Ecoscience* 19, 344–355. <https://doi.org/10.2980/19-4-3506>
- Lombardi, F., Marchetti, M., Corona, P., Merlini, P., Chirici, G., Tognetti, R., Burrascano, S., Alivernini, A., Puletti, N., 2015. Quantifying the effect of sampling plot size on the estimation of structural indicators in old-growth forest stands. *For. Ecol. Manag.* 346, 89–97. <https://doi.org/10.1016/j.foreco.2015.02.011>
- Lonsdale, D., Pautasso, M., Holdenrieder, O., 2008. Wood-decaying fungi in forest: Conservation needs and management options. *Eur. J. Res.* 127, 1–22. <https://doi.org/10.1007/s10342-007-0182-6>
- Marchetti, M., Tognetti, R., Lombardi, F., Chiavetta, U., Palumbo, G., Sellitto, M., Colombo, C., Iovieno, P., Alfani, A., Baldantoni, D., Barbati, A., Ferrari, B., Bonacquisti, S., Capotorti, G., Copiz, R., Blasi, C., 2010. Ecological portrayal of old-growth forests and persistent woodlands in the Cilento and Vallo di Diano National Park (southern Italy). *Plant Biosyst.* 144, 130–147. <https://doi.org/10.1080/11263500903560470>
- Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest USA. *For. Ecol. Manag.* 257, 1453–1464. <https://doi.org/10.1016/j.foreco.2008.11.027>
- Mikusinski, G., Angelstam, P., 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt* 118, 277–283. ([online] URL). <http://www.researchgate.net/publication/240310747>
- Millennium Ecosystem Assessment, 2003. *Ecosystems and Humanwell-being; A Framework for Assessment*. Island Press, Washington, D.C., USA, pp. 266.
- Motta, R., Berretti, R., Lingua, E., Piusi, P., 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. *For. Ecol. Manag.* 235, 155–163. <https://doi.org/10.1016/j.foreco.2006.08.007>
- Müller, J., Büttler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *Eur. J. For. Res.* 129, 981–992. <https://doi.org/10.1007/s10342-010-0400-5>
- Nieto, A., Alexander, K.N.A., 2010. *European Red List of Saproxyllic Beetles*. Publications Office of the European Union, Luxembourg.
- Odor, P., Standovář, T., 2001. Richness of bryophyte vegetation in near-natural and managed beech stands: the effects of management-induced differences in dead wood. *Ecol. Bull.* 49, 219–229. ([online] URL). <http://www.jstor.org/stable/20113278>
- Paillet, Y., Bergès, L., Hjäältén, J., Ödör, P., Avon, C., Bernhardt-Romermaun, M., Bjilisma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, I., Sebastia, M.T., Schmidt, W., Standovar, T., Tothmeresz, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>
- Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. *For. Ecol. Manag.* 346, 51–64. <https://doi.org/10.1016/j.foreco.2015.02.037>
- Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., Guilbert, E., 2018. The indicator side of tree microhabitat: a multi-taxon approach based on bats, birds and saproxyllic beetles. *J. Appl. Ecol.* 55, 2147–2159. <https://doi.org/10.1111/1365-2664.13181>
- Paine, R.T., 1969. A note on trophic complexity and community stability. *Am. Nat.* 103, 91–93.
- Parisi, F., Lombardi, F., Sciarretta, A., Tognetti, R., Campanaro, A., Marchetti, M., Trematerra, P., 2016. Spatial patterns of saproxyllic beetles in a relic silver fir forest (Central Italy), relationships with forest structure and biodiversity indicators. *For. Ecol. Manag.* 381, 217–234. <https://doi.org/10.1016/j.FORECO.2016.09.041>
- Parisi, F., Pioli, S., Lombardi, F., Fravolini, G., Marchetti, M., Tognetti, R., 2018. Linking deadwood traits with saproxyllic invertebrates and fungi in European forests – a review. *iForest* 11, 423–436. <https://doi.org/10.3832/IFOR2670-011>
- Parisi, F., Di Febraro, M., Lombardi, F., Biscaccianti, A.B., Campanaro, A., Tognetti, R., Marchetti, M., 2019. Relationships between stand structural attributes and saproxyllic beetle abundance in a Mediterranean broadleaved mixed forest. *For. Ecol. Manag.* 432, 957–966. <https://doi.org/10.1016/j.foreco.2018.10.040>
- Parisi, F., Frate, L., Lombardi, F., Tognetti, R., Campanaro, A., Biscaccianti, A.B., Marchetti, M., 2020a. Diversity patterns of Coleoptera and saproxyllic communities in unmanaged forests of Mediterranean mountains. *Ecol. Indic.* 110, 105873. <https://doi.org/10.1016/j.ecolind.2019.105873>
- Parisi, F., Platia, G., Mancini, M., De Cristofaro, A., 2020b. Confirmation of *Crepidophorus mutilatus* (Rosenhauer, 1847) in Italy (Coleoptera: Elateridae), with notes on its distribution and conservation. *Coleopt. Bull.* 74, 489–494. <https://doi.org/10.1649/0010-065X-74.3.489>
- Parisi, F., Lombardi, F., Marziliano, Pasquale, A., Russo, D., De Cristofaro, A., Marchetti, M., Tognetti, R., 2020c. Diversity of saproxyllic beetle communities in chestnut agroforestry systems. *iForest* 13, 456–465. <https://doi.org/10.3832/IFOR3478-013>
- PerceI, G., Laroche, F., Bouget, C., 2019. The scale of saproxyllic beetles response to landscape structure depends on their habitat stability. *Landscape Ecol.* 34, 1905–1918. <https://doi.org/10.1007/s10980-019-00857-0>
- Pioli, S., Antonucci, S., Giovannelli, A., Traversi, M.L., Borruso, L., Bani, A., Brusetti, L., Tognetti, R., 2018. Community fingerprinting reveals increasing wood-inhabiting fungal diversity in unmanaged Mediterranean forests. *For. Ecol. Manag.* 408, 202–210. <https://doi.org/10.1016/j.foreco.2017.10.052>
- Pohjanmies, T., Eyvindson, K., Mönkkönen, M., 2019. Forest management optimization across spatial scales to reconcile economic and conservation objectives. *PLoS One* 14, 0218213. <https://doi.org/10.1371/journal.pone.0218213>
- Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T.A.S., Parsons, S., Joern, A., 2013. Invertebrates, ecosystem services and climate change. *Biol. Rev.* 88, 327–348. <https://doi.org/10.1111/brv.12002>
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [WWW Document]. URL <https://www.r-project.org/>
- Regnery, B., Couvet, D., Kubarek, L., Julien, J.-F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecol. Indic.* 34, 221–230. <https://doi.org/10.1016/j.ecolind.2013.05.003>
- Rohlf, F.J., Corti, M., 2000. Use of two-block partial least-squares to study covariation in shape. *Syst. Biol.* 49, 740–753. <https://doi.org/10.1080/106351500750049806>
- Rondinini, C., Chiozza, F., 2010. Quantitative methods for defining percentage area targets for habitat types in conservation planning. *Biol. Conserv.* 143, 1646–1653. <https://doi.org/10.1016/j.biocon.2010.03.037>
- Sabatini, F.M., Burrascano, S., Tuomisto, H., Blasi, C., 2014. Ground layer plant species turnover and beta diversity in Southern-European old-growth forests. *Plos One* 9, 95244. <https://doi.org/10.1371/journal.pone.0095244>
- Sabatini, F.M., Burrascano, S., Azzella, M.M., Barbati, A., De Paulis, S., Di Santo, D., Facioni, L., Giuliarelli, D., Lombardi, F., Maggi, O., Mattioli, W., Parisi, F., Persiani, A., Ravera, S., Blasi, C., 2016. One taxon does not fit all: Herb-layer diversity and stand structural complexity are weak predictors of biodiversity in *Fagus sylvatica* forests. *Ecol. Indic.* 69, 126–137. <https://doi.org/10.1016/j.ecolind.2016.04.012>
- Sanchez, G., 2012. plsdepot: Partial Least Squares (PLS) Data Analysis Methods. R package version 0.1.17 [WWW Document]. URL <https://cran.r-project.org/package=plsdepot>
- Sanderman, J., Amundson, R., 2003. Biogeochemistry of Decomposition and Detrital Processing. In: Schlesinger, W.H. (Ed.), *Treatise on Geochemistry* 8. Elsevier Ltd., pp. 682–2003.
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.-D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C., 2017. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* 55, 267–278. <https://doi.org/10.1111/1365-2664.12950>
- Schouten, M.A., Barendregt, A., Verweij, P.A., Kalkman, V.J., Kleukers, R.M.J.C., Lenders, H.J.R., Siebel, H.N., 2010. Defining hotspots of characteristic species for multiple taxonomic groups in the Netherlands. *Biodivers. Conserv.* 19, 2517–2536. <https://doi.org/10.1007/s10531-010-9857-2>
- Schwalter, T.D., 2013. *Insects and sustainability of ecosystem services*. In: *Social Environmental Sustainability Series*. CRC Press/Taylor & Francis Group, BocaRaton, FL, USA, pp. 362.
- Schwalter, T.D., 2016. *Insect Ecology: An Ecosystem Approach*, 4th ed. Academic Press, pp. 774.

- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv. Biol.* 29, 382–390. <https://doi.org/10.1111/cobi.12427>
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49, 11–41. ([online] URL). <http://www.jstor.org/stable/20113262> .
- Siitonen, J., 2012. In: Stokland, J.N., Siitonen, J., Jonsson, B.G. (Eds.), *Microhabitats. Biodiversity in Dead Wood*. Cambridge University Press, Cambridge.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. *Biodiversity in Dead Wood*. Cambridge University Press, New York (US).
- Tabacchi, G., Di Cosmo, L., Gasparini, P., 2011. Aboveground tree volume and phytomass prediction equations for forest species in Italy. *Eur. J. For. Res.* 130, 911–934. <https://doi.org/10.1007/s10342-011-0481-9>
- Thorn, S., Seibold, S., Leverkus, A.B., Müller, J., Noss, R.F., Stork, N., Vogel, S., Lindenmayer, D.B., 2020a. The living dead - acknowledging life after tree death to stop forest degradation. *Front. Ecol. Environ.* 18, 505–512. <https://doi.org/10.1002/fee.2252>
- Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., H. Feldhaar, J.B., Fontaine, P.J., Fornwalt, R., María, H., Hernández, R.L., Hutto Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlik, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Zmihorski, M., Leverkus, A.B., 2020b. Estimating retention benchmarks for salvage logging to protect biodiversity. *Nat. Commun.* 11, 1–8. <https://doi.org/10.1038/s41467-020-18612-4>
- Vanderwel, M.C., Malcolm, J.R., Smith, S.M., Islam, N., 2006. Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. *For. Ecol. Manag.* 225, 190–199. <https://doi.org/10.1016/j.foreco.2005.12.051>
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer.
- Williams-Guillén, K., Olimpi, E., Maas, B., Taylor, P.J., Arlettaz, R., 2016. Bats in the anthropogenic matrix: challenges and opportunities for the conservation of Chiroptera and their ecosystem services in agricultural landscapes. In: *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer, Cham, pp. 151–186.
- Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. *For. Ecol. Manag.* 255, 1251–1261. <https://doi.org/10.1016/j.foreco.2007.10.029>