



## Diversity of beetle species and functional traits along gradients of deadwood suggests weak environmental filtering

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### ARTICLE INFO

#### Keywords:

Abundance

Forest

Italy

Joint species distribution model

Saproxyllic

Trophic group

### ABSTRACT

**Background:** Gradients in local environmental characteristics may favour the abundance of species with particular traits, while other species decline, or favour species with different traits at the same time, without an increase in average species abundances. Therefore, we asked: do variations in species and traits differ along gradients of deadwood variables? Do species abundance and trait occurrence change with species richness within or between functional groups? Thus, we analysed the beetle assemblages of five forest sites located in Italy, along the Apennines mountains.

**Methods:** From 2012 to 2018 we sampled beetles and five deadwood types in 193 plots to characterise the deadwood gradient: standing dead trees, snags, dead downed trees, coarse woody debris, and stumps. We modelled beetle species relative abundances and trophic traits occurrences against the deadwood variables using joint species distribution models.

**Results:** Out of 462 species, only 77 showed significant responses to at least one deadwood type, with a weak mean response across species. Trophic groups showed mostly negative responses to deadwood variables. Species abundance increased with species richness among sites only for phytophagous and saproxyllophagous. Trait occurrence did not increase with species richness among sites, except for phytophagous and saproxyllophagous. However, trait occurrence changed significantly with species richness of several trophic groups within some sites. We found that increases in species richness do not result in decreases in species abundance of a given trophic group, but rather null or positive relationships were found suggesting low interspecific competition.

**Conclusions:** Our findings suggest that in Mediterranean mountain forests there is still room for increasing the level of naturalness, at least for what concerns deadwood management. On one side, our findings suggest that competition for deadwood substrates is still low, on the other side they indicate that increasing deadwood volume and types to improve overall beetle richness may increase also beetle abundances.

### 1. Introduction

The variation of functional traits within species assemblages and along environmental gradients can inform ecosystem functioning, being traits associated with ecosystem resilience and resource availability (Winfree et al., 2015; Sakschewski et al., 2016). A functional trait is ‘a well-defined, measurable property of organisms, usually measured at the

individual level and used comparatively across species’ (McGill et al., 2006). Being related to physiological (e.g., basal metabolic rate), morphological (e.g., body size) or behavioural (e.g., trophic level) characteristics of an organism (Nock et al., 2016), functional traits influence how species ‘respond to the environment and/or their effects on ecosystem properties’ (Violle et al., 2007). High trait diversity found at sites with similar abiotic conditions signals the availability of multiple niches (De Bello et al.,

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2009; Laughlin et al., 2012) and it can correspond to high local functional diversity (i.e., diversity of the functional groups of species, such as trophic groups; Petchev and Gaston, 2002). In such a situation, average species abundances are predicted to be lower due to competitive exclusion and niche overlap (Sugihara et al., 2003; Mason et al., 2008). On the other hand, it entails also that abiotic conditions can act as environmental filters and favour the abundance of species whose niches match the local environmental conditions (Mouillot et al., 2007; Shipley et al., 2011). However, the evidence for the latter is somewhat contradictory and the effects of environmental filtering on species abundances and trait occurrence seem to be tightly linked with the effects of species co-existence and biotic interactions (Cadotte and Tucker, 2017; Basile et al., 2021a). The variation of species and traits can ultimately regulate the overall ecosystem function (Cardinale et al., 2012), and their relationship can assume different forms, depending on the environment (Halpern and Floeter, 2008; Seymour et al., 2015).

Trait variation along environmental gradients may differ among sites, making the use of traits in predictive studies limited (Burner et al., 2021). Although they are thought to be more informative about species assembly rules than species themselves, the evidence in this direction is limited. Indeed, patterns of diversity may be better inferred from the information retrieved from species rather than traits, due to the natural tendency of some traits to be associated among species (Clark, 2016). Other confounding factors are environmental disturbances, which may hamper our ability to infer diversity or abundance patterns from traits (Grime, 2006). For instance, trait occurrence can be determined by anthropogenic alteration of environments among New Zealand bird assemblages of native and exotic forests, and open environments (Barnagaud et al., 2022). Moreover, trait diversity can be influenced by human disturbance in the form of management (Petermann et al., 2020). Traits may also disclose information about rare species, otherwise difficult to access due to data limitations (Ovaskainen et al., 2017; Basile, 2022).

Conversely, species responses along environmental gradients are widely studied and tend to be similar among sites (Balestrieri et al., 2015; D'Amen et al., 2018; Basile et al., 2021b; Burner et al., 2021). The increase in species abundance may include only those species with traits favored by the environmental gradients, but, at the same time, high competition for resources may limit the abundance of those species (Mason et al., 2008; Muscarella and Uriarte, 2016). It is, therefore, pivotal to consider both species and traits in ecological modelling for understanding species variation and their responses to environmental conditions (Clark et al., 2017; Ovaskainen et al., 2017). In particular, responses to human-conditioned environmental gradients need a better understanding to propose management solutions. A contradiction, however, emerges when considering environmental management for biodiversity, such as close-to-nature forest management (Bauhus et al., 2013; Gustafsson et al., 2020): an improvement in local environmental conditions, such as an increase in deadwood volume, may (i) favour the abundance of species with particular traits, while other species may decline; or (ii) favour species with different traits at the same time, without an increase in average species abundances.

One typical environmental gradient linked with important resources and generally targeted by management is deadwood (Lassauce et al., 2011; Bouget et al., 2013; Doerfler et al., 2017; Vítková et al., 2018). Deadwood occurs in forests in different forms (e.g., snags or coarse woody debris) and decay stages. Depending on these characteristics and the surrounding environment, it can deliver multiple functions to biodiversity, as in the case of saproxylic beetles or woodpeckers (Parisi et al., 2016; Gutzat and Dormann, 2018; Thorn et al., 2020; Porro et al., 2021). The importance of deadwood for forest biodiversity needs to be assessed also in terms of species and traits variation with it. Specifically, it is important to understand if species assembly along deadwood gradients is determined by changes in species abundance of different functional groups or if the entire community benefits from it, due to the complex and mostly inaccessible web of biotic interactions (D'Amen et al., 2018; Basile et al., 2021a). Therefore, in this study we aim to

address the following questions.

1. Do variations in species and traits differ along gradients of deadwood variables?
2. Do species abundance and trait occurrence change with species richness within or between functional groups?

We focused on the communities of saproxylic and non-saproxylic adult beetles, which include species highly responsive to forest management and, particularly, to deadwood (Parisi et al., 2019). We conduct our investigation in several mountain forests located along the Apennines (Italian Peninsula).

## 2. Materials and methods

### 2.1. Datasets compilations and study areas

We compiled data from five forest sites in the Apennines mountains (Fig. 1). Beetle data were obtained from the annotated checklists found in Campanaro and Parisi (2021).

In each study site, we established multiple circular sampling plots of 530 m<sup>2</sup> following Lombardi et al. (2015). For each plot, UTM-WGS84 coordinates were recorded using a Juno SB Global Positioning System (GPS) (Trimble, Sunnyvale, California). Collectively, we sampled 193 plots encompassing different forest types and management histories (Table 1).

### 2.2. Data collection

#### 2.2.1. Deadwood survey

In each plot, deadwood was surveyed distinguishing standing dead trees (SDT), snags, dead downed trees (DDT), coarse woody debris (CWD), and stumps. Standing dead trees are characterized by the presence of the crown, while snags refer to stems without a crown. Sampling rules for deadwood components, dimensional limits, and data recorded for each deadwood type are detailed in Table 2. The volume of SDT and DDT was calculated using double-entry volume equations (Tabacchi et al., 2011), while the volume of snags, CWD, and stumps were calculated using the cone trunk formula (Lombardi et al., 2012). The mean volume for each deadwood component at each site is detailed in Table 3.

$$V = \pi \times (H/3) \times [(D_{\text{top}}/2)^2 + (D_{\text{min}}/2)^2 + (D_{\text{top}}/2) \times (D_{\text{min}}/2)] \quad (1)$$

where  $V$  = volume (m<sup>3</sup>),  $H$  = height or length (m),  $D_{\text{top}}$  = diameter at the top of the trunk (m), and  $D_{\text{min}}$  = minimum diameter (m).

#### 2.2.2. Beetle sampling

The sampling of beetles was carried out at each plot from 2012 to 2018 using two trapping methods: window flight traps for flying beetles and emergence traps for ground-dwelling beetles. Emergence traps were emptied only once, at the end of the sampling period, while window flight traps were checked approximately every 30 days from June to October. All the traps were removed during winter. Nomenclature and systematics followed Audisio et al. (2015) and Bouchard et al. (2011). Species strictly considered as saproxylic (*sensu* Carpaneto et al., 2015) were grouped according to the prevalent trophic strategy, defined by Audisio et al. (2015) and Carpaneto et al. (2015): i) xylophagous (organisms feeding exclusively or mainly on wood), ii) saproxylophagous (organisms feeding exclusively or largely on fungi-infected wood), iii) mycetophagous (organisms feeding exclusively or mainly on fungi), and iv) predator (organisms that primarily obtain food by consuming other organisms or their parts). Non-saproxylic beetles were divided into two main trophic groups: rhizophagous (organisms feeding on roots) (Oliveira and Salvadori, 2012), and phytophagous (organisms that primarily consume plants) (Odegaard, 2000). In addition, the body length of each species was measured. In the case of species with only one individual, the



Fig. 1. Location of the five study sites.

Table 1

List of the study sites, modified from Parisi et al. (2022a).

Study site	Coordinates <sup>a</sup>	No. of plots	Sampling year	Protected area	EUNIS Habitat type	Forest management	Management regime
Abeti Soprani (AS)	41.8608 N 14.2936 E	50	2012, 2013	–	Southern Apennine <i>Abies alba</i> forests	Unmanaged forest	Old high forest
Bosco Pennataro (BP)	41.7488 N 14.1972 E	50	2014, 2015	UNESCO “Collemeluccio-Montedimezzo-Alto Molise”	Thermophilous deciduous woodland	Unmanaged forest	High forest on old coppice
Cilento (CI)	40.4705 N 15.4317 E	14	2013, 2016	Cilento, Vallo di Diano e Alburni National Park	<i>Fagus</i> forest on non-acid soils	Unmanaged forest	Old high forest
Gran Sasso (GS)	42.5096 N 13.5679 E	19	2013, 2016	Gran Sasso e Monti della Laga National Park	<i>Fagus</i> forest on non-acid soils	Unmanaged forest	Old high forest
Matese (MT)	41.4522 N 14.3502 E	60	2018	Matese National Park	Southern Italian <i>Fagus</i> forests	Managed forest	Mature coppice with standards; group system (high forest)

<sup>a</sup> UTM datum WGS84 (EPSG 4326).

body length was measured on the individual, while in the case of species with several individuals, the body length was measured on 10 specimens and the average value was calculated.

### 2.3. Beetle diversity and trait modelling with deadwood

We modelled species relative abundances and trait occurrences using the deadwood components (Table 2) as predictors in joint species distribution models fitted with Bayesian inference (Clark et al., 2017). By incorporating species traits in the form of community-weighted mean traits, the joint species distribution model infers trait variation within and between species, the diversity of species with certain traits, and the environmental variation that influences both species and trait diversity (Clark, 2016). The response variable was the matrix of species relative abundances per plot, which were derived from trap counts. Besides the estimates of species responses to the deadwood predictors, the model returned also a species-by-species and a trait-by-trait covariance matrix. Each deadwood predictor was scaled and centred before analysis. Modelled traits included body length as a continuous variable and trophic groups as seven binary variables (0, 1). We also included the study

site as a random effect. Given the large number of species and zeros in the species matrix which could slow down the analysis and bias the inferences, the initial species matrix was reduced by excluding all the species that occurred in less than two plots. In addition, we used a dimension reduction algorithm to trim species that bore no information on the responses to the predictors (Taylor-Rodríguez et al., 2017). The model was fitted using a Gibbs sampler as a Markov chain Monte Carlo algorithm (MCMC). Non-informative priors were used for all distributions and significant predictors were selected using 95% Bayesian credible intervals (equivalent to confidence intervals in frequentist approaches). The root mean square predictive error (RMSPE) was used to evaluate model fit and predictive performance. We used 25,000 iterations with a burn-in of 5000 iterations. MCMC chains convergence was assessed visually (see Supplementary data: Fig. S1). Statistical analysis was conducted in R (R Core Team, 2021) using the package ‘gjam’ (Clark and Taylor-Rodríguez, 2022). Finally, to assess the change in species abundance and trait occurrence with species richness of the entire beetle assemblage and trophic groups, we regressed the predicted relative abundances and community-weighted trait means against observed species richness within and among sites using linear regressions.

**Table 2**

Dimensional limits and sampling rules of deadwood. CWD = coarse woody debris; DDT = dead downed trees; SDT = standing dead trees; DBH = diameter at breast height;  $D_{min}$  = minimum diameter;  $D_{top}$  = diameter at the top of the trunk;  $H$  = height for SDT, snags and stumps, or length for DDT and CWD.

Deadwood component	Dimensional limits	Sampling rule	Measurements
CWD	$D_{min} \geq 5$ cm $H \geq 100$ cm	Inventoried if its diameter at the thinner-end is $\geq 5$ cm and its thicker end is within the boundary of the plot	$D_{min}, D_{top}, H$
DDT	$DBH \geq 5$ cm $H \geq 130$ cm	Downed dead trees (in one piece or more pieces unambiguously recognizable as a single tree) were inventoried if the thickest part of its stem is within the boundary of the plot	DBH and $H$
SDT	$DBH \geq 5$ cm $H \geq 130$ cm	Standing single tree with crown, inventoried if its DBH is $\geq 5$ cm and its stem base is within the boundary of the primary plot	DBH and $H$
Snags	$DBH \geq 5$ cm $H \geq 130$ cm	Characterized by a height $\geq 1.3$ m, with absence of crown	$D_{min}, D_{top}, H$
Stumps	$D_{top} \geq 5$ cm $H < 130$ cm	Stumps were considered when their diameter at the cutting or breaking point was $\geq 5$ cm and height $< 1.3$ m	$D_{min}, D_{top}, H$

**Table 3**

Mean volume ( $\pm$ SD) ( $m^3$ ) for each deadwood component at each site. For site and deadwood abbreviations, see Tables 1 and 2

Deadwood component	Site				
	AS	BP	CI	GS	MT
CWD	11.87 ( $\pm 20.40$ )	6.16 ( $\pm 5.99$ )	0.25 ( $\pm 0.59$ )	0.19 ( $\pm 0.29$ )	0.36 ( $\pm 0.96$ )
DDT	2.23 ( $\pm 13.40$ )	0.92 ( $\pm 4.58$ )	0.10 ( $\pm 0.29$ )	0.62 ( $\pm 2.58$ )	9.62 ( $\pm 28.62$ )
SDT	2.03 ( $\pm 4.07$ )	0.33 ( $\pm 0.79$ )	1.94 ( $\pm 3.00$ )	1.32 ( $\pm 3.10$ )	0.37 ( $\pm 1.10$ )
Snags	14.66 ( $\pm 32.47$ )	1.20 ( $\pm 2.24$ )	0.03 ( $\pm 0.05$ )	0.01 ( $\pm 0.02$ )	0.30 ( $\pm 0.65$ )
Stumps	9.76 ( $\pm 7.71$ )	0.31 ( $\pm 0.61$ )	4.94 ( $\pm 6.69$ )	6.57 ( $\pm 7.21$ )	12.48 ( $\pm 33.95$ )

**3. Results**

We collected 18,505 beetle specimens of 640 species belonging to the following families: Staphylinidae (17% of the species), Curculionidae (12%), Elateridae (7%), Nitidulidae (6%), Scarabaeidae (5%), Cerambycidae (5%), others (48%).

Regarding the trophic groups, the most frequent were predators

**Table 4**

Percentages of species collected belonging to each trophic group.

Trophic group	Percentage	Number of individuals
Coprophagous	3.9	344
Detriticolous	2.2	24
Mycetobiontic	2.3	634
Mycophagous	8.7	731
Myrmecophilous	0.2	1
Necrophagous	1.1	204
Phytophagous	14.5	1025
Pollinivorous	5.6	270
Predator	25.5	2600
Rhizophagous	8.6	8355
Saprophagous	1.4	61
Saproxylophagous	9.4	564
Unknown	2.3	72
Xylophagous	13.8	3620

(25.5% of the species), phytophagous (14.5%), and xylophagous (13.8%) (Table 4). Some trophic groups occurred less than 30 times in the dataset, comprising coprophagous (3.9% of the species), detriticolous (2.2%), micetobiontic (2.3%), myrmecophilous (0.2%), necrophagous (1.1%), pollinivorous (5.6%), saprophagous (1.4%), and unknown (2.3%), and were modelled together as ‘other’.

The final model showed good convergence of the predictor estimates (Fig. S1) and included 462 species, after excluding the species occurring in less than two plots. The predictive error of the model indicated by the RMSPE was 0.0105, with the saproxylophagous species showing the smallest average RMSPE per group (0.0049) and the rhizophagous showing the highest (0.0113). Trophic groups showed different sensitivity to deadwood predictors, with the largest difference among groups for DDT, which accounted for the most observed variation in species abundances (Fig. S2). Species residual correlation was overall weak (mean = 0  $\pm$  0.05 SD), with 299 species pairs having a correlation > 0.5 (max = 0.98). Covariance within trophic group was always positive ( $p < 0.05$ ), whereas covariance among groups showed also negative values (Fig. S3).

**3.1. Do variation in species and traits differs along deadwood gradients?**

Out of the 462 species included in the model, only seventy-seven showed significant responses to at least one deadwood predictor, with a mean response across species of  $-0.006 \pm 0.02$  SD (Fig. 2). Similarly, trophic groups showed mostly negative responses to deadwood predictors, averaging  $-0.54 \pm 1.03$  SD (Fig. 3).

**3.2. Do species abundance and trait occurrence change with species richness within trophic categories?**

The fitted relative abundances indicated clear increases with species richness among sites only for phytophagous (0.00002;  $p < 0.01$ ) and saproxylophagous (0.00002;  $p < 0.01$ ). All other trophic groups did not show significant relationship between species abundance and species richness (Fig. 4). However, the relationship did not hold within sites, with no significant cases (Fig. S4).

Trait occurrence expressed as community-weighted trait means, did not change with species richness among sites for most of the trophic groups (Fig. 5). The only exceptions were phytophagous (0.001;  $p < 0.01$ ) and saproxylophagous (0.001;  $p < 0.01$ ), which showed positive relationships. However, trait occurrence increased significantly with species richness within some sites (Fig. S5), including xylophagous at GS (0.003;  $p < 0.01$ ) and MT (0.005;  $p < 0.01$ ), and rhizophagous at BP (0.005;  $p < 0.01$ ). Significant decreases were instead observed for xylophagous at BP ( $-0.003$ ;  $p < 0.05$ ), predator at MT ( $-0.004$ ;  $p < 0.05$ ), and phytophagous at CI ( $-0.001$ ;  $p < 0.05$ ).

**4. Discussion**

We modelled the association of forest beetles with deadwood gradients, including saproxylic and non-saproxylic trophic groups, with specimens from temperate Mediterranean mountain forests. We found that the volume of five types of deadwood does not represent an environmental gradient that can affect significantly the abundance of the beetle assemblage. In general, abundance and trait occurrence did not change along the deadwood gradients, despite some negative responses were detected. Nevertheless, beetle abundance and trait occurrence could be more correlated with other environmental gradients, such as the volume of living trees or the share of broadleaved trees (Lassaue et al., 2011; Rappa et al., 2022). Indeed, species richness of saproxylic beetles can show weak correlations with the volume of deadwood, when considering the deadwood separately by components (i.e., CWD, DDT, SDT, snags, and stumps) (Lassaue et al., 2011). In managed forests with more deadwood than our study area, the biomass of saproxylic species was found increasing with lying deadwood volume but their abundance

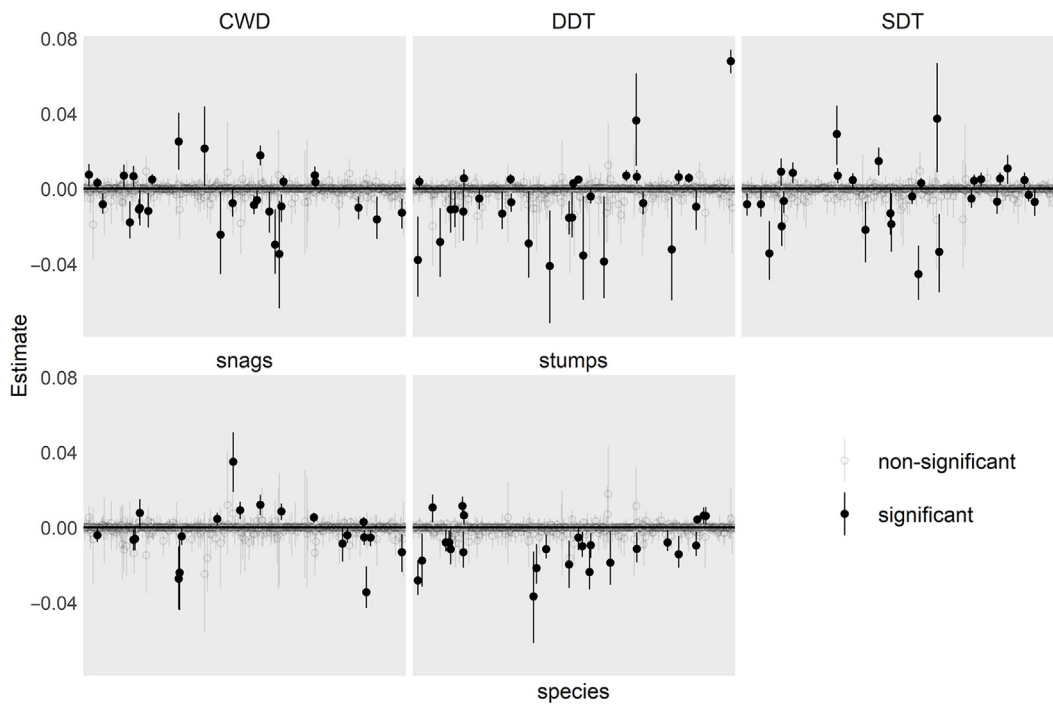


Fig. 2. Estimated responses of 462 beetle species to deadwood predictors. Each circle corresponds to one species response and each bar indicates the 95% confidence interval.

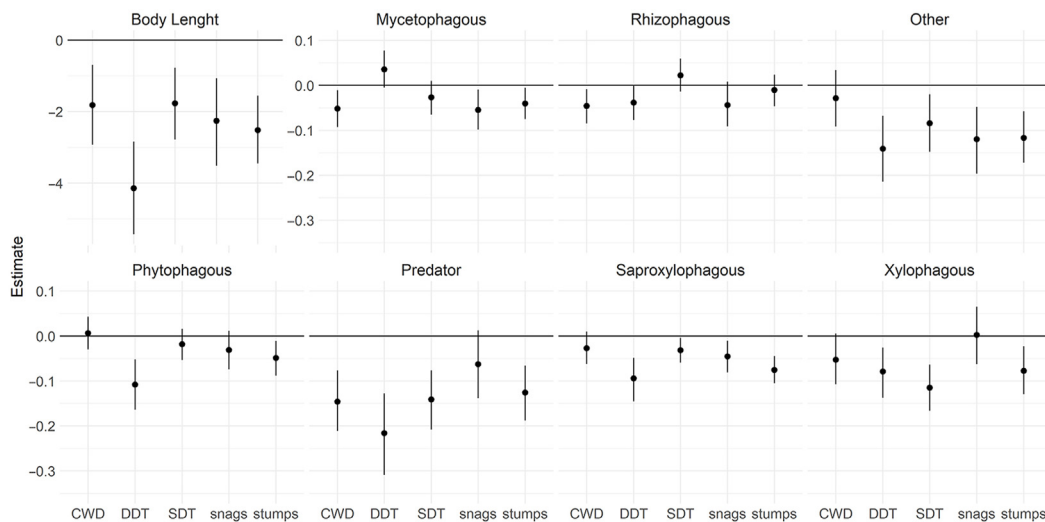
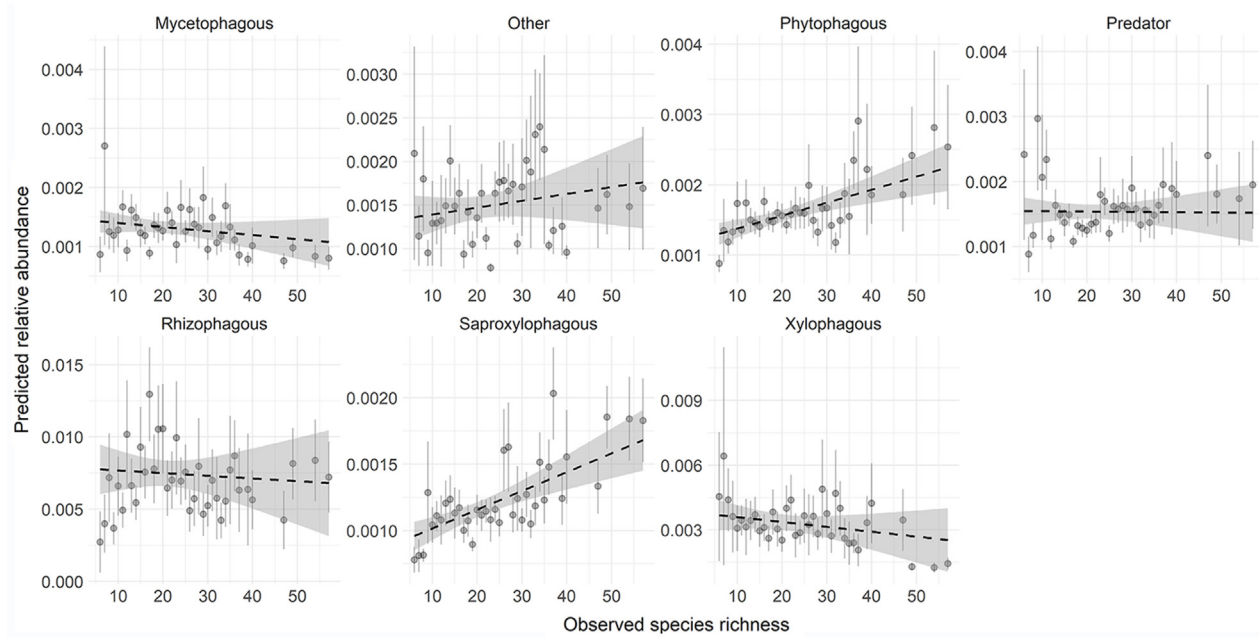


Fig. 3. Estimated responses of traits to deadwood predictors, comprising body length and seven trophic groups. Responses are shown with 95% confidence interval. CWD = coarse woody debris; DDT = dead downed trees; SDT = standing dead trees.

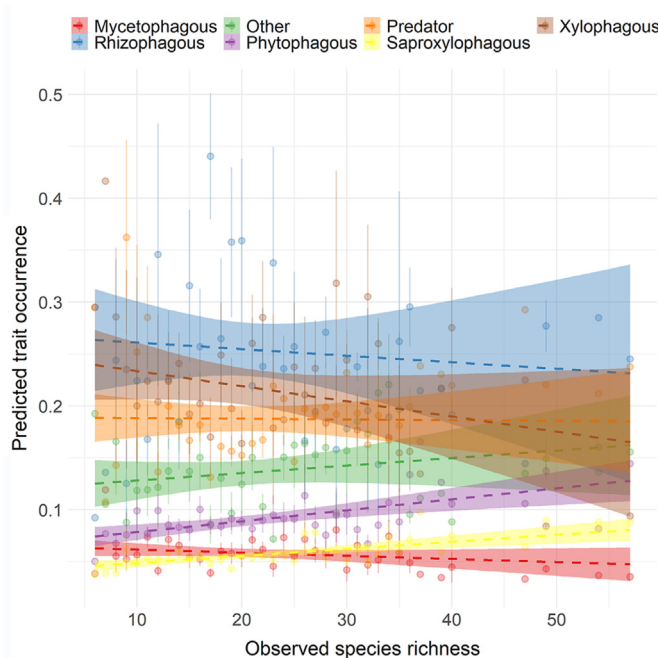
did not show such correlation (Rappa et al., 2022). In our case, we found significant relationships only for the species negatively related with the volume of deadwood components, causing also the responses of the trophic groups to steer toward negative values. Hence, we concluded that the increase in deadwood volume is likely to affect negatively the abundance of a minor part of the beetle assemblage, while not really influencing most of it. The minor decrease in species abundances along the deadwood gradients, however, was not associated with a significant decrease in the diversity of species and traits, though with some exceptions: decreases in species richness were associated with decreases in the occurrence rate of saproxylophagous and phytophagous species. Species richness is related to the volume of deadwood at the level of the stand (Ranius and Fahrig, 2006; Müller et al., 2015) and at the level of the individual deadwood piece (Hammond et al., 2004). In our case, we

observed that the abundance of saproxylophagous and phytophagous beetles increased with species richness. This may point towards the absence of competitive exclusion among species, indicating also that deadwood may not be a sought-after resource in our study area.

Indeed, the volume of deadwood is not the only driver of beetle assemblages. Variables linked to qualitative aspects of deadwood, such as decay stage, tree species, deadwood type, and its position (i.e., sun exposure) are important factors influencing both composition and richness of saproxylic beetles (Seibold et al., 2016; Vogel et al., 2020; Lettenmaier et al., 2022). For instance, early decay deadwood is associated with increased saproxylic beetle activity (Saint-Germain et al., 2007), since fresh deadwood offers large amounts of nutrient-rich resources in terms of phloem and sapwood, suitable for xylophagous species (Hammond et al., 2004). On the other hand, Burner et al. (2021) showed that



**Fig. 4.** Linear regressions between observed species richness and fitted relative abundance for the species in each trophic group. Circles show mean abundances with standard errors. Lines and shades show the regression with 95% confidence intervals.



**Fig. 5.** Linear regressions between observed species richness and fitted community-weighted trait means. Circles show means with standard errors. Lines and shades show the regressions with 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

advanced deadwood decomposition significantly reduces the species richness of saproxylic beetles. In our case, data about the decay stage of deadwood was lacking from some sites, limiting the analysis and the interpretation of our results. Therefore, future analysis should consider also the decay stage in order to have a more detailed picture of the changes in the beetle assemblage.

Overall, we observed that changes in trait occurrence are weakly related to species richness, except for some trophic groups, including

saproxylophagous and phytophagous. Competition can limit the abundance of species sharing the functional traits favored by environmental variables (Mason et al., 2008). However, we found that increases in species richness did not result in decreases in species abundance of a given trophic group, but rather null or positive responses were found.

While our study focused on deadwood volume, more in depth analysis on climate conditions would be necessary to evaluate the effect of environmental factors (e.g., temperature, humidity) on beetle richness and abundance. Indeed, temperature and moisture play a fundamental role in the decomposition process. Some species, for instance, need dry and sun-exposed deadwood (Parisi et al., 2018). Seibold et al. (2021) found that high temperatures can affect positively beetles' richness, increasing their metabolic rate and larval development, while high precipitation with low evaporation can have a negative impact, due to low aeration or pathogen occurrence. Indeed, sun exposure may lead to the presence of different ecological niches, and thus food substrates, that support a great diversity of beetle trophic groups (Parisi et al., 2022b).

#### 4.1. Management implications

Our findings suggest that in Mediterranean mountain forests there is still room for increasing the level of naturalness, at least for what concerns deadwood management (Wirth et al., 2009; Parisi et al., 2016; Siitonen et al., 2000). The variability in the quality and quantity of deadwood substrates is essential to preserve the diversity of saproxylic and non-saproxylic beetles in complex forest landscapes, where conservation and production objectives coexist (McGeoch et al., 2007; Sabatini et al., 2016). By modelling the complex interactions between beetle species and deadwood, we observed that the abundance of saproxylophagous and phytophagous species increased with their richness. On one side, this suggests that competition for deadwood substrates may be low, on the other side it indicates that increasing deadwood alone may not necessarily improve overall beetle diversity (Parisi et al., 2018).

In addition, 2.8% of the sampled species belong to the IUCN risk categories CR, EN and VU, and were often sampled as single specimens. The rarity or the strongly localized presence of these species could be explained by the scarce quantity and the scattered localization of deadwood of large diameter, which was found to be essential for rare and threatened species (Grove, 2002). Besides, the total absence of the most

advanced decomposition stages for some areas (i.e., Bosco Pennataro, Matese) could have influenced their occurrence (Lombardi et al., 2012; Parisi et al., 2019, 2020b). Indeed, the retention of standing and lying deadwood, the preservation of particularly large, old trees (Gustafsson et al., 2020; Thorn et al., 2020; Parisi et al., 2021), the increase of heterogeneity (e.g., through the establishment of “senescence islands” in forest ecosystems, see Parisi et al., 2018), and the maintenance of mature and old-growth stands across the landscape should be promoted for forest biodiversity conservation.

## Funding

This work received no external funding.

## Availability of data and materials

All data generated or analysed during this study are included in this published article and its supplementary information files.

## Authors' contributions

Marco Basile: Conceptualization; Data curation; Data analysis; Writing original draft, review and editing. Francesco Parisi: Data collection; Data curation; Writing original draft, review and editing. Roberto Tognetti, Saverio Francini, Fabio Lombardi, Marco Marchetti, Davide Travaglini, Gherardo Chirici: Writing review and editing. Elena De Santis: Writing original draft, review & editing.

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Declaration of competing interest

The authors declare that they have no competing interests.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2023.100090>.

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