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Diversity patterns of Coleoptera and saproxylic communities in unmanaged forests of Mediterranean mountains



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ABSTRACT

Beetle communities are excellent indicators to monitor biodiversity in forest environments. The most common indicators monitored for assessing the effectiveness of the sustainable forest management measures are deadwood amount, forest structure, and microhabitat traits. In Mediterranean mountain forests, however, the relationships between stand-level attributes and species diversity indicators have been still poorly studied. We have investigated the patterns of species diversity of beetle communities in relation to stand structural traits in two unmanaged forests located in central Apennines (Italy). The two forest stands are characterized by different tree species composition and management history. The experimental area extends over approximately 300 ha, within which 50 circular plots of 530 m² were sampled for each studied forest. Coleoptera were collected using window flight traps and emergence traps on decaying deadwood. We evaluated i) the differences in species diversity (richness, Shannon diversity and Simpson diversity) between the two forests and ii) the beetle Shannon diversity and composition in relation to selected forest variables, with a particular focus on saproxylic species. Principal Component Analysis followed by rarefaction analysis were applied to examine differences in species diversity. Within each forest stand, a Boosted Regression Tree model and a Non-Metric Multidimensional Scaling were performed to relate the species Shannon diversity and community assemblages to the forest structural attributes. Results revealed how these forest structural attributes have a fundamental role in influencing the diversity of Coleoptera and their assemblages. Forest vertical heterogeneity, snag volume and tree dominance were the most important variables for saproxylic assemblages in these Mediterranean mountain forests, while the amount of coarse woody debris positively affected the overall beetle diversity and that of saproxylic species. At stand level, differences in species diversity were mainly driven by tree composition, probably indicating that food resources, determined by tree species, are of primary importance in determining species assemblages and beetle diversity in these forests; while at plot level, we found that the variables, which drove species composition and beetle diversity, varied between the two forests. This study provides the basis for the integration of independent biodiversity indicators in sustainable solutions for the conservation of unmanaged forests in Mediterranean mountain systems.

1. Introduction

Forest ecosystems are under constant dynamic changes, driven predominantly by the silvicultural practices and disturbance intensities, and influenced by social, political and economic drivers (Chen et al., 2008). The current distribution and structure of forest ecosystems in the Mediterranean region is the legacy of centuries of forest use and landscape transformation. Forest exploitation and landscape degradation have also influenced the presence of endemisms and, more in general, the biodiversity occurring in mountainous areas of the Mediterranean

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Basin (State of Mediterranean Forests, 2018). Nevertheless, in the last 50–60 years, a diffuse land abandonment has occurred in many mountain and inner areas of the Mediterranean region (Scarascia-Mugnozza et al., 2000), leading to an increment of the forest canopy cover and to the natural recovery of formerly managed forests, even if their composition and structure still reflect the past human activity (Bowman et al., 2013).

Forest management, especially timber extraction, modifies many forest traits. Specifically, forest management alters tree age structure, canopy cover, diameter distribution, and stand density, often simplifying the vertical and horizontal forest structure. Deadwood volumes and microhabitat attributes are also affected by the intensity and frequency of thinning (Lombardi et al., 2018). Intensive management practices influence microclimatic conditions within forest stands, such as light availability and quality, as well as moisture and nutrient fluxes, which in turn have an impact on deadwood decomposition rates, as well as species assemblages and diversity (Davies et al., 2008; Grove, 2002; Thomas et al., 2009). In the Mediterranean region, mountain forests have been heavily impacted for centuries by livestock grazing, and silvicultural treatments have been mainly aimed at fuelwood production, often promoting the regeneration of one or few tree species, which have resulted in a prolonged history of deadwood removal (Dudley and Vallauri, 2004; New, 2010). On the other hand, Parisi et al. (2018) suggested that specific forest management practices may help maintain ecological connectivity, increase landscape heterogeneity, and promote stand complexity, in turn enhancing biodiversity (insects in Mediterranean mountain forests). In particular, establishing "senescence islands" and ensuring the presence of big and old trees may add to natural processes that create suitable reproductive sites for saproxylic organisms (Pioli et al., 2018).

The variability of deadwood volume affects the biodiversity of saproxylic organisms, including saproxylic beetles (Brin et al., 2009; Martikainen, 2001). In boreal environments, abundance and diversity of beetle communities (Coleoptera) have declined steeply in response to a history of extensive forest management and deadwood removal (Gibb et al., 2006; Lindhe et al., 2005). In general, beetle communities have several key functions in forests, being prey for other organisms or predators themselves, pollinators, herbivores and decomposers (Redolfi De Zan et al., 2014). Among these trophic categories, saproxylic beetles depend upon deadwood or wood-decaying fungi for some portion of their life cycle (Bani et al., 2018; Parisi et al., 2018), and contribute to the decomposition processes, significantly optimizing the forest nutrient cycles (Stokland et al., 2012). In Europe, research on the effects of forest management on beetle communities has been mainly focused on temperate and boreal forests (Brin et al., 2009; Gibb et al., 2006; Lindhe et al., 2005; Lassauce et al., 2011). Nevertheless, relatively few studies that link forestry practices and saproxylic communities are currently available for Mediterranean mountain forests (see Bani et al., 2018; Parisi et al., 2018). These studies point to deadwood as one of the best indicators of species richness, especially for saproxylic species; as a consequence, deadwood enrichment is often recommended as a conservative management practice to support saproxylic organisms (Müller and Bütler, 2010; Parisi et al., 2016, 2019).

The loss of biodiversity in forests is not only linked to deadwood removal (Seibold et al., 2015). The simplification of forest structure and changes in canopy cover, especially in the Mediterranean context, have often induced the disappearance of sun-exposed dead trees, which host an important portion of the saproxylic community (García et al., 2018). In Mediterranean regions, particularly rich in beetle species and with high number of endemisms (Oleksa et al., 2007; Carpaneto et al., 2010; Redolfi De Zan et al., 2014), landscape homogenization has affected forest functions and diversity traits in many areas, reducing the density of habitat patches (Buisson et al., 2013; Clavel et al., 2011; Devictor et al., 2008; Parisi et al., 2019). Since the availability of habitats at a specific site is a function of landscape heterogeneity and deadwood amount (e.g., Seibold et al., 2017), it is possible to speculate that the number of saproxylic species in unmanaged forests might provide a useful reference for pursuing effective conservation measures in Mediterranean mountains. Indeed, spatial homogenization of community composition of saproxylic beetles during deadwood succession would indicate a vulnerability of detritivore networks to reduced tree species and habitat diversity, threatening biogeochemical cycles (Wende et al., 2017). Indeed, saproxylic beetle communities, but also fungi (which constitute trophic niche of many saproxylic species) often associated with deadwood, change with time according to the stage of wood decay, which reflects changing in physicochemical wood conditions (Stokland et al., 2012).

The presence of saproxylic beetles is strongly influenced by the occurrence of large and regularly distributed patches of mature and undisturbed forests (Parisi et al., 2016). Habitat types preferred by saproxylic beetles are hardwood forests, followed by coniferous forests, and several threatened species are often associated with large hollow deciduous trees or with the fruiting bodies of large arboreal fungi (Carpaneto et al., 2015; Persiani et al., 2015; Sabatini et al., 2016). In Mediterranean mountains, forest fires add to habitat loss and tree removal as major threats to beetle species (Lachat and Bütler, 2007). However, the cessation of intense forest operations in many mountain areas of the Italian Peninsula is determining an increase in deadwood volume and structural complexity of these forests, as well as higher frequency diversity of microhabitats.

Understanding the relationship between forest features and beetle diversity is essential for evaluating the contribution to biodiversity conservation of land use change in these ecosystems (Sitzia et al., 2015). In the present study, we focused on Coleoptera and saproxylic beetle diversity and their relationship with indicators of forest biodiversity (e.g., deadwood) in Mediterranean mountain forests, already known to be suitable for biodiversity studies in unmanaged forests, in which the amount of deadwood ranges between 2% and 30% (Fridman and Walheim, 2000). The objective of this work was to assess the difference in patterns of species richness between beetle communities of a silver fir forest and a mixed broadleaved forest, characterized by the same management history and located in central Apennines (Italy). The analysis considered the whole beetle community, as well as the sole saproxylic component, and took advantage of statistically rigorous diversity indices and advanced machine learning techniques. We hypothesized that tree species composition and forest management legacy might be reflected in species diversity and composition of beetle communities specific of the two forest types.

2. Material and methods

2.1. Study area

The study was conducted in two mountain sites located in the central Apennines (Italy) (Fig. A1). The two sites, considered representative of montane beech and coniferous forests of the Mediterranean, Anatolian and Macaronesian regions (EEA, 2006), are located within a 12-km radius of each other and both are within the temperate bioclimatic region, humid-*meso*-temperate type.

"Abeti Soprani" (hereinafter referred to AS – 41°51'39''N, 14°17'37''E) is an almost pure silver fir (*Abies alba* Mill.) forest (sometimes associated with *Fagus sylvatica* L. at the highest elevations and with *Quercus cerris* L. at the lowest elevations) near Pescopennataro, 160 km east of Rome. The study area is located at an elevation ranging from 1000 to 1450 m a.s.l. The slope is north facing, and the geology is dominated by Miocenic-clay soils and Cretacic white limestone. Mean annual temperature is 8.4°C, with a total annual precipitation of 1124 mm (1927–1987). "Abeti Soprani" is an unevenaged forest stand, with an average age of 90–100 years, extending over 343 ha. The forest is a relict stand dominated by silver fir, typical of the fir forests once widespread in the Mediterranean and Anatolian regions, which nowadays survive only in small areas of the Italian Peninsula.

Table 1

Environmental variables describing forest features.

Forest variable	Description
Canopy cover	Canopy cover visually estimated (%)
Basal area	Sum of the cross-sectional area at breast height (1.3 m aboveground) of individual tree stems (m ² ha ⁻¹)
CWD	Coarse woody debris $(m^3 ha^{-1})$
SDT	Standing dead trees $(m^3 ha^{-1})$
STUMP	Stumps $(m^3 ha^{-1})$
SNAG	Snags $(m^3 ha^{-1})$
Mtot	Total number of microhabitats (number ha^{-1})
Height	Mean tree height (m)
SDT height	Standard deviation of the height, a measure of vertical heterogeneity (m).
DBH SDT	Standard deviation of the diameter at breast height, a measure of spatial heterogeneity (cm)
Tree rich	Richness of tree species
Tree dominance	1-Simpson diversity index; tree_dominance is 0 when all tree species are equally distributed and reach 1 when there is only one species.
Tree composition	Percentage of coniferous species in the species composition (%)

"Bosco Pennataro" (hereinafter referred to BP - 41°44'56"N, 14°11′50″E) is a broadleaved mixed forest located near Vastogirardi, 150 km east of Rome. The elevation ranges between 900 and 1100 m a.s.l., and mean minimum and maximum temperatures are 2.5 °C and 14.8 °C, respectively. The 30-year total annual precipitation is 1012 mm. The forest extends over approximately 300 ha; it is characterized by a mixture of old coppices and patches of mature forest stands grown from natural regeneration. These complex structures derive from the absence of any silvicultural intervention in the area during the last 60 years. The site is part of the MaB-UNESCO Reserve of "Collemeluccio-Montedimezzo-Alto Molise". The species combinations vary in relation to the exposure, slope, microclimate, substrate composition and historical human disturbances. Q. cerris L. is the dominant tree species with the presence of *F. sylvatica* and other broadleaves, such as Carpinus betulus L., Sorbus torminalis L., Acer opalus Mill., A. pseudoplatanus L., A. campestre L., A. cappadocicum Gled. subsp. lobelii. (Ten.) A.E. Murray.

2.2. Survey of the forest structural traits

The experimental areas extend over about 480 ha. In each site, 50 circular sampling plots of 530 m² were established following the approach of Lombardi et al. (2015): 43 plots were located at a regular distance of 250 m to each other, following a systematic aligned grid, while 7 plots were randomly positioned at a shorter distance (Fig. A1). For each plot, UTM datum WGS 1984 coordinates (Zone 32 T) and elevation (m a.s.l.) were recorded using the Juno SB Global Positioning System (GPS) (Trimble, Sunnyvale, California). All living trees (minimum diameter at breast height, $DBH \ge 10 \text{ cm}$) and deadwood (minimum diameter \geq 5 cm) were sampled at each plot, recording the following parameters: tree DBH and height, canopy cover and species for living trees. Dead downed trees, snags, coarse woody debris (CWD) and stumps were also surveyed, measuring their length/height, minimum and maximum diameter and recording the species. Standing dead trees were characterized by the presence of crown, while snags referred to stems without crown. 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). The decay stage of deadwood was assigned using the fiveclass scale used by Hunter (1990). We also counted a set of 23 treerelated microhabitats in the same sample plots. They were 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, mould pockets) and then classified according to Winter and Möller (2008).

2.3. Sampling of beetle fauna

The 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. In AS, all traps were positioned for two consecutive years, in 2012 (from June to October) and in 2013 (from April to September), for a total of 4 and 5 surveys, respectively; in BP, the traps were installed in 2014 and 2015 (from June to October), for a total of six and four surveys, respectively. Windows flight traps were checked approximately every 20 days. Emergence traps were emptied only once, at the end of the sampling period. All monitoring systems were removed in winter.

Nomenclature of genera and species follow Löbl and Smetana (2003, 2007, 2008, 2010, 2011, 2013), Löbl and Löbl (2015, 2016) and Audisio et al. (2015), in a few cases modified according to the opinion of the specialists involved (genera *Anisandrus, Involvulus, Mycetochara*); systematics and nomenclature at the higher rank follow Bouchard et al. (2011). All the taxa collected during the field activities are alphabetically listed in the Appendix (see Table A1).

Species considered strictly saproxylic (sensu Speight, 1989; Alexander, 2010; Carpaneto et al., 2015) are also reported in Table A1, together with their risk category at the Italian level (see Audisio et al., 2015; Carpaneto et al., 2015).

2.4. Data analysis

In order to characterize the Coleoptera communities in the surveyed forests, we first compared the two study sites in terms of both saproxylic species diversity and forest structural traits. Wilcoxon-Mann-Whitney test and related effect size were used to test differences in forest structure. Then, Principal Component Analysis (PCA) was applied to 13 forest variables, as detailed in Table 1.

Species diversity in the two forests was assessed using the Hill's number or the effective number of species (species richness, Shannon diversity and Simpson diversity). We applied the method recently developed by Hsieh et al. (2016), which allows comparing species diversity across assemblages, using rarefaction and extrapolation sampling curves. Briefly, Hill's number expresses the effective number of species (or the number of equally-common species for a given index) of a community, which is a more intuitive and statistically rigorous alternative to other diversity indices (see Chao et al., 2014, for a recent review). Hsieh et al. (2016) provided simple functions to compute rarefaction and extrapolation sampling curves for the three most widely used members of the Hill's number family (q = 0 species richness, q = 1 Shannon diversity and q = 2 Simpson diversity). We used the iNEXT R package to compute and compare the species diversity among the groups. In particular, we used the sampling-unit-based incidence data (or frequency) to compute such curves.

We then analyzed the relationship between the diversity of Coleoptera and forest structural traits for both the forest sites, separately. We selected only non-correlated forest variables (Pearson correlation values < 0.7). For each plot, the exponential of the Shannon Index was calculated in order to characterize the diversity of the total Coleoptera communities (Total SDI - tSDI). Here we choose the Shannon Index due to its unique ability to weigh elements precisely by their frequency, without disproportionately favoring either rare or common species (Jost, 2006). To analyze the relationship between tSDI and forest variables, we fitted a Boosted Regression Tree model (BRT). BRT is a machine learning technique, which combines the advantages of regression tree-based model and boosting techniques (Elith et al., 2008). We fitted a BRT model using the function gbm.step implemented in the dismo R packages (Hijmans et al., 2017). Specifically, the function uses cross-validation for selecting optimal settings. The model was evaluated using ten-fold cross-validation to determine the optimal combinations of the learning rate and tree complexity. We also dropped unimportant variables from the model, using the function gbm.simpilfy of the dismo package. We repeated the same analysis using only saproxylic species (Shannon Diversity of saproxylic community - sSDI). Results were then visualized using a partial dependence plot (Friedman, 2001), showing the effect of a variable on the response after accounting for the average effects of all the other variables in the model.

A non-metric multidimensional scaling (NMDS) was performed to investigate the Coleoptera communities across plots, in relation to the forest structural parameters. We first log-transformed abundance data and then we performed NMDS, using the Bray-Curtis distance (metaMDS function of the vegan package – Oksanen et al., 2018). Finally, all the forest variables (previously standardized to zero mean and unit variance) were individually tested to verify the significance with the NMDS ordination using the envfit function of the vegan package, with 1000 permutations. We excluded all the singleton species from the assemblage composition analyses, as rare species have little effect on the analysis but high uncertainty whether they origin from the stand or elsewhere.

3. Results

3.1. Main forest structural features

The analysis of forest variables revealed that AS and BP differed, in addition to tree composition, in tree richness, tree dominance, amount of STUMP and number of microhabitats, which were the variables with the strongest effect (Table 2). Specifically, BP was more diverse in terms of tree species and had a higher number of microhabitats than AS. On the contrary, AS showed higher values of STUMP and Basal_area. The other variables had less influence in determining differences between the two forests.

3.2. Material identification

3.2.1. Abeti Soprani

A total of 4607 specimens were collected during 2012 and 2013, repartitioned as follow: 468 specimens belonging to 66 species in 2012, and 4139 specimens belonging to 164 species in 2013. A total of 46 families were detected and Elateridae was the most common group: two species, *Nothodes parvulus* and *Athous vittatus*, represented over the 60% of the family sampled, with 2411 and 303 sampled specimens, respectively. Elateridae represented 85% of the total specimens collected, followed by Curculionidae (8.9%), Tenebrionidae (8%), Melyridae (2.3%), and Cerambycidae (3.3%). The remaining 41 families represented < 10% of the total sampled families.

Among the 179 species collected, 83 (46.3%) were saproxylic. Within the saproxylic fauna, 18 species (22.2%) are included in the risk categories of the Italian Red List for saproxylic beetles (Carpaneto et al., 2015): 12 species belong to the Near Threatened (NT), while four to the Vulnerable (VU), and one refers to each of the Endangered (EN) and Critically Endangered (CR) categories. Finally, one species is attributable to the DD category (Data Deficient) (Table A1).

3.2.2. Bosco Pennataro

A total of 3983 specimens were collected between 2014 and 2015, repartitioned as follow: 2700 specimens belonging to 224 species in 2014, and 1276 specimens belonging to 116 species in 2015. In this case, as well, 46 families were observed. The most abundant species were *Hylesinus taranio* (Curculionidae) with 856 specimens, *Dacne bipustulata* (Erotilydae) with 584 and *Nothodes parvulus* (Elateridae) with 404, corresponding to 48% of the total sampled species. Curculionidae represented 28.1% of the total specimens, followed by Elateridae (17.8%), Erotylidae (15.5%), Staphylinidae (9.6%), Scarabaeidae (5%), and Tenebrionidae (4.8%). The remaining 40 families represented 19.4% of the total.

Among the 226 species collected, 101 (44.7%) were saproxylic. Twenty-seven saproxylic species (27%) belong to the risk categories reported in the Red List of Italian saproxylic beetles (Carpaneto et al., 2015): 20 species refer to the Near Threatened (NT), 3 to the Vulnerable (VU), 1 to the Endangered (EN) and 3 to the Critically Endangered (CR) categories; finally, two species belong to the DD category (Table A1).

Table 2

Average values and standard deviation of the forest variables. Differences between the two forests were evaluated using a Wilcoxon-Mann-Whitney test and related effect size.

	Abeti Soprani		Bosco Pennataro		Wilcoxon-Mann-Whitney z	p-value	Effect size (r)
Forest variables	Mean value	SD	Mean value	SD			
Canopy cover	66	12.2	68.98	9.7	-0.99125	0.3233	-0.0991
Basal_area	44.29	14.4	33.09	10.7	4.1432	< 0.001	0.4143
CWD	11.87	20.4	6.15	5.9	0.3592	0.7220	0.0359
SDT	2.03	4.07	0.34	0.7	2.0617	0.0396	0.2061
STUMP	9.87	7.71	0.31	0.6	7.9963	< 0.001	0.7996
SNAG	14.66	32.4	1.2	2.2	1.0318	0.3039	0.1031
Mtot	162.07	56.5	332.91	153.4	-6.5261	< 0.001	-0.6526
Height	14.31	1.9	13.62	2.2	1.6132	0.1075	0.1613
STD-DBH	16.6	3.9	14.59	3.4	2.7197	0.0066	0.2719
STD-height	6.27	0.8	6.34	1.4	0.7859	0.4339	0.0786
Tree rich	2.68	0.8	5.84	1.7	-7.9833	< 0.001	-0.7983
Tree dominance	0.57	0.1	0.35	0.1	6.4664	< 0.001	0.6466
Tree composition	55.7	22.08	0.38	2.7	9.009	< 0.001	0.9009



Fig. 1. a) PCA for forests variables. Plots were grouped according to the forest sites: black dots = AS; grey triangles = BP. b) Sample-size-based rarefaction curves with 95% confidence intervals (shaded areas) for the three Hill's number (q = 0 species richness, q = 1 Shannon diversity and q = 2 Simpson diversity), considering all the species. c) Sample-size-based rarefaction curves with 95% confidence intervals (shaded areas) for the Hill's number (q = 0 species richness, q = 1 Shannon diversity and q = 2 Simpson diversity), considering saproxylic species.

3.3. Relationship between stand structural attributes and species diversity/ assemblages two axes explained 46.45% of the total variance, with the first axis explaining about 29.7% of it. Tree_rich and Mtot were negatively correlated with the first axis, whereas tree dominance, tree composition and STUMP were positively correlated. Considering the second axis, the

Fig. 1a shows the results obtained by applying the PCA. The first

standard deviations of DBH and height were positively correlated. All the plots sampled in BP are located on the right side of the PCA: they are characterized by high tree species richness and diversity, with a large number of microhabitats. On the contrary, AS is characterized by few tree species (mainly silver fir), with a relatively high volume of deadwood (STUMP). Great differences between the two forests were related to tree_composition, STUMP, tree richness, Mtot and tree dominance (Table 2).

Tree species richness was higher in BP (170 vs. 153, +10%), although the difference between BP and AS was not significant (confidence interval overlaps – Fig. 1b). For the Shannon diversity (q = 1), the number of equally-common species was higher in BP than AS of about 17% (86.18 and 71.67, respectively). For the Simpson diversity (q = 2), BP had 56.30 equally common species, while AS showed a value of 44.37, more than 20% lower. There was a large drop in the effective number of species as q increased.

Regarding the saproxylic species (Fig. 1c), BP had a considerably higher number of saproxylic species than AS (92 vs. 55, +37%). This tendency was confirmed also by the Shannon diversity (47.79 vs. 27.63, +42%) and by the Simpson diversity (33.16 vs. 20.17, +39%).

3.4. BRT model analysis

3.4.1. Abeti Soprani

Across the 12 non-correlated variables considered, the final model for total Shannon Diversity Index (tSDI) selected only three variables (Fig. 2): STUMP, the standard deviation of tree height and tree composition. The relative importance of the three variables were 49.2%, 30.6% and 20.2%, respectively. There was a negative relationship between STUMP volume and tSDI, but also between tree composition and tSDI. In particular, tSDI suddenly dropped at low values of STUMP ($\sim 7 \text{ m}^3 \text{ ha}^{-1}$), stabilizing thereafter. A drop occurred in tSDI at tree composition of 40% (considering silver fir presence). The tSDI tends to increase at high values of the standard deviation of tree height.

Considering only the saproxylic species, the model considers six variables (Fig. 3). The most important variables were STUMP (22.8%), which showed a negative relationship with diversity, followed by STD_heigth (22.7%), Mtot (19.8%), basal area (19.5%), tree composition (11.8%) and tree dominance (3.4%).

Specifically, sSDI increased at medium-high values of STD_height and showed a peak in matching the low medium value of Mtot. Basal area and tree composition showed a negative relationship with the diversity of saproxylic species.

3.4.2. Bosco pennataro

The BRT model for tSDI selected 5 variables (Fig. 4). The most

important one is CWD (37.7%), followed by STD_DBH (23.1%), tree dominance (17.2%), height (11.2%) and STD_height (10.8%).

Results obtained for tSDI indicates a high level of diversity as CWD volume, tree height and STD_height increased, whereas tSDI decreased as the tree dominance increased. Furthermore, tSDI showed a positive peak and intermediate values of STD_DBH.

Regarding saproxylic diversity (Fig. 5), CWD was the most important variable (43.3%), followed by tree dominance (24.3%), STD_height (16.8%) and height (15.6%).

The diversity of saproxylic species was higher as CWD volume, STD_height and height increased; on the contrary, sSDI decreased as the tree dominance increased.

3.5. Coleoptera communities

3.5.1. Abeti Soprani

The NMDS obtained for AS reveals how the composition of Coleoptera communities was influenced by SDT_height ($r^2 = 0.211$, p = 0.003) and SNAG volume ($r^2 = 0.1809$, p = 0.008) (Fig. 6a).

Among all the species collected, *Agriotes litigiosus* (Elateridae), *Globicornis fasciata* (Dermestidae), *Zacladus geranii* (Curculionidae) and *Alosterna tabacicolor* (Cerambycidae) showed a preference for forest structures characterized by high vertical diversity. Addittionally, a group of species formed by *Quedius ochripennis* (Staphylinidae), *Mycetochara linearis* (Mycetophagidae), *Dodecastichus consentaneus* (Curculionidae) and *Bryoporus multipunctus* (Staphylinidae) showed to prefer forest plots where high volumes of SNAG occur (Fig. 6a, b).

Regarding the saproxylic species, SDT_height ($r^2 = 0.245$, p = 0.002), SNAG ($r^2 = 0.125$, p = 0.045) and tree_dominance ($r^2 = 0.124$, p = 0.046) influenced the composition assemblage (Fig. 7a, b).

Aplocnemus nigricornis (Melyridae), Melasis buprestoides (Eucnemidae) and Opilo mollis (Cleridae) were strongly associated with SNAG volume; Pissodes piceae (Curculionidae) and Ampedus glycereus (Elateridae) preferred forest plots characterized by high vertical heterogeneity; Tetrops praeustus (Cerambycidae) tended to be more abundant in monospecific plots.

3.5.2. Bosco Pennataro

In BP, none of the forest variables explained the total species assemblage (data not shown). On the contrary, saproxylic species assemblages were marginally explained by the canopy_cover ($r^2 = 0.109$; p = 0.074) and CWD ($r^2 = 0.094$, p = 0.095) (Fig. 8a, b). A group of saproxylic species formed by *Rutpela maculata*, *Leiopus nebulosus* (Cerambycidae), *Epuraea fuscicollis* (Nitidulidae) and *Corticeus unicolor* (Tenebrionidae) showed a preference for large volumes of CWD;



Fig. 2. Partial dependence plots of the influence of forest variables on the Shannon Diversity Index for the total species in AS. Percentages in brackets represent the relative variable importance of the BRT model.



Fig. 3. Partial dependence plots of the influence of forest variables on the Shannon Diversity Index of saproxylic species for AS. Percentages in brackets represent the relative variable importance of the BRT model.

Epuraea melanocephala (Nitidulidae) and *Laemophloeus monilis* (Laemophloeidae) preferred high values of canopy cover.

4. Discussion

In this work, the importance of stand structural indicators was investigated by testing the correlations between beetle species richness and forest biodiversity indicators, as surrogates for the species diversity of saproxylic organisms. Results reinforce the importance of deadwood volume and quality for biodiversity monitoring. Surveying stands structural traits was, indeed, easier than monitoring living organisms themselves (e.g., Lassauce et al., 2011). This information is important to implement effective planning strategies that aim to reconcile the conflicting objectives of forest management (namely timber harvesting) at the local/regional scale and those of biodiversity conservation (e.g., in mountain environments) at the continental/global scale, particularly when considering commercial and environmental trade-offs (Pohjanmies et al., 2019).

Abeti Soprani (AS) and Bosco Pennataro (BP) strongly differed in terms of compositional traits (tree composition, richness and dominance) and structural attributes (stump and microhabitat). Although these forests were left unmanaged for 50–60 years, the legacy of past management was still visible in the actual structure. The large number of microhabitats in the mixed broadleaved forest of BP can be attributable to the high tree species richness and diversity. Broadleaved forests have been found to host a higher number of microhabitats than coniferous ones (e.g., Vuidot et al., 2011). Nevertheless, the coniferous

forest of AS showed a larger amount of deadwood than BP, in particular for stumps. In general, higher habitat diversity or larger population sizes of individual saproxylic species have been explained by a larger amount of CWD (e.g., Ranius et al., 2011). The average size and type of deadwood, its stage of decomposition, as well as the temporal availability of host woody debris may explain the local abundance of saproxylic species and differences between forest types. Indeed, several saproxylic species require a continuous supply of deadwood in high amount and can be confined to protected/restricted forest stands with sufficient microhabitat availability (Müller and Bütler, 2010). This indicates that forest managers, for biodiversity conservation purposes, should increase locally the amount of deadwood and retain a large variability of deadwood types and host species through time, in order to supply the minimum number of different niches to maintain viable populations of the overall saproxylic beetle community (Seibold et al., 2017

Deadwood removal by local communities can be a possible cause for the lower amount of deadwood in BP since oak wood (the most common type in BP) has been usually used for firewood, whereas silver fir (dominant species in AS) has not been utilized for the same scope. Lombardi et al. (2012) evidenced that stumps in AS are the most abundant deadwood type and most of them are of natural origin (also suggesting that AS is somewhat evolving toward a mixed forest type (Lombardi et al., 2008). Müller et al. (2015) found that local saproxylic beetle communities differed in their host preference depending on the stage of deadwood decay, the type of forest stand (broadleaved vs. conifer species) and the region (north to south transect in Germany).



Fig. 4. Partial dependence plots of the influence of forest variables on the Shannon Diversity Index of the total species for BP. Percentages in brackets represent the relative variable importance of the BRT model.



Fig. 5. Partial dependence plots of the influence of forest variables on the Shannon Diversity Index of the saproxylic species for BP. Percentages in brackets represent the relative variable importance of the BRT model.



Fig. 6. Biplot of the NMDS for all the species collected in AS: a) biplot with fitted forest variables; b) biplot representing the species. Squares and black points represent plots and species in the ordination space. Only 20% of the species with the best fitting are reported.

Changes in tree species composition, such as the transition from broadleaved or mixed forest to coniferous forest, may impair the positive effects of species diversity on ecosystem functions and services (Hisano et al., 2018), as well as stand productivity and resilience (Jactel et al., 2018). On the other hand, heterogeneous disturbance patterns may create habitat patches, broadening niche availability and increasing community diversity (Seibold et al., 2017). Information on the spatial and temporal variability of habitat heterogeneity and species diversity in the unmanaged AF and BP forests will help prescribe best management practices and conservation strategies locally tailored.

According to Vallauri et al. (2005), deadwood-related biodiversity

alone represents about 30% of the global forest biodiversity, reaching the 50% for beetles (Bütler et al., 2006; Lachat and Bütler, 2007). In Italy, species of beetles considered as saproxylics reach 15% of the whole Italian beetle fauna (Carpaneto et al., 2015). However, available data on the contingent of saproxylic beetles, compared to the whole beetle fauna occurring in forest ecosystems, are not exhaustive at a regional or national scale. In our study, saproxylic beetles represented about 46% of the whole beetle community (AS, 47%; BP, 45%), thus positioning between global estimates (Vallauri et al., 2005) and regional values (e.g., Germany; Grove, 2002). Unpublished data on saproxylic beetles collected in several forests with different management



Fig. 7. Biplot of the NMDS for all the saproxylic species collected in AS: a) biplot with fitted forest variables; b) biplot representing the species. Squares and black points represent plots and species in the ordination space. Only 20% of the saproxylic species with the best fitting are shown.



Fig. 8. Biplot of the NMDS for all the saproxylic species collected in BP. a) biplot with fitted forest variables; b) biplot representing the species. Squares and black points represent plots and species in the ordination space. Only 20% of the saproxylic species with the best fitting are reported.

history in Central and Southern Italy showed values between 25% and 55% of the whole beetle fauna (Biscaccianti, unpublished results). Therefore, unmanaged AS and BP forests ranked in the upper quartile of the diversity index.

Despite the high volume of deadwood found in AS, the saproxylic richness and diversity were notably lower. The current structure of these forests is the result of past forest management (Lombardi et al., 2013), which has favored the regeneration of silver fir in AS, at the expense of deciduous species, thus determining lower diversity in the beetle coenosis – 85 saproxylic species out of 179. Several species are strongly associated to relict fir forests, at least in the Apennines, such as *Eurythyrea austriaca* (Buprestidae), *Callidium aeneum* (Cerambycidae), *Pissodes piceae*, *Cryphalus piceae* (Curculionidae), *Serropalpus barbatus* (Melandryidae). On the contrary, BP offers a variety of microhabitats and microclimatic conditions (i.e., light availability, moisture level, etc.) that has diversified the spatial availability of resources, supporting higher diversity in the beetle coenosis – 103 saproxylic species out of 226. However, a very low number of strictly stenotopic species occurs in this mixed deciduous forest.

According to our initial hypothesis, we found that Coleoptera diversity and species assemblages were affected by both forest structural traits and tree species composition. Variables related to vertical heterogeneity (STD height) and tree diversity (tree composition and tree dominance) were important in both AS and BP. The analysis revealed that, in AS, increasing stump volume affected negatively both the overall beetle diversity and that of saproxylic species. A similar relationship was found by Sitzia et al. (2015) for the volume of stumps. which was negatively correlated with the number of longhorn and bark beetles. In our case, stumps, primarily of natural origin (Lombardi et al., 2012) and often filled with water, probably favored saproxylic Diptera (Ulyshen and Wagner, 2013) at the expense of Coleoptera species. The standard deviation of tree height, which can be considered a proxy of vertical structure heterogeneity, influenced positively the overall beetle diversity and that of saproxylic species in AS and BP. While deadwood is recognized as a fundamental prerequisite for larval development of saproxylic species, adults may have other requirements (i.e., substrate, microclimate - Wermelinger et al., 2007). Indeed, the heterogeneity in the vertical profile of forest stands determines high availability of food resources, such as leaves, twigs and thin branches, hosting also microhabitats, which are important food resources (Larrieu and Cabanettes, 2012). This may also partially explain the negative relationship between saproxylic diversity and basal area found in AS, where relatively homogeneous dominant canopy trees reduce the heterogeneity of the forest structure (Parisi et al., 2016).

Tree composition (percentage of coniferous species in the plot) and dominance played a negative role in species diversity in both AS and BP. We hypothesize that, in our case, an increase in the proportion of coniferous species in the stand (namely silver fir) probably affected the level of trophic specialization for Coleoptera species, reducing their diversity. The dominance of a few tree species in forest composition would reduce the variety of trophic resources, leading to poor overall species diversity (Wermelinger et al., 2007). Nevertheless, the number of microhabitats positively affected saproxylic diversity in AS, suggesting the presence of different niches for specialized organisms (xylophagous species, species living in tree hollows, species associated with fungi, species associated with sap exudates, etc.). In BP, the amount of CWD positively affected the overall beetle diversity and that of saproxylic species, CWD being a key factor in determining saproxylic species diversity (Lassauce et al., 2011). In particular, dry deadwood with bark represents the optimal substrate for oviposition of early successional beetles, important to ecosystem functioning (Lassauce et al., 2011). Although many of these species are not threatened, e.g., most bark beetles, they form a large part of overall saproxylic diversity and affect later-successional species by building entrance ports for other species (Müller et al., 2008), promoting wood decomposition and introducing fungal species (Hofstetter et al., 2015). Therefore, a higher diversity of early successional species is likely supportive for species of conservation concern (Quinto et al., 2014, 2015; Gossner et al., 2016).

Saproxylic beetles include highly specialized species, with well-defined habits, habitats and specific environmental conditions. Consequently, they are considered suitable indicators for forest ecosystem assessment (Audisio et al., 2009; Persiani et al., 2010; Zehetmair et al., 2014; Carpaneto et al., 2015). In fact, saproxylic beetles play an important role in the forest ecosystem food chain, particularly in the recycling of nutrients, since they depend on – or are involved in – deadwood decay processes. However, current information on status, trends and population distribution of these species are poor particularly in the Mediterranean area (Garcia et al., 2018). Overall, our results indicate that the forest vertical heterogeneity, snag volume and tree dominance were the most important variables for saproxylic assemblages in these Mediterranean mountain forests, while the amount of CWD positively affected the overall beetle diversity and that of saproxylic species. In general, quantity and quality of CWD are key factors in determining the diversity of saproxylic species (Ranius and Jansson, 2000; Lassauce et al., 2011; Lachat et al., 2013). However, our results demonstrate that, in these forests at an intermediate evolutionary stage, the amount (at least) of CWD is a key factor not for saproxylic species only, but also for the whole beetle fauna. Fig. A1

5. Conclusion

In this paper, we have shown how these Mediterranean mountain forests are particularly rich in beetle species. In addition, a large amount of these species (mainly saproxylic) are included in one of the IUCN risk categories. A reliable list of indicator species of saproxylic beetles for these unmanaged forest stands may become useful for conservation commitments, with consideration of rare species. The rarefaction and extrapolation approach enabled the precise comparison of beetle diversity metrics, increasing the effectiveness of ecological inventories for habitat evaluation in this forest ecosystem.

At stand level, differences in species diversity were mainly driven by tree composition (i.e., coniferous forest vs. deciduous or mixed forest), probably indicating that food resources, determined by tree species, are of primary importance in determining species assemblages and beetle diversity in these forests. At plot level, we found that the variables, which drove species composition and beetle diversity, varied between AS and BP. In particular, though deadwood played a fundamental role in maintaining high levels of biodiversity (especially CWD), other factors, such as forest structural heterogeneity and tree species diversity, significantly contributed to saproxylic diversity.

The recognition of statistical changes in biodiversity indices through advanced analytical tools is crucial for cost-effective ecological surveys of forests based on sampling units to determine the species richness for management purposes. In these Mediterranean mountain systems, promoting both vertical and spatial heterogeneity of mixed forests, in addition to deadwood accumulation, will increase or maintain the high level of beetle diversity. Setting aside forest patches of high conservation value may greatly increase the biodiversity of these communities at a landscape scale. In particular, we recommend the adoption of forest planning and management practices that favour deadwood accumulation and heterogeneity within forest stands in support of saproxylic species, as well as increase the extent of old-growth forest patches in the rural landscape to maintain saproxylic species in viable populations. In this sense, ex-ante and ex-post analyses are highly recommended for research purposes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105873.

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