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Micro-habitat drivers of saproxylic beetle assemblages in old woodlands of Mediterranean cork oak (*Quercus suber*)

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Abstract

1. Cork oak landscapes are fascinating ecosystems, historically managed for cork extraction. The persistence in this habitat of many hollow veteran trees provides suitable micro-habitats for saproxylic beetles.
2. We investigated the saproxylic beetle community of two isolated cork oak woodlands of central Italy with different degree of recovery after human transformation: (1) an open woodland and (2) a dense mixed woodland, both dominated by cork oak trees.
3. We found endemic, rare and threatened saproxylic beetles in both the areas, confirming the important conservation value of cork oak landscapes. In the open woodland we observed a higher number of species in all trophic categories, except for mycophagous specialists. Several microhabitat variables reflected the different stage of recovery of the two woodlands.
4. Our findings suggest the crucial role of diversified environments in protected areas: even a small difference in the degree of recovery (i.e., tree closeness) can affect the number of beetle species. Specifically, we found (1) more xerophilous species in the open woodland and (2) more mesophilous species in the dense mixed woodland.

KEYWORDS
beetle ecology, deadwood, hollow trees, insect communities, trap sampling, trophic guilds

INTRODUCTION

Hollow veteran trees are important habitats for biodiversity conservation in forest ecosystems, as many species of animals (e.g., hole nesting birds, small mammals and invertebrates such as wood living beetles) depend on tree cavities. Many of these organisms, associated to tree cavities and dead wood, have disappeared from large forests due to intensive timber exploitation, but survived in small remnant woodlands or even monumental trees in urban areas (Davies et al., 2008).

Species somehow associated to deadwood micro-habitats are often referred as saproxylic, that is species that feed on rotten wood (saproxylophagous), those predating or parasitizing other animals (zoophagous) living in the same environment and those feeding on arboreal fungi (dendromycophagous; cf. Carpaneto et al., 2015; Grove, 2002; Speight, 1989; Stokland & Siitonen, 2012; Ulyshen, 2018). Generally, saproxylic insects, mainly beetle species, are mostly associated to deadwood of old trees, such as in trunks, branches or inside the hollows filled with wood mould (i.e., wood softened by decomposing fungi, often enriched by droppings of insect larvae; Bütler et al., 2013; Dajoz, 2000; Micó, 2018; Speight, 1989). Many authors have classified the veteran trees as keystone structures for forest animals and saproxylic beetles as a keystone group for forest ecosystems (Buse, 2012; Bütler et al., 2013; Carpaneto et al., 2015; Lindenmayer et al., 2012; McLean & Speight, 1993; Müller et al., 2013; Parmain & Bouget, 2018; Speight, 1989; Warren & Key, 1989).

Saproxylic beetles are an important guild of the order Coleoptera, estimated approximately around 2000 and 4000 species in Italy and Europe, respectively (cf. Carpaneto et al., 2015). They are considered one of the most endangered invertebrate groups in Europe, as their habitat has severely decreased (McLean & Speight, 1993). Many species of saproxylic beetles were classified in the red lists dedicated to this insect guild in European countries (Carpaneto et al., 2015; Nieto & Alexander, 2010).

Recent studies have focused on identifying the main factors affecting species richness of saproxylic beetles; these studies highlighted the importance of several factors such as the size of the trunks, the age of the trees, the tree stands, the sun exposure and temperature, the amount and diversity of dead wood, the height of the hollow entrance, the size of the hollow, the wood mould volume, and the isolation from other forest fragments (Gossner et al., 2016; Gough et al., 2014; Micó, 2018; Micó et al., 2015; Micó et al., 2020; Miklín et al., 2018; Parmain & Bouget, 2018; Pilskog et al., 2016; Ranius et al., 2009; Ranius & Jansson, 2000; Sverdrup-Thygeson et al., 2010; Vodka et al., 2009; Wetherbee et al., 2020; Widerberg et al., 2012).

In Europe, hollow oaks (*Quercus* spp.) provide important habitat for wood-living beetles and other animals (Burner et al., 2021; Pilskog et al., 2020; Sverdrup-Thygeson et al., 2010). In northern European countries, where the pedunculate oak (*Quercus robur* L.) is the most widespread oak species, this tree species is considered the most important for invertebrates associated with tree hollows (Ranius et al., 2005; Siitonen & Ranius, 2015). Further studies carried out throughout Europe found similar saproxylic beetle communities in species richness and composition, associated to other tree species, in forests and even in open landscapes (Parmain & Bouget, 2018; Ranius & Jansson, 2000; Sverdrup-Thygeson et al., 2010; Widerberg et al., 2012).

Cork oak *Quercus suber* (Linnaeus 1753), is a medium-sized evergreen tree species belonging to the family Fagaceae and native to the Western Mediterranean basin. Its natural distribution includes the Iberian Peninsula (Portugal and Spain), southern France (from Aquitaine to Provence and Corsica), Italy (northern and central Tyrrhenian coast, Sardinia, Sicilia, Calabria and Apulia) and North Africa (Morocco, Algeria and Tunisia) (Barstow & Harvey-Brown, 2017). Cork oak population is still assumed to be large but decreasing even though the extent of this decline has not been fully assessed. Threats are certainly due to either forest mismanagement or habitat conversion, mainly in terms of expansion of intensive agriculture or timber forestry. Currently, the species is assessed as Least Concern at global level, because the estimated extent of occurrence exceeds the criteria for a threatened category and owing to the legal protection given its distribution throughout Europe (Barstow & Harvey-Brown, 2017). Nevertheless, the risk of becoming Near Threatened or Vulnerable is high for several local contexts because of illegal logging, climatic change and the ongoing abandonment of cork industry (Aronson et al., 2009; Kim et al., 2017).

Despite the ecological, biogeographic, economic and historical interest of Cork oak woodlands (Aronson et al., 2009) due to the ancient cork industry still extant in some areas, the biological communities associated to them have never been investigated in Italy, neither in terms of taxonomic composition nor as regards the ecological relationships between living organisms and environmental parameters. In Spain, on the contrary, the evergreen open woodlands dominated by cork oak and the western holm oak (*Quercus rotundifolia*) have been studied in terms in light of biodiversity conservation, in particular focusing on the guild of saproxylic beetles, revealing the important role of these forests in biodiversity conservation (Micó et al., 2015, 2020; Quinto et al., 2012, 2014, 2015; Ramilo et al., 2017; Ramírez-Hernández et al., 2014; Sanchez-Galvan et al., 2018).

Thus, the aim of this study is to compare the saproxylic beetle community of two isolated cork oak woodlands differing in ecological features due to different temporal gap of abandonment by human industry. Specifically, we want to: (1) to highlight the differences between the two assemblages (rarity, risk category, endemic degree, hot and dry tolerance, trophic roles), (2) to assess the importance of the two assemblages for biodiversity conservation (richness) and ecological functioning in food webs (abundance and trophic roles) and (3) to foresee the consequences of land use change, that is, abandonment of historical cork extraction and recovery of native forest, by comparing the same parameters.

METHODS

Study area

All specimens were collected during an ecological project on saproxylic beetle communities of old oaks in Europe, carried out jointly by Linköping University (Sweden) and Roma Tre University (Italy). Samples were performed in two study sites 'Sughereta di Pomezia' (12°30′59.08″ E, 41°26′10″ N) and 'Bosco Polverino' (13°11′14″ E, 41°39′47.59″ N), both situated in the Tyrrhenian subcoastal zone of the Latium region, central Italy (Figure 1).

Notwithstanding these two woodlands are dominated by the same species (*Quercus suber*) in the tree layer, they show different ecological features. In one of these areas (Pomezia), the cork exploitation was stopped 40 years ago, while in the other one (Polverino) such activity was abandoned about 80 years (Novak et al., 2012). This different temporal gap of abandonment by human industry implied a dissimilar aspect of the two woodlands.

The first study area, 'Sughereta di Pomezia', is a small fragment of open woodland (about 60 ha; 50–80 m a.s.l.) characterized by old cork oak trees and a sparse evergreen bushy layer, surrounded by cultivated areas and human settlements. In the last two decades, grazing

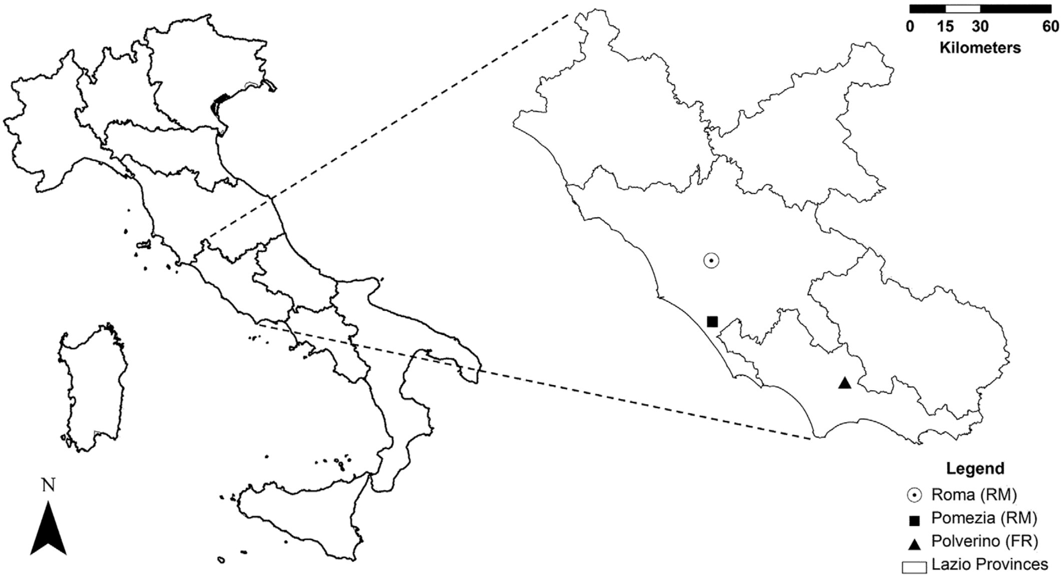

FIGURE 1 Study area

activity became progressively reduced to a low number of sheep. The second study area, 'Bosco Polverino', is another small fragment (about 107 ha) of mixed evergreen/deciduous forest, surrounded by cultivated areas. This area is located in the Latina province, near Priverno, at an altitude of 20–70 m a.s.l. The tree layer is mostly formed by evergreen oaks (*Quercus suber* and *Quercus ilex*) mixed with deciduous oaks (*Quercus cerris, Quercus frainetto, Quercus pubescens*). According to the native countrymen, before the 60s of the 20th century, the cork oak was almost the only tree species occurring in the site, favoured by man for the traditional exploitation of the bark. In the last decades of the past century, the commercial importance of cork started to decline and this fact determined the gradual abandonment of such industry. The consequent increased competition with deciduous trees from neighbouring woodlands produced the mixed (deciduous and evergreen) species composition and the dense forest aspect of the area.

The different temporal gap of abandonment by human industry implied a dissimilar aspect of the two woodland: in the first case (Pomezia), it still retained a wooded pasture aspect (open woodland with a bushy underground of evergreen species), with trees that have been kept spaced among them due to the continuous clearing action of livestock (sheep and cattle); in the second case (Polverino), the invasion by native bush and trees started a reforestation process, with cork oaks still dominant at tree layer, while the undergrowth is rebuilding a close and dense mixed deciduous woodland, similar to local native young forests (Novak et al., 2012). This vegetation density affected light, temperature and humidity gradients, factors that led us to expect qualitative and quantitative differences in beetle assemblages (Seibold et al., 2016). Both the study areas harbour a high number of old hollow cork oaks and induced us to investigate richness, diversity and species composition of saproxylic beetle assemblages.

Currently the 'Sughereta di Pomezia', is included in the 'Riserva Naturale della Sughereta di Pomezia (L.R. 12, 10/08/2016)', while

TABLE 1 List of the microhabitat variables used for analysing saproxylic richness and composition (from Chiari et al., 2012). Mean (μ) and SD are provided

Variable	Value (μ ± SD)	
TWR: Type of the rotten wood in the visible part of the cavity	/	
WMM: Wood Mould Moisture	/	
PWMSo: Proportion of Wood Mould/Soil	/	
FDS: Foliage density sun	81.06	±25.39
FDC: Foliage density cavity	65.18	±34.32
S: Slant of entrance hole	/	
DIAM: Trunk diameter	274	±82.41
H: Cavity height from the ground	40.76	±54.13
AEH: Area of entrance hole	5466.92	±5651
DWM: Distance to wood mould	10.24	±22.55
WMA: Wood mould area	4273.36	±4318.38
DEWM: Depth of wood mould	13.35	±7.17
AWM: Amount of wood mould	24300.97	±29768.87
TD: Trap distance from the ground	135.59	±54.35

'Bosco Polverino' is classified as Special Area of Conservation (IT6040004), according to the European Union Habitats Directive, and is managed for conservation and recreational purpose towards the recovery of old-growth trees of all species.

Sampling design

For collecting saproxylic beetles, traps were set exclusively on old hollow trees. We selected eight trees in 'Sughereta di Pomezia' and nine trees in 'Bosco Polverino', located in a stand of 2–10 ha and in a distance of about 500 m from other hollow trees. For each tree, we measured a total of 14 microhabitat variables related to cavity features that we considered as potentially important for the local species richness and composition in the different microhabitats, that is, temperature, fungal activity and activity of birds and mammals (Tables 1 and S1, for more information see also Chiari et al., 2012). We considered the chosen parameters because most of them have been proved to be crucial in other studies (Micó, 2018; Micó et al., 2015, 2020; Miklín et al., 2018; Parmain & Bouget, 2018; Ranius, 2002; Ranius et al., 2009; Ranius & Jansson, 2000; Sverdrup-Thygeson et al., 2010; Vodka et al., 2009; Wetherbee et al., 2020; Widerberg et al., 2012).

Saproxylic beetles were sampled with two trap types: pitfall traps (PT) placed inside the trunk cavity and windows traps (WT) set near the trunk (<1 m) in front the cavity. For each tree, a windows trap and a pitfall trap were placed. The windows traps consisted of a 30 × 60 cm wide transparent plastic plate with a tray underneath (Jansson & Lundberg, 2000). Their positions were 0–7 m from the ground, depending on where the cavity entrance was located on the studied tree. The pitfall traps were plastic cups with a top diameter of 6.5 cm. They were placed in the wood mould at the bottom of the cavity. Both types of traps were partially (about ½ of the volume) filled with ethylene glycol and water (50:50 v/v), adding some detergent to reduce surface tension. All traps were checked at 3 weeks interval from April to August of 2009 and 2010. As our sampling scheme did not cover the entire flight periods for all species, some early and late species may not be represented in this study.

In this paper, we considered only beetles whose larval biology is sufficiently well-known to be considered saproxylic and therefore occurring in the database for the Italian IUCN Red List (Carpaneto et al., 2015) which includes all the species reliable to be recognized in the saproxylic guild.

Materials

The beetle specimens collected were classified by two of us (Nicklas Jansson and Giuseppe M. Carpaneto) as coordinators, with the collaboration of several specialists, whose names are listed in the acknowledgements. The voucher specimens are conserved in the local insect collections of Linköping University (Sweden) and Roma Tre University (Italy); several specimens of systematic and biogeographical interest were given to the specialists who required them for their personal collections and taxonomic studies.

Nomenclature and classification (including the hierarchic relations among families) followed Bouchard et al. (2011). Basic information on the trophic roles among the saproxylic organisms is still very scarce and their ecological niches are poorly known. We used the information produced by a team of taxonomists specialized in various families, and gathered into the Italian red list of saproxylic beetles (Carpaneto et al., 2015). According to the feeding behaviour of their larvae, we considered the following categories of saproxylic beetles: saproxylophagous (SX, mainly feeding on still compacted dead wood of standing or fallen trees); tree cavity saproxylophagous (SP, feeding of wood debris or dust inside tree cavities); xylophagous (XY, also feeding on healthy tree wood), dendrolymphophagous (SF, feeding on fermented sap or exudates produced by attacked trees), predators (PR, mainly feeding on other invertebrates), mycophagous (MY, feeding on fungi, including micromycetes, yeasts and myxomycetes; some of these species feed only on large mushrooms or arboreal fungi). Saproxylic species belonging to category represented by less than three specimens were not included in the further analysis.

The trophic traits analysed in this study were extrapolated from those reported in the Italian red list of saproxylic beetles (Carpaneto et al., 2015) and merged into fewer categories for simplifying the analysis and making the results more understandable.

As regards the conservation status of the species we grouped species theme as 'threatened' if listed under the Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) categories, and 'not-threatened' if listed under the Least Concern (LC) or Near Threatened (NT) categories.

Statistical analysis

We evaluated the effect of microhabitat drivers on saproxylic beetles richness, diversity and assemblage composition. As a measure of species richness and diversity, we considered three response variables: (1) total and threatened species richness ('SR' and 'TSR' respectively), and (2) the exponential Shannon diversity index (Jost, 2007; henceforth 'Shannon diversity, 'ShDiv') calculated on the whole community (total number of species). This index weighs species by their abundance, thus reducing the influence of rare species on the metric and therefore helping to detect effects of micro-variables on diversity caused by differences in the evenness of samples (Hill, 1973).

As a measure of species composition, we considered two response variable: (1) the taxonomical dissimilarity between each pair of sample calculated using Bray-Curtis distance with standardized and square root-transformed abundance data; (2) The community-weighted means (CWM) of trophic traits dissimilarity between each pair of sample calculated using a Gower's dissimilarity matrix. In our study, the community-weighted means express the mean trophic traits value between species occurring in each sample, weighted by the relative abundance of each species (Violle et al., 2007). We derived a 'CWM-by-sample' matrix by multiplying the sample-by-species matrix with a species-by-trait matrix using the function 'functcomp' of the 'FD' package in R software (Laliberté et al., 2014; Laliberté & Legendre, 2010).

To analyse differences in species richness, in Threatened Species Richness and in Shannon diversity among sites (Polverino and Pomezia), traps (Pitfall and Windows) and years of sampling, we performed the Mann–Whitney *U*-test using the wilcoxon. test *R* function.

To analyse differences in species and community-weighted means of trophic traits composition among sites, traps and years of sampling we performed a non-parametric a two-way PERMANOVA procedure. This is a semi-parametric test analogous to multivariate analysis of variance but with pseudo *F*-ratios and *p*-values generated

TABLE 3 Results of multi-model inference conducted on species composition and community weighed mean (CWM) of trophic guild using generalized linear models

Responce variable	Covariates	β	SE	*p*	*W*
Species composition	**Intercept**	77.131	1.076	<0.001	
	AWM	0.029	0.009	<0.01	0.27
	FDC	0.054	0.013	<0.001	0.27
	TD	0.102	0.018	<0.001	0.27
	TWR	0.061	0.017	<0.001	0.11
	DEWM	0.039	0.013	<0.01	0.07
CWM	**Intercept**	9.951	0.339	<0.001	
	DIAM	0.074	0.011	<0.001	0.33
	TD	0.054	0.009	<0.001	0.33
	TWR	0.026	0.007	<0.001	0.19
	WMM	0.027	0.008	<0.001	0.14

Note: Only models with ΔAIC_c <2 are shown. Average standardized coefficient (β), standard error (SE), *p*-values (*p*) and relative importance from Akaike weights (*W*) are shown. Predictor variables are: AWM, amount of wood mould; DEWM, depth of wood mould; DIAM, trunk diameter; FDC, foliage density cavity; TD, trap distance from the ground; TWR, type of the rotten wood in the visible part of the cavity; WMM, wood Mould moisture.

by 9999 permutations (Anderson et al., 2006; Clarke & Gorley, 2006). PERMANOVA analysis was performed on two Bray-Curtis Similarity matrices based on standardized and square root transformed species abundance and CWM data, respectively. The design was a two-way PERMANOVA with Site as one factor with two levels (Polverino, POL and Pomezia, POM), traps as one factor with two levels (Pitfall, PT and Windows, WT) and Years as one factor with two levels. The design was run using a permutation of residuals under a full model (9999 permutations) with Type III (partial) sums of squares. Multivariate patterns were shown by a principal coordinates analysis (PCO) plot (Gower, 2005). Both PERMANOVA and PCO analysis were performed by using the software PERMANOVA + for PRIMER (Anderson et al., 2006; Clarke & Gorley, 2006).

Finally, to identify which microhabitat variables among those selected (Table S1) were most related to species richness, species diversity, species composition and community-weighted means of trophic trait composition, we applied an information theoretic approach (Burnham & Anderson, 2004) through model selection and multi-model inference (testing all possible combinations of predictor variables excluding combinations that include correlated variables [based on Pearson' correlation coefficient], $|r| > 0.7$; Dormann et al., 2013). Specifically, the Akaike information criterion (AIC; Akaike, 1973) was used, and models were ranked based on ΔAIC (considering only models with ΔAIC <2; Burnham & Anderson, 2004). We estimated standardized regression β-coefficients (and their relative standard errors) as well as significance and importance (calculated as the sum of the Akaike weights, *W*) of all the predictor variables entered in the best model(s) through model averaging. Specifically, we carried out generalized linear models (GLMs) and multi-model inference using the *R* package 'MUMIN' (v. 1.0.0. Barton, 2009), initially grouping all data collected through pitfall and windows traps in both Polverino and Pomezia study sites (Table 3) while, in a second step, we split data based on traps and study sites (Tables S4-S5).

RESULTS

We collected and identified a total of 14,288 beetles belonging to 284 species and 43 families (Table S2). After removing species not included in the IUCN red list of Italian saproxylic beetles (Carpaneto et al., 2015), which includes all saproxylic beetles inhabit the country, we focused on 12,511 individuals (2044 in PTs and 10,603 in WTs) belonging to 192 species (100 in PTs and 185 in WTs) and 35 families (Table S3). Seventeen of these selected species were threatened (eight endangered, seven vulnerable, two critical endangered) (Table S3). Among them, according to their trophic trait we found: 60 saproxylophagous, 48 mycophagous, 37 predators, 33 xylophagous, 8 tree cavity saproxylophagous and 7 dendrolymphophagous.

For taxonomical and trophic guild composition analysis, rare species (singleton and doubleton, total = 60) were omitted.

Cork oak woodland saproxylic assemblages

The trap types used for collecting saproxylic species (WT and PT) and the site where these beetles were collected (Polverino and Pomezia) are both important drivers of the compositional differences among samples (Figure 2). Indeed, both the trap type and sites showed a high significant effect on species composition (Permanova: traps pseudo-$f = 8.803$, $p < 0.001$; sites pseudo-$f = 10.025$, $p < 0.001$) and a minor but still significant effect on community-weighted means of trophic traits composition (Permanova: traps pseudo-$f = 12.531$, $p < 0.01$; sites pseudo-$f = 7.900$, $p < 0.01$).

The number of species did not vary between Polverino and Pomezia while Shannon diversity index, and the proportion of all trophic categories (except for predators) differed significantly among sites with Pomezia being always higher than Polverino (Figure 3,

TABLE 4 Results of multi-model inference carried on (1) species richness and diversity trait (SR, species richness; ShDiv, Shannon diversity; TSR, threatened species richness) and (2) the proportion of each trophic trait (MY, proportion of mycophagous; PR, proportion of predators; SF, proportion of Dendrolymphophagous; SX, proportion of Saproxylophagous; XY, proportion of Xylophagous; SP, tree cavity saproxylophagous), through generalized linear models

	SR	ShDiv	TSR	MY	PR	SF	SP	SX	XY
S							0.062 (0)*		
DEWM							0.017*	−0.053	
FDC	−3.954*	−0.344***	−0.927***	0.132*	−0.04**	0.015*			−0.036**
FDS					0.025*			−0.086**	0.023*
H			−0.569*						0.032**
AWM						0.032***	0.02*		−0.084*
PWMSo		0.533(S)*		−0.452(S)**	0.0518 (S)*			−0.278(WMS)**	
TD		−0.312***	−0.523**	0.066*				−0.116***	0.02*
DIAM		0.169*		0.151**					−0.026*
DWM			0.611**	0.197***		−0.021**	−0.023**		
TWR				−0.218(0)* 0.226(1)*				−0.291 (0)**	
WMM				0.221(1)* 0.219(2)**			0.051(2)*	−0.185(2)*	0.061(1)*
AEH							0.027*		
WMA				−0.284***					−0.021*

Note: Average standardized coefficient (β) of significant predictors from models with ΔAIC_c <2 are shown. Levels of the categorical variables are provided in brackets (see Table S6 for details). Asterisks indicate the level of significance (*p < 0.05; **p < 0.01; and***p < <0.001). Predictor variables are: AEH, area of entrance hole; AWM, amount of wood mould; DEWM, depth of wood mould; DIAM, trunk diameter; DWM, distance to wood mould; FDC, foliage density cavity; FDS, foliage density sun; H, cavity height from the ground; PWMSo, Proportion of wood mould/soil; S, slant of entrance hole; TD, trap distance from the ground; TWR, type of the rotten wood in the visible part of the cavity; WMA, wood mould area; WMM, wood Mould moisture.

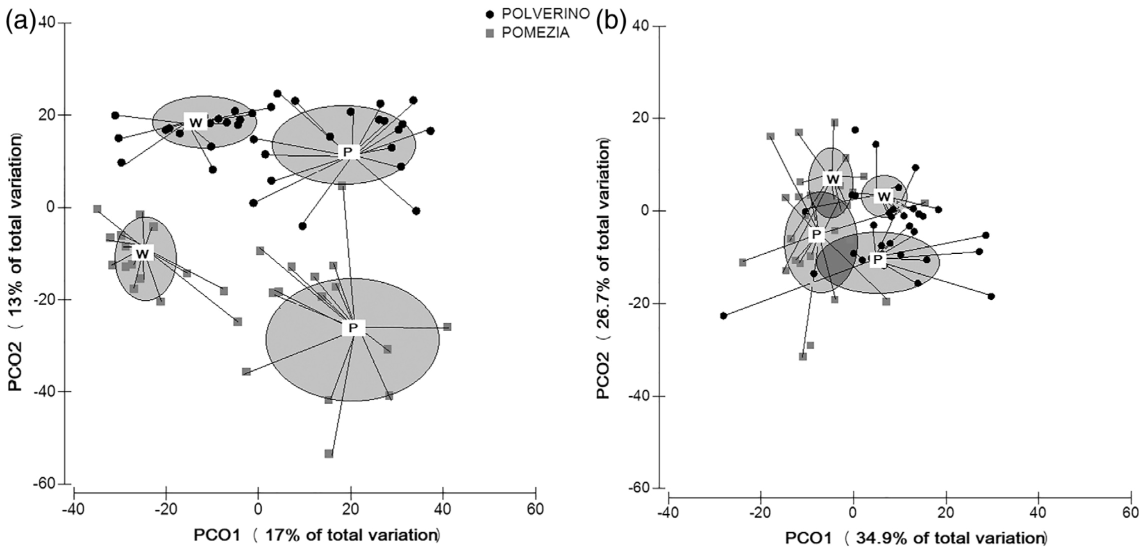

FIGURE 2 Taxonomic (a) and CWM of trophic trait (b) composition of the saproxylic communities grouped by trap type (P, pitfall; W, windows) and study area (Polverino and Pomezia). Each point represents a community in a principal coordinate analysis (PCO) space based on Bray-Curtis taxonomical and functional dissimilarities between communities. The proportion of explained variance for the first and second axis of each plot is shown

Table 2). Only the proportion of mycophagous of Windows Traps assemblage was significantly higher in Polverino (Figure 3f). All taxonomical metrics and the proportion of two trophic categories, mycophagous and xylophagous, differed significantly among trap type (Figure 3, Table 2) with window traps always higher than pitfall traps.

Effect of microhabitat variables on saproxylic assemblages

Multi-model inference showed that the best predictor model driving the composition of saproxylic beetle communities included five microsite variables: amount of wood mould, foliage density sun, trap distance from the ground, type of the rotten wood and depth of wood mould. All of them where significantly related to species composition but amount of wood mould, foliage density sun and trap distance from the ground where the most important one, accounting for almost the total Akaike weight (Table 3). The pitfall traps assemblage was mostly affected by trap distance from the ground in Polverino site and by the area of entrance hole and trunk diameter in Pomezia site (Table S4). The windows trap assemblage was mostly affected by the proportion of wood mould and foliage density sun in Polverino and by the distance to wood mould and the cavity foliage density in Pomezia (Table S4).

The community weighed mean (CWM) of trophic traits responded partially to the same microsite predictor found for species composition. Indeed, the best model driving these functional communities included again trap distance from the ground and type of the rotten wood but also two different variables: trunk diameter and wood mould moisture (Table 3). trunk diameter and trap distance from the ground where identified as the most important drivers for the CWM of trophic traits. In particular, the proportion of trophic trait found in pitfall traps were mostly affected by trunk diameter in both Polverino and Pomezia sites (Table S5) while those found in windows traps were mostly affected by foliage density sun in Polverino and by trunk diameter and the cavity foliage density in Pomezia (Table S5).

All the microsite variables analysed act on at least one taxonomic metric and one trophic trait (Tables 4 and S6). The cavity foliage density is undoubtedly the main factor affecting the saproxylic assemblages under study: this factor significantly structured species composition in almost all the assemblages and affected negatively the total species richness (included the threatened ones) and diversity. We also found a clear vertical stratification of saproxylic assemblages based on trap position (Tables 4 and S6). Our results showed an equal vertical distribution of predators and a general increasing of species richness and diversity with the decreasing of cavity height from the ground. Moreover, we found that, with the increasing of cavity height from the ground only some trophic categories dominated, reducing the overall functional diversity. These two categories are the mycophagous (including mycetophagous) and xylophagous beetles which represented the most numerous beetles in our assemblages, but resulted proportionately more abundant in higher cavities.

Trunk diameter is another important variable for the saproxylic assemblages under study. We did not find any effect of tree diameter on the overall species richness and on threatened species richness. Conversely our results showed a strong and positive relationship between large trees and species diversity.

The microhabitat variables distance to wood mould, proportion of wood mould/soil and wood mould moisture were included in the best models for at least four of the metrics considered. Among them, the distance to wood mould was one of the most important variables for

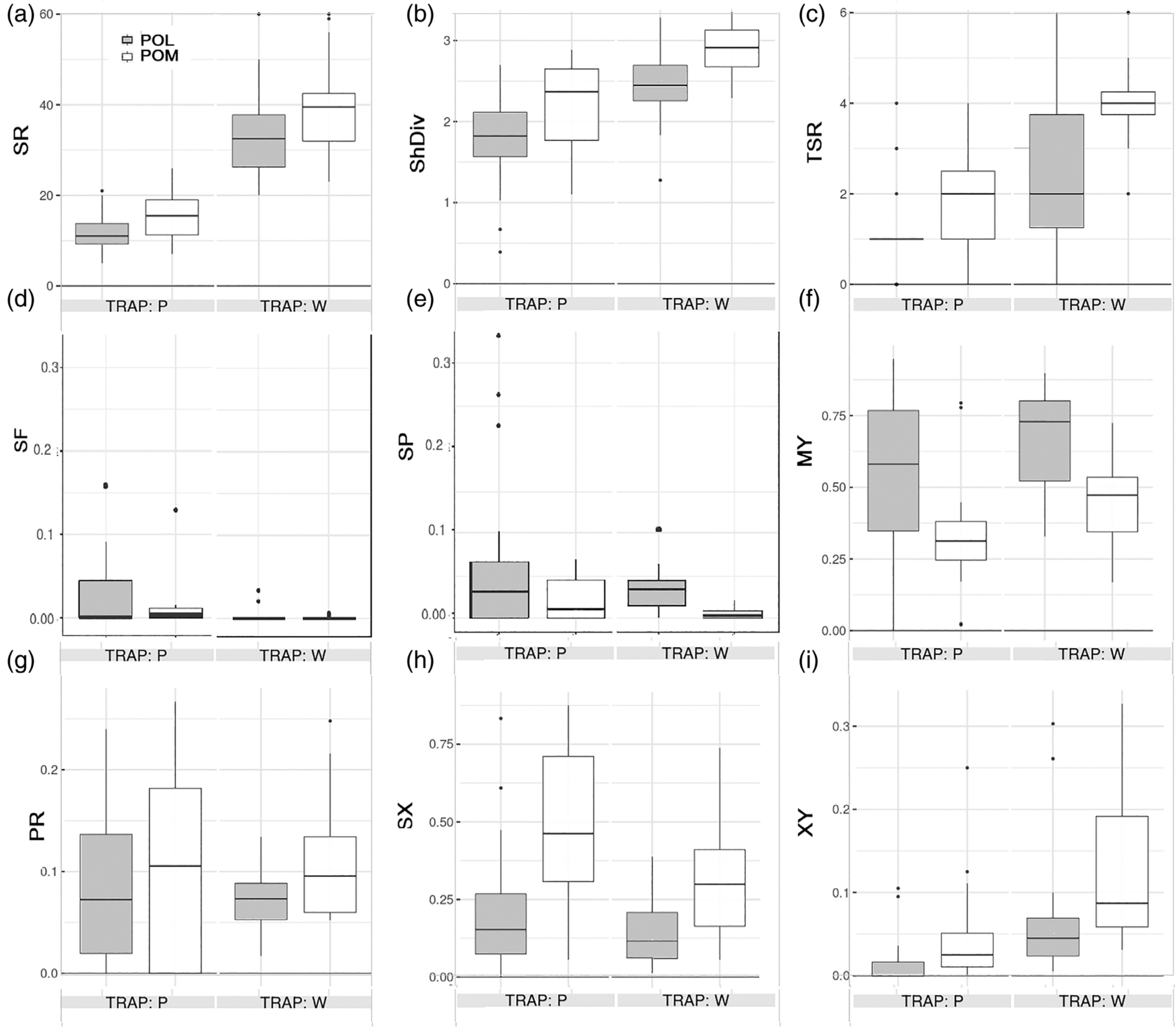

FIGURE 3 Boxplot showing the saproxylic beetles richness and diversity (a, b); the threatened species richness (c) and the community weighed mean values of dendrolymphophagous (SF), tree cavity Saproxylophagous (SP), mycophagous (MY), predators (PR), saproxylophagous (SX) and xylophagous (XY) grouped by the trap type and the study area

threatened species richness, mycophagous beetles, dendrolymphophagous and tree cavity saproxylophagous beetles acting positively on the first two and negatively on the others.

Cavities with very humid wood mould seem to be elective habitats for mycophagous and tree cavity saproxylophagous beetles while are avoided by saproxylophagous ones. Xylophagous beetles are proportionally more abundant in cavities with moist wood mould.

The proportion of wood mould/soil found in the cavity was one of the most important variables for mycophagous and saproxylophagous beetles. In particular the predominance of soil in the cavity (S) affected negatively the proportion of mycophagous beetles while the presence in the cavity of an equal mixture of soil and wood mould (WMS) affected negatively the proportion of saproxylophagous species.

Foliage density is one of the most important variables for xylophagous beetles while the amount of wood mould present in the cavity is the most relevant variables affecting dendrolymphophagous species. The less common microsite variables included in the models are: depth of wood mould, slant of entrance hole, area of entrance hole, wood mould area, cavity height from the ground and type of the rotten wood. The wood mould area in the cavity negatively affected the proportion of mycophagous species. Cavity height from the ground had mainly a positive effect on the proportion of xylophagous beetles. The absence of rotten wood in the cavity (0) had a strong negative effect on saproxylophagous beetles.

TABLE 2 Mann–Whitney *U*-tests comparing the effect of traps, sites and years on saproxylic beetles species, functional diversity and the proportion of each trophic trait (MY, proportion of Mycophagous; PR, proportion of predators; SR, species richness; ShDiv, Shannon diversity; SF, proportion of Dendrolymphophagous; SX, proportion of Saproxylophagous; TSR, threatened species richness; XY, proportion of Xylophagous; SP, tree cavity saproxylophagous). In bold significant values

	Traps ($W = 34$; $P = 34$)		Sites (POL = 36; POM = 32)		Years (2009 = 34; 2010 = 34)	
	z	*p*	*z*	*p*	*z*	*p*
SR	−6.884	**<0.001**	−1.487	0.136	−1.429	0.152
ShDiv	−4.538	**<0.001**	−3.367	**<0.001**	−0.356	0.722
TSR	−4.266	**<0.001**	−2.931	**<0.01**	−2.368	0.027
MY	−2.03	**0.042**	−3.84	**<0.001**	−0.147	0.882
PR	−0.491	0.623	−1.457	0.145	−1.436	0.151
SF	−0.029	0.976	−3.47	**<0.001**	−0.196	0.844
SP	−0.563	0.573	−3.221	**<0.01**	−0.075	0.940
SX	−1.797	0.072	−3.95	**<0.001**	−0.043	0.965
XY	−4.463	**<0.001**	−2.672	**<0.01**	−4.463	0.532

DISCUSSION

We found a high number of threatened beetles mainly linked to advanced deadwood decomposition stage and to stable microclimate conditions, confirming the important ecological role of cork woodlands and the high conservation value of old hollow trees as elective habitat for many vulnerable species (Quinto et al., 2014). We observed the predominance of different components of species diversity and trophic traits as well as the effect of several microsite variables according to sites and trap type assemblages, indicating high heterogeneous environments (Scarascia-Mugnozza et al., 2000). The use of two different trap types is a source of variability as species with different ecological needs are captured (Peuhu et al., 2019; Stefanelli et al., 2014). Furthermore, in our case, another source of variability is represented by the difference between the two woodlands in terms of maturity and historical management. The maturity of the woodlands and the historical tree management affect the availability of tree microhabitats with a consequent effect on variety and diversity of species (Quinto et al., 2014). Mature woodland sites with higher tree heterogeneity and larger trees, larger hollows, higher hollow openings and greater volumes of wood mould, house greater species diversity compared to less mature and preserved sites. Moreover, different or even unmanaged woodlands can model substrate availability and offer different tree microhabitats, which benefit certain saproxylic groups (Marcos-García & Galante, 2013; Ranius et al., 2009).

Cork oak woodland saproxylic assemblages

Among the species collected, 17 were classified as threatened by the Italian red list of saproxylic beetle (Carpaneto et al., 2015). Among them, the endangered beetle *Allecula suberina* Novák 2012 (Novak et al., 2012), is a recently described species, still now only known of Pomezia and Polverino, and caught with both trap types. So it was considered as a species associated to the trunk cavities in old cork oaks, but further investigations could be undertaken for confirming this assertion. Two species, *Pityophagus quercus* (Nitidulidae) and *Eledonoprius armatus* (Tenebrionidae), classified respectively as endangered and critically endangered, were already discussed for the sites investigated (Audisio et al., 2011; Carpaneto et al., 2013). The presence of *P. quercus* at the Bosco Polverino was reported by Audisio et al. (2011) and it was the first record of the species for Italy. *P. quercus*, host of the ancient primary xerophilous and meso-xerophilous oak forests of south-central Europe (Barnouin et al., 2011; Müller et al., 2005), is considered among the most important entomological 'markers' of old-growth forests (Audisio et al., 2011). The capture of this species in a dense regrown woodland seems to indicate that the species can persist in a human-managed woodland with a reduced nucleus of specimens for long time. The same consideration could be made for *E. armatus*, considered to be a relict species of the primeval European forests (Espanol, 1985; Müller et al., 2005). It has a scattered occurrence in Europe being restricted to approximately 50 localities from central and southern Europe (Carpaneto et al., 2013). According to the literature, the species of this genus have a narrow ecological niche (Brustel et al., 2004; Soldati et al., 2009) the most important feature of which is its dependence on hollow old deciduous trees colonized by bracket fungi that are their primary food resource. The persistence of old hollow oaks with bracket fungi, even if strongly perturbed by human management, can allow the conservation of this species with reduced populations.

The present recovery status of the Polverino woodland allows the conservation of a high abundance of mycophagous species, secondary saproxylic beetles linked to advanced dead wood decay stages (Campanaro et al., 2010; Lee et al., 2014). Their abundance could be due to the high tree density of this close forest and consequent humidity that could have favoured the abundance and diversity of fungi (Carpaneto et al., 2015).

Saproxylophagous beetles were the most abundant group found in Pomezia and this may be due to the high availability of old hollow trees with a great amount of wood mould and open spaces among trees which allow moderate conditions of humidity inside the cavities. They partially overlap with mycophagous beetles at the intermediate stage of wood decay (Parisi et al., 2018), but many species, feeding often on still compacted dead wood (Carpaneto et al., 2015), colonize earlier stages of decaying wood. These findings clearly reflect the different degree of recovery after human transformation. Pomezia shows the open physiognomic features of an habitat where cork is still harvested although with a low rate, while the regrowth of natural trees and bushes is hampered by frequent sheep grazing (Novak et al., 2012). On the contrary, Polverino is a close and humid forest because cork harvesting was almost abandoned since some decades and grazing is not a continuous event (Novak et al., 2012). The lack of the two above mentioned species (*P. quercus* and *E. armatus*) in Pomezia let us to suggest that the survived nucleus of these species in this location is so small that the probability to capture specimens in very low.

Effects of microsite variables on saproxylic assemblages

Our results indicate that saproxylic beetles are influenced by several microhabitat variables which change according to the sites and trap type assemblage.

Species and trophic guilds composition are affected by different parameters. Some factors strongly influence species turnover such as the light condition in the cavity due to the percentage of the sky covered by foliage seen from the entrance of the cavity (FDC).The general importance of the insolation produced by canopy openness for saproxylic beetles is widely known (Della Rocca et al., 2014; Müller et al., 2010; Ranius & Jansson, 2000) and could be explained by the micro-climatic effects of sun exposure on deadwood substrate quality (Bouget et al., 2014).

Other factors which influence the proportion of each trophic category within the assemblage are tree diameter and, to a lesser extent, the type of rotten wood in the visible part of the cavity. Large pieces of woody debris generally host a large number of species (Grove, 2002; Hottola et al., 2009; Nordén & Paltto, 2001) and are widely recognized as critical habitats for rare or threatened beetle species (Hammond et al., 2004; Langor et al., 2008). However, saproxylic species linked to cavities occupy already large trees. Therefore, it is likely that size variability provided by these large trees provides higher substrate heterogeneity and higher stability, two factors that can lead to an increasing in species richness and functional diversity (Lutz et al., 2013). Only mycophagous beetles resulted to be strongly affected by tree size, being in proportion more abundant in large trees and driving this effect on the whole species composition. The vertical stratification of saproxylic beetles assemblages found in our study is highly linked to cavity distance from the ground. The effect of hollow height on saproxylic assemblages could be related to changes in qualitative features of cavity and wood mould (Micó et al., 2015; Taylor & Ranius, 2014). Moreover, tree diameter and hollow height above ground (possibly related to hollow depth) have previously been identified as important factors affecting hollow microclimate (Isaac et al., 2008) buffering internal microclimate against external fluctuations. This could represent consequently the ideal condition for the development on many fungus species which can favour the presence of beetles such as those investigated in our study. Moreover, among saproxylic beetles investigated, the mycophagous species seem to prefer cavities with high distance to wood mould (deep cavity), high quality wood mould, small wood mould surface (low rate of wood mould dehydration) and extremely wet conditions (high rate of relative humidity): all parameters which are more likely to occur in cavities located at greater height (Micó et al., 2015). Unlike what has been reported in the literature so far (Ranius, 2002; Schauer et al., 2018), we found a general preference of beetles for moist or humid microclimate inside the cavities and no preferences were found for dry cavities. This phenomenon could be due to the difference between North European and Mediterranean climate, and to the intrinsic characteristic of the Mediterranean cork oak woodlands, characterized by relatively open canopy and long period of drought (Quinto et al., 2014; Santana et al., 2011). In these woodlands, water content is one of the most important limiting factors. During the hot summer months, trees with cavities able to provide stable microclimate conditions and a suitable level of humidity (i.e., favourable conditions for fungi) are very rare in the Mediterranean littoral zones.

CONCLUSIONS

Cork oak landscapes are a fascinating ecosystem favoured by man and managed for cork extraction, but also inhabited by many animal species, included rare saproxylic species (Berrahmouni et al., 2009; Zavala et al., 2004). The presence, in the investigated woodlands, of many endemic, rare and threatened species and in some cases also recently described taxa for the science, confirmed the important conservation value of cork oak landscapes and pointed out the current lack of knowledge of the entomofauna associated with this habitat, especially in some Mediterranean countries such as Italy.

Both the investigated locations allowed for the existence of a high biodiversity of beetles at both taxonomical and functional level, and are home to highly specialized communities with different habitat requirements that reflect different forest management. These findings suggest the crucial role of diversified environments and the importance of maintaining extensive management practices for preserving saproxylic biodiversity in cork oak forests (Marchetti, 2004). In particular, the persistence of old hollow trees and the presence of close to mature forest patches in an open (savannah like) woodland, could guarantee adequate microclimatic conditions for several species that would disappear in a scenario of increasing drought severity which Mediterranean ecosystems are facing (Kim et al., 2017).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Detailed description of the microhabitat variables used for analysing saproxylic richness and composition (from Chiari et al., 2012). Mean (μ) and SD are provided.

Table S2. List of all the beetles species collected during the two field seasons in Polverino and Pomezia woodlands. The table shows: the total number of individuals per species; the IUCN category; the Trophic Categories (the Original TC, reported in the Italian red list of saproxylic beetles by Carpaneto et al. (2015), and the new one [simplified], Group TC, created for this paper). The species excluded for all the analysis (because not strictly saproxylics) and those excluded for the compositional analysis (because singleton or doubleton) are also showed.

Table S3. List of all the saproxylic beetles considered for the analysis. For each species the table shows: the IUCN category; the trophic category (obtained by grouping the original trophic categories in more simplified categories, see Table S2 for details); the number of individuals found in each site and in each trap type.

Table S4. Results of multimodel inference conducted on species composition using generalized linear models, GLMs. Only models with ΔAIC_c <2 are shown. Average standardized coefficient (β), standard error (SE), *p*-values (*p*) and relative importance from akaike weights (*W*) are shown. Predictor variables are: S, Slant of entrance hole; DEWM, Depth of wood mould; FDC, Foliage density cavity; FDS, Foliage density sun; H, cavity height from the ground; AWM, Amount of wood mould; PWMSo, Proportion of Wood mould/Soil; TD, trap distance from the ground; DIAM, Trunk diameter; DWM, Distance to wood mould; TWR, Type of the rotten wood in the visible part of the cavity; WMM, Wood Mould Moisture; AEH, Area of entrance hole; WMA, wood mould area.

Table S5. Results of multimodel inference conducted on CWM of trophic category using generalized linear models, GLMs. Only models with ΔAIC_c <2 are shown. Average standardized coefficient (β), standard error (SE), *p*-values (*p*) and relative importance from akaike weights (*W*) are shown. Predictor variables are: S, Slant of entrance hole; DEWM, Depth of wood mould; FDC, Foliage density cavity; FDS, Foliage density sun; H, cavity height from the ground; AWM, Amount of wood mould; PWMSo, Proportion of Wood mould/Soil; TD, trap distance from the ground; DIAM, Trunk diameter; DWM, Distance to wood mould; TWR, Type of the rotten wood in the visible part of the cavity; WMM, Wood Mould Moisture; AEH, Area of entrance hole; WMA, wood mould area.

Table S6. Results of multimodel inference of the whole saproxylic assemblage using generalized linear models, GLMs. Only significant variables from models with ΔAIC_c <2 are shown. Average standardized coefficient (β), standard error (SE), *p*-values (****p* < 0.001; ***p* < 0.01; and **p* < 0.05) and relative importance from akaike weights are shown. Predictor variables are: S, Slant of entrance hole; DEWM, Depth of wood mould; FDC, Foliage density cavity; FDS, Foliage density sun; H, cavity height from the ground; AWM, Amount of wood mould; PWMSo, Proportion of Wood mould/Soil; TD, trap distance from the ground; DIAM, Trunk diameter; DWM, Distance to wood mould; TWR, Type of the rotten Wood in the visible part of the cavity; WMM, Wood Mould Moisture; AEH, Area of entrance hole; WMA, Wood Mould Area.

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