On how the abandonment of traditional forest management practices could reduce saproxylic diversity in the Mediterranean Region

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ABSTRACT

Forests of the Mediterranean Basin provide a wide range of provisioning and regulating services that are currently jeopardised by land-use change. Although many ecosystem services are mediated by insects, most of the studies that have focused on how to enhance diversity in traditionally managed forests are about plants and vertebrates. *Quercus pyrenaica* woodlands of the Western Iberian Peninsula constitute a scenario in which traditional human practices (i.e., extensive livestock grazing, pollarding, firewood, forest thinning, etc.), and their progressive abandonment, have generated differences in landscape that affect habitat and microhabitat structures. We used saproxylic beetles (deadwood-dependent species) as biological indicators because they are the most diverse taxa and provide important ecosystem services related to deadwood decomposition, forest pest control and pollination. We modelled the response of two taxonomic (species richness and abundance), one ecological (species diversity of order 1) and two functional (functional richness and redundancy) diversity metrics to the environmental variables that result from traditional management or its abandonment at habitat and microhabitat levels. We included 16 explanatory variables related to forest structure, tree microhabitats and abiotic factors, which were grouped into eight principal components. Linear regression was the best fitting model for data. The resulting models were used to perform diversity predictions in different scenarios. We found that abandonment of some traditional forest management activities in the Mediterranean Region reduced taxonomic saproxylic beetle diversity, which may be further aggravated by climate change. We suggest minimal management actions to improve taxonomic and ecological saproxylic beetle diversity related to habitat and tree management (i.e., maintenance of >20% scrub coverage, >20 m³/ha of deadwood on soil and >20 hollow trees/ha). However, actions that boost saproxylic biodiversity do not ensure the community's higher functional resilience. We should also promote tree microhabitat diversity to reduce the vulnerability of saproxylic beetle functions to environmental changes.

1. Introduction

Forests of the Mediterranean Basin provide a wide range of provisioning and regulating services that are currently jeopardised by land-use change and climatic change (Morán-Ordóñez et al., 2021; Rathore et al., 2019; Martinez-Harms et al., 2017). In the Iberian Peninsula, *dehesa* –savannah-like open woodland with scattered old trees as a result of former traditional agrosilvopastoral practices (Ramírez-Hernández et al., 2014; Plieninger et al., 2003)– has been the best example of forest transformation for sustainable use for combining exploitation (extensive livestock grazing) and habitat conservation (Dawson & Fry, 1998). This millennial activity in forests (note that *dehesas* date back to the 10th century), has resulted in a habitat composed of an open tree layer with an understory dominated by winter annuals and, to a lesser extent, by small evergreen scrubland (Martín Vicente & Fernández Alés, 2006). The special *dehesa* structure allows the organisms typical of forest areas and those of open grassland systems to co-exist (Díaz et al., 1997, 2003; Sánchez Martínez et al., 2012). Accordingly, it hosts a high diversity of plants, insects and birds that also provide valuable ecosystem services (Plieninger & Wilbrand, 2001; Galante, 2021).

However, the maintenance of traditionally managed forests, of which *dehesas* are the best example, is linked with the continuity of

traditional activities (livestock grazing, pollarding, forest thinning, etc.) (Moreno & Pulido, 2009). Consequently, both the intensification or abandonment of agricultural and pastoral activities can dismiss the ecological value of silvopastoral systems (Bugalho et al., 2011). In this way, since the 1960s, the progressive abandonment of traditional uses threatens the existence of this cultural landscape as we know it. By way of example, eliminating livestock from the equation leads to denser scrub, which negatively affects plant diversity (Carmona, 2014). In the same way, lack of tree management (i.e., pollarding) dismisses the creation rate of important microhabitats for the conservation of forest biodiversity, such as tree hollows, which host birds, mammals and invertebrates that perform relevant ecosystem functions (Regnery et al., 2013; Micó et al., 2021).

Mainstream biodiversity conservation/protection of ecosystem functions is one of the 20 actions included in Agenda 2030 for Sustainable Development (SDG) because biodiversity is integral to ecosystem health (FAO, 2018). Although many ecosystem services are mediated by insects (i.e., pollination, pest control, nutrient cycling), most studies that have focused on how to enhance diversity and productivity in traditionally managed forests, including *dehesas*, are about plants and vertebrates (Díaz et al., 1997, 2003; Bugalho et al., 2011; Galante, 2021). However, traditional forest management activities or their abandonment can affect insects as the main forest diversity component (Ulyshen & Šobotník, 2018; Ramilo et al., 2017).

Taking into account that land-use change is one of the main sources of diversity loss in planetary terms, guidelines to optimise the insect diversity of these human-made ecosystems are urgently needed to ensure their conservation and to strengthen their services. Many efforts have been made to provide information about which forest management-related parameters can favour insect diversity in the Mediterranean Region. However, these studies do not often specify the minimum changes needed to ensure adequate diversity (Karpiński et al., 2021; Vogel et al., 2020). This lack of precision is the main handicap for taking a step towards real conservation. We therefore aimed to develop a suitable predictive model of insect diversity, which is based on differential responses to environmental factors, to estimate diversity trends in different scenarios.

Within this framework, we aim to: (1) model the response of different diversity metrics (species richness and abundance, species diversity of order 1, functional richness and redundancy) to the environmental variables that result from different traditional management activities or their abandonment[1] at habitat and microhabitat levels. Combining taxonomic, ecological and functional approaches will help to better understand the diversity of traditional managed forests and to identify potential vulnerabilities to preserve functions (Watts & Mason, 2015; Pérez-Sánchez et al., 2021). The resulting models will serve to: (2) perform diversity predictions in different scenarios, which will allow us to recommend concrete management actions to boost biodiversity. We also include abiotic factors related to temperature and humidity in models to estimate the extent to which climate change may, or may not, aggravate the situation.

For this purpose, we used saproxylic beetles, which are those that depend directly on dying or dead wood, and also indirectly (i.e., on wood-rotting fungi or other saproxylic organisms), during at least part of their life cycle (Speight, 1989; Ulyshen & Šobotník, 2018), as biological indicators because they are one of the main components of forest fauna and provide important ecosystem services related to not only wood decomposition, but also to forest pest control and pollination (Stokland et al., 2012; Micó et al., 2020).

Quercus pyrenaica woodlands of Western Spain provide a scenario in which past and/or current traditional human practices (i.e., extensive livestock grazing, pollarding, collection of firewood, forest thinning, etc.) affect habitat and microhabitat structures. In this way, the various degrees of forest thinning in the past have generated differences in landscape, from *dehesas* with big isolated trees (fewer than 20 trees per ha) to forests of about 300 trees per ha. The current absence, presence or degree of extensive livestock grazing and firewood collection also contributes to differences in the forest structure related to scrub coverage and with the abundance of dead wood on soil, respectively. In addition, and as stated above, tree management (i.e., pollarding) contributes to the formation of tree microhabitats (i.e. tree hollows and wounds) that are key for saproxylic fauna. The progressive abandonment of these traditional activities imprints a greater heterogeneity on the environmental variables of the landscape.

We expect to find differences in the response of diversity metrics to environmental variables because not all types and degrees of traditional forest management favour saproxylic diversity in the same way (Ramilo et al., 2017). Moreover, the variables favouring taxonomic diversity will not necessarily ensure higher functional resilience (Pérez-Sánchez et al., 2021). We hypothesise that some environmental factors that derive from the abandonment of certain management actions will reduce saproxylic beetle diversity. We also expect to suggest minimal management actions that will boost the saproxylic diversity of these human-made woodlands.

2. Methods

2.1. Study area and sampling design

The study area constitutes one of the largest continuous areas of *Quercus pyrenaica* Wild. forests in the Iberian Peninsula, and covers a total area of 174236 ha with different degrees of protection (the El Rebollar and Sierra de las Quilamas Natural Areas, the Batuecas-Sierra de Francia Natural Park and the Sierra de Béjar UNESCO Biosphere Reserve) (Fig. 1). These areas include old-growth forests[2] with either traditional management practices (forest thinning, pollarding, extensive livestock grazing, etc.) or were managed in the past. The study area, thus, covers high landscape heterogeneity that goes from typical *dehesas* with big isolated trees (<20 trees per ha) to woodlands (>300 trees per ha). In this gradient of forest openness, the ongoing presence of other traditional management activities, such as grazing, firewood collection, and the different extents to which these activites are abandoned, have led to differences in habitat (i. e., scrub coverage, amount of deadwood, etc.) and at microhabitat level (Fig. 1, Table S1).

The sampled areas lie at an altitude of 700–1100 m. The mean annual temperature is 10–14 °C and the mean rainfall is about 1000 mm (Oliver-Moscardó & Luis-Calabuig, 1979; García Rodríguez et al., 1984; Llamas et al., 2011). Forest is dominated by *Q. pyrenaica*, and its undergrowth canopy is dominated by several species, such as *Genista* spp., *Cytisus* spp., *Cistus* spp., *Erica* spp. and *Crataegus monogyna* Jacq (Micó et al., 2021).

2.2. Beetle sampling and dataset

Thirteen localities were selected (Fig. 1). The site selection criteria were intended to reflect the heterogeneity of the old-growth *Quercus pyrenaica* habitats in the region in terms of forest structure and availability of tree microhabitats (see Supplementary Table S1, Fig. 1 and Chapter 2.1.).

We established three circular plots in each one with an 18 m-radius around all the traps and a total area of 0.1 ha per plot. The plots in each locality were placed 20 to 113 (M = 58) metres away from one another, always in the same habitat.

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[1] The abandonment of traditional management means that these types of traditional activities have substantially reduced or have disappeared altogether. In this study, the abandonment of management never moves in the direction of more intensive management.

[2] No pristine forest exists in the region. Here we refer to forest composed of old trees in which the mean trunk diameter is bigger than 20 cm.
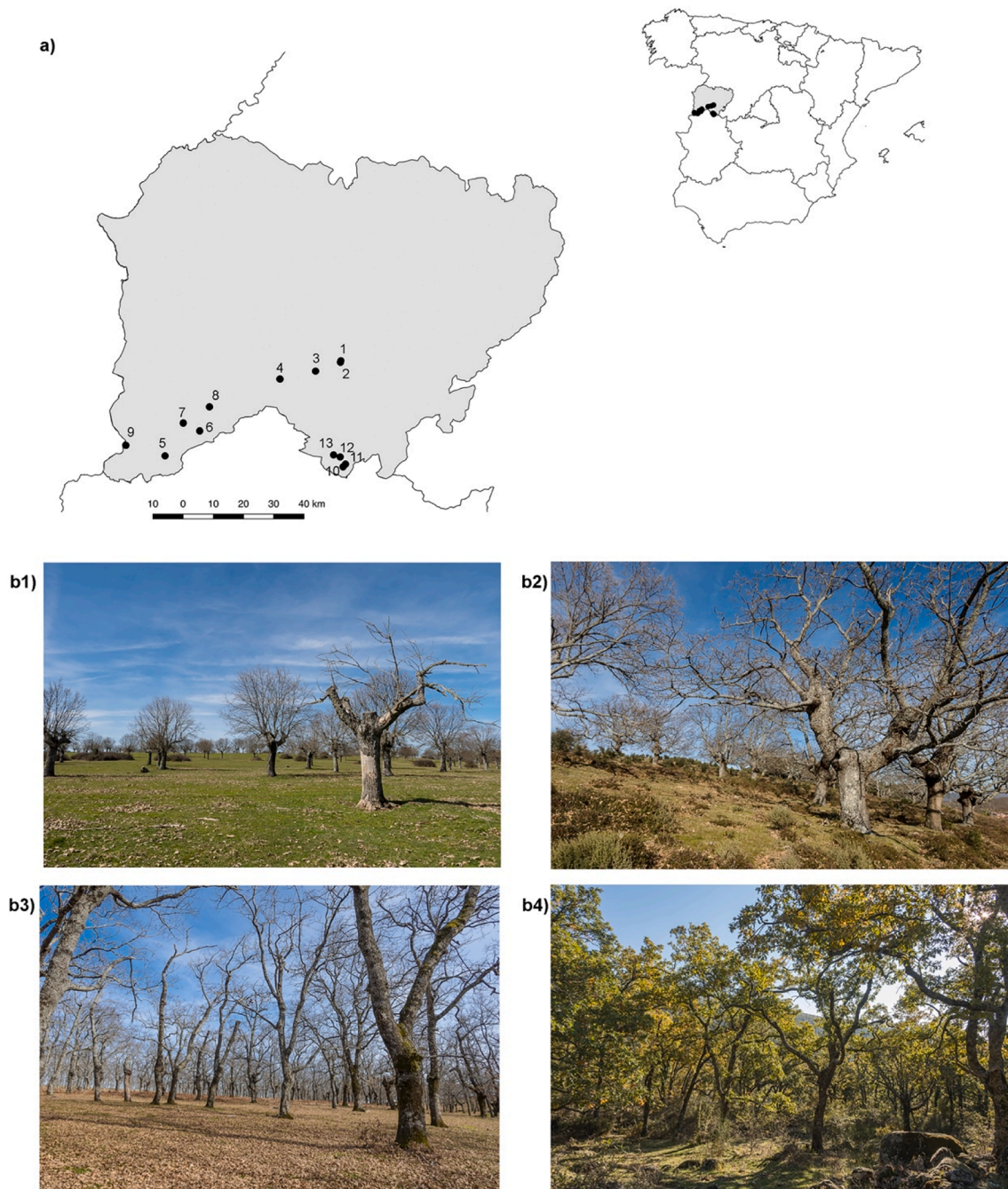
Fig. 1. (a) Study area with the location of the different plots. (b1) Structure of a currently managed *dehesa* showing the typical big trees, but with sparse scrub coverage; (b2) an abandoned *dehesa* showing the bush encroachment as a result of livestock grazing activity currently lacking; (b3) structure of more closed forest with livestock grazing activities and (b4) with less livestock activity.

Saproxylic beetles were collected using flight interception traps ("window traps"; Ramilo et al., 2017). Each trap consists of two transparent sheets (73 cm long, 42 cm wide) lying over a funnel and a collection container with 70% propyleneglycol as the preservative liquid for collected species (Bouget et al., 2008; Micó et al., 2020). Three flight interception traps were placed in all 13 localities, one per circular plot, which totalled 39.

Beetles were collected from April 2017 to April 2018. The collector container in each trap was replaced monthly. Beetle species were identified with the support of specialists in different beetle families (see 'Acknowledgments') and they were deposited in the entomological collection of the University of Alicante (Collection CEUA-CIBIO, Spain).

The nomenclature was in accordance with Fauna Europaea (https://www.faunaeur.org/), Bouchard et al. (2011) and the Catalogue of Palaearctic Coleoptera (Löbl & Smetana 2004, 2010).

2.3. Environmental data

Sixteen environmental variables were measured in each plot (size 0.1 ha) in every locality (Table 1). The data of the environmental variables of each locality were extrapolated to a 1-hectare surface to facilitate further comparisons (Supplementary Table S1). Ten variables were related to forest structure and tree microhabitats (Table 1). In addition, six abiotic factors at the habitat level related to temperature and relative

Table 1
Environmental variables measured in each plot to evaluate their effect on beetles' diversity.

Type of Variable	Variable	Description and justification	References
Forest structure	TreeDen	Number of trees per hectare. Forest openness affects saproxylic diversity	(Sverdrup-Thygeson and Birkemoe, 2009; Horák, 2017)
	MeanDiam	Mean diameter of trees at 1,30 cm at breast height. Bigger trees offer more, and larger microhabitats	(Quinto et al., 2014; Horák, 2017)
	Canopy	Percentage of canopy coverage. Provides a measure of forest openness	(Ramírez-Hernández et al., 2014)
	Scrub	Percentage of scrub coverage. Affects beetle diversity.	(Ramírez-Hernández et al., 2014)
	DDW	Volume (m^3) of fallen dead wood ($\geq$7 cm in perimeter) per hectare. The amount of dead wood has a strongly affects species diversity.	(Larrieu et al., 2018; Karpiński et al., 2021).
	SDW	Volume (m^3) of standing dead wood ($\geq$7 cm in perimeter) per hectare. Dead wood position affects saproxylic community	(Larrieu et al., 2018)
Tree Microhabitats	Excrescences	Burr and cankers, mainly caused by reactive growth to parasitic or microbial intrusion, where tree create specific structures to isolate the pathogen.It is measured as the number of trees with trunk excrescences (with a diameter of $\geq$ 10 cm) per hectare. This microhabitat hosts a diverse community	(Winter and Möller, 2008; Kraus et al., 2016; Larrieu et al., 2018; Ramilo et al., 2017)
	Hollows	Measured as the number of trees with tree hollows ($\geq$10 cm in diameter) per hectare. This microhabitat is a keystone for saproxylic beetles	(Müller et al., 2013; Micó et al., 2020)
	CerGalleries	Number of trees with visible damage caused by *Cerambyx* beetles per hectare. Such damage facilitates the subsequent colonisation by other saproxylic species.	(Buse et al. 2008; Micó et al., 2015)
	TreeCanopyLoss	Number of trees with more than 50% of dead branches in the tree canopy per hectare. Provides a sign of tree decay that offers several microhabitats	(Larrieu et al., 2018)
Abiotic	TMax	Maximum temperature (°C)	
	TMin	Minimum temperature (°C)	
	TMean	Mean temperature (°C). Affects services provision in forests, and also saproxylic insect diversity.	(;Morán-Ordóñez et al., 2021;Kamboyi, 2019)
	HMax	Maximum relative humidity %	
	HMin	Minimum relative humidity %	
	HMean	Mean relative humidity %	

humidity (RH) were measured using two dataloggers (*HOBO U23 Pro v2 Temperature/Relative Humidity Data Loggers* with a *U23-001* sensor) in each locality (Table 1). Data loggers were attached to tree trunks. They were programmed to record temperature and RH values every 4 h throughout the sampling year.

2.4. Functional trait selection and measurements

We analysed eight functional traits belonging to two functional groups: seven morphological and one phenological functional trait (Table 2). Except for body size, which was a direct measurement, the rest of the characters were calculated based on a combination of other morphological measures (Table 2, Fig. 2). For the morphological measurements, photographs from three to ten individuals (M = 5) of each species were taken depending on availability. Photos were produced from individual stacked images, taken with a camera (Leica DFC450) attached to a binocular stereomicroscope (Leica M205 C), which allowed us to have all the specimens in full focus. Measurements were taken on photos using version 4.6.1 of the Leica Application Suite (LAS) software. Some measurements, such as body size, body depth and eye surface, required a photograph in the lateral view, while those of width required a dorsal image (see Table 2 and Fig. 2 for measurement details and units).

2.5. Data analysis

We first checked the inventory completeness of our sampling for each locality using the sample coverage estimator described by Chao & Jost (2012). Sample coverage determines the percentage of observed species in relation to the number of predicted species. We utilised 100 replicate bootstrapping runs to estimate 95% confidence intervals with the SPADE software (Chao & Shen, 2010).

2.6. Taxonomic and ecological diversity metrics analyses

Three taxonomic diversity metrics were analysed per locality (the

data from the three traps in each locality were collected together to calculate these indices): abundance (henceforth Ab), species richness (henceforth S) and species diversity of order 1 ($q = 1$) (henceforth ^1D), which is one of the named Hill numbers (Jost, 2006). S and Ab have been traditionally used as a direct way to measure biodiversity, while ^1D provides the number of effective species. ^1D weights each species by its frequency in the sample without favouring either common or rare species (Jost, 2006) and can, therefore, be interpreted as the number of common (or typical) species in an assemblage. ^1D was calculated by the SPADE software (Chao & Shen 2010). Using these different metrics can help to better understand the community's response to environmental variables (Ramilo et al., 2017).

2.7. Functional diversity metrics analysis

We calculated two functional diversity metrics for each locality: a standardised functional richness index (SESFRic) and functional redundancy (FRed).

Singletons and doubletons were firstly removed from the data matrix because more than two specimens are needed to calculate any phenological trait (Micó et al., 2020). We also removed any species that lacked trait information.

Species traits were log-transformed and scaled to zero mean and unit variance. We estimated Gower's dissimilarity matrix between all pairs of species, which was subsequently used to perform a Principal Coordinates Analysis (PCoA). This strategy allowed dimensionality reduction, especially if some variables can correlate with one another (Carmona et al., 2016a, 2016b). We retained the first four PCoA axes that represented 89.7% of the total variation in the trait matrix, and used the scores of the species on these axes to estimate the functional diversity index (Micó et al., 2020). We employed the R package TPD (Carmona, 2017; Carmona et al., 2019) to obtain a trait probability density function (TPD) for each species and assemblage. We calculated functional richness diversity (as an indicator of the amount of functional space occupied by an assemblage) corrected by species richness to take functional richness independently of this taxonomic measure (Villéger

Table 2

Definition and description of the 8 functional traits used for the calculation of the functional diversity indices (SESFRic and FRed). The measurements of the morphological traits are shown in Fig. 2.

| Functional group	Trait	Functional significance	References
Phenological	**Number of months active**: Number of months in which adults of species were active throughout the year.	This trait can be considered as key predictor of species extinction risk as consequence of climate change since species that are active a higher number of months are exposed to a wider range of abiotic conditions and, so, have more chances to adapt to new climatic conditions.	(Gillespie et al., 2017; Micó et al., 2020; Moretti et al., 2017; Pearson et al., 2014; Pérez-Sánchez et al., 2020)
Morphological	**Body length:** Total lateral length from anterior margin of head to the apex of abdomen (mm).	Body size has been considered as predictor of species microhabitat. Moreover, it can act as response trait to changes in the environment and as effect trait able to estimate the magnitude of the effect of the species action in the ecosystem.	(Cunningham & Murray 2007; Barton et al., 2011; Fountain-Jones et al., 2017; Gillespie et al., 2017; Micó et al., 2020; Pérez-Sánchez et al., 2020)
	Robustness: it was calculated by regressing five traits (pronotum dorsal maximum width length and depth, elytra and head maximum dorsal width) on body length and averaging the residuals of these regressions.	It provides information about the microhabitat use since flattened body shapes are more common in assemblages within confined than in open microhabitats (i.e., under bark versus in tree hollows)	(Barton et al., 2011; Micó et al., 2020; Pérez-Sánchez et al., 2020)
	Ratio Elytra length: Ratio between maximum lateral length of the elytra and maximum length from the base of the elytra to the apex of abdomen (mm).	This trait gives information on microhabitat use, since long elytra provide wing protection in rugged habitats. Moreover, it can be also connected with flight ability, since shorter elytra indicate better dispersal efficiency in some beetles.	(Forsythe, 1983; Ribera et al., 1999a; Barton et al., 2011; Johansson et al., 2012; Micó et al., 2020)
	Eye size: Ratio between eye surface and head width (mm²).	This trait acts as predictor of species microhabitat use and lifestyle.	(Bauer 1981; Woodcock et al., 2010)
	Antenna length: Ratio between antenna length (maximum length from the base of the antenna to its apex) and body length (mm).	This trait acts as predictor of species microhabitat use and lifestyle.	(Pérez-Sánchez et al., 2020; Ribera et al., 1999b; Talarico et al., 2011; Woodcock et al., 2010)
	Wing loading: Ratio between	This trait is a surrogate of species	

Table 2 (*continued*)

| Functional group	Trait	Functional significance	References
	body mass and wing surface (mg/mm²)	flying abilities. Species with a low wing loading present flight more energetically efficient than species with high wing loading.	(Angelo & Slansky, 1984; Gibb et al., 2006)
	Wing Aspect ratio: Ratio between wing length and wing width.	This trait provides information about species flight type. Species with high aspect ratio present a flight adapted to fast flapping, while species with low aspect ratio would present gliding flight.	(Norberg, 1990; Wootton, 1992; Gibb et al., 2006)
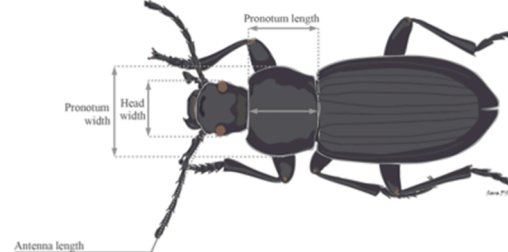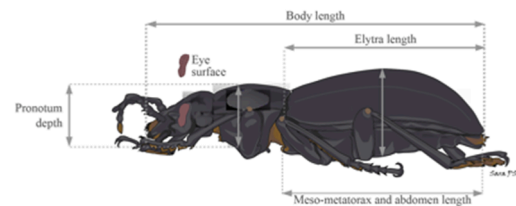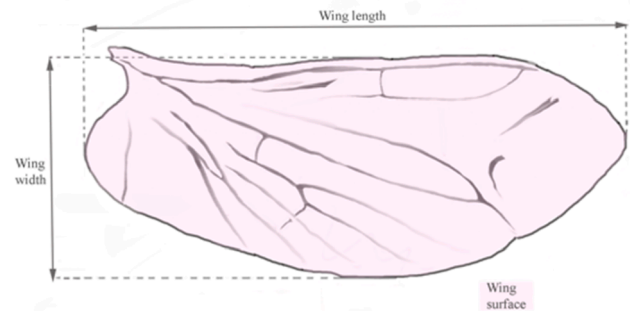
Fig. 2. Scheme of the morphological trait measurements in each individual from (a) a dorsal view and (b) a lateral view. Maximum dorsal width of the head and body, and maximum width, length and lateral depth of the pronotum, were used to calculate robustness. Elytra, *meso*-metathorax and abdomen length were employed to calculate the Elytra ratio. (c) Wing measurements utilised to calculate the wing loading and wing aspect ratio. Information and definition of the traits in Table 2. Modified from Pérez-Sánchez et al (2021).

et al., 2008). For this purpose, we compared the observed FRic values to a null model generated by means of a matrix-swap null model based on the species presence-absence matrix (Manly, 1995). We restricted permutations so that only the species co-existing in the same study locality were swapped. We performed 1,000 randomisations and estimated the standardised effect size (SESFRic = [observed FRic – (mean of simulated FRic)/(SD of simulated FRic)]) as an indicator of functional richness independently of species richness (Carmona et al., 2015) (henceforth SESFRic). We also calculated the functional redundancy (FRed) of the species in each locality. This functional diversity component shows the effect of the removal of random species. For example, an assemblage with high redundancy indicates that the removal of a random species should not strongly affect its functional structure (Ricotta et al., 2016). This metric can, thus, be understood as a measure of a community's functional resilience (Pérez-Sánchez, 2021). In the same way as FRic, this component is not independent of species richness (Carmona et al., 2016a; Micó et al., 2020). Thus we calculated this component by dividing it by its upper bound (species richness-1) to remove the species richness effect.

All the analyses were performed with the R software (R Core Team, 2017).

2.8. Modelling

Before model selection, the principal components technique was previously applied to avoid possible multicollinearity problems for variables and to maintain the information of most explanatory variables. Principal components (PC) were calculated per type of information of the explanatory variables using the Statgraphics 17 software. Eight PCs were obtained (Tables 3, 4). The percentage of accumulated variance always exceeded 80%. Components 1 and 2 joined forest structure in forest openness and deadwood amount terms. Component 3 showed forest structure in canopy and scrub coverage terms. Components 4 and 5 joined microhabitat availability on living trees. Finally, components 6, 7 and 8 joined the abiotic factors related to temperature and RH. Each PC was affected differently and to a distinct degree for the different environmental variables (Table 3). The values of the eight PCs for each sampling site (Table 4) were calculated to estimate the prediction models.

For model selection, we first tested how well our data fit in the different suitable models. As all the variables were quantitative and continuous, multiple regression model and General Linear Models (GLM) were considered to be the most suitable models. However in this case, multiple regression better fit than GLM (see Supplementary Table S2). The resulting valid models (Table 5) were then used to perform diversity predictions.

Tests and models were carried out with the Statgraphics 17 software.

2.9. Predictions

By employing the models shown in Table 5, a series of assumptions were made in different possible scenarios by predefining the values of the environmental explanatory variables. The obtained predictions provided an estimated measure of the value that could be expected under the conditions of the scenario proposed for each diversity metrics. We also provided the estimate for the 95% confidence interval (Figs. 3-6). Predictions were represented as linear graphs using the ggplot2 package in the R software (R Core Team, 2017).

3. Results

10,498 individuals belonging to 285 saproxylic beetle species and 43 families were identified (Supplementary Table S3).

The inventory completeness of the whole sample was 99.3%. Likewise, the inventory completeness values in each locality were also consistently high and always over 91%.

For the functional metrics, after omitting rare species (singletons and doubletons; 108 species) and those with some lacking traits (39 spp.) (see the data analysis), the analysis focused on 7258 individuals of 138 species across 22 beetle families (see Supplementary Table S3).

3.1. Modelling the response of insect diversity to the environmental variables and predicting biodiversity

Valid models were obtained that fulfilled the hypotheses for all the employed taxonomic (Ab, S) and ecological diversity metrics (^1D), and also for functional redundancy (FRed) (Table 5). Functional richness (represented by SESFric; see the Methods section) was the only response variable that did not fit any model (Supplementary Table S2).

Diversity metrics differed in both the number and identity of the environmental variables that affected them. While abundance (Ab) was the metric affected by more environmental variables (seven of the eight

Table 3

Weights of the explanatory variables in the principal components. Components 1 and 2 (PC1 and PC2) joined forest structure in forest openness and deadwood amount terms (TreeDen: Number of trees per hectare, MeanDiam: Mean diameter of trees at 1.30 cm at breast height, DDW: Volume (m^3) of fallen dead wood, SDW: Volume (m^3) of standing dead wood, both per hectare). Component 3 (PC3) showed forest structure in canopy and scrub coverage terms (Canopy: Percentage of canopy coverage, Scrub: Percentage of scrub coverage. Affect beetle diversity). Components 4 and 5 (PC4 and PC5) joined microhabitat availability in living trees (Excrescences: number of trees with trunk excrescences, Hollows: number of trees with tree hollows, CerGalleries: Number of trees with visible damage caused by *Cerambyx* beetles, TreeCanopyLoss: Number of trees with more than 50% of dead branches, all per hectare). Components 6, 7 and 8 (PC6, PC7 and PC8) joined the abiotic factors related to temperature (TMax, TMin and respectively TMean refer to maximum, minimum and mean temperature) and relative humidity (RH) (HMax, HMin and HMean respectively refer to maximum, minimum and mean humidity). Bold depicts the most important variables for each principal component.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Canopy	–	–	**0.7071**	–	–	–	–	–
Scrub	–	–	**0.7071**	–	–	–	–	–
TreeDen	**0.5991**	0.2070	–	–	–	–	–	–
MeanDiam	**−0.6715**	−0.1704	–	–	–	–	–	–
DDW	0.0036	**0.7887**	–	–	–	–	–	–
SDW	−0.4361	**0.5533**	–	–	–	–	–	–
Excrescences	–	–	–	0.3967	**0.5988**	–	–	–
Hollows	–	–	–	**−0.6749**	−0.1545	–	–	–
CerGaleries	–	–	–	**−0.5923**	0.3507	–	–	–
TreeCanopyLoss	–	–	–	−0.1907	**0.7033**	–	–	–
TMax	–	–	–	–	–	0.2833	−0.1149	**0.7691**
TMin	–	–	–	–	–	**0.4905**	0.0937	−0.0740
TMean	–	–	–	–	–	**0.5251**	−0.0336	0.3059
HMax	–	–	–	–	–	−0.2190	**0.7560**	0.3149
HMin	–	–	–	–	–	−0.3003	**−0.6353**	0.2339
HMean	–	–	–	–	–	**−0.5150**	0.0408	0.3944

Table 4
Values of the Principal Components (PC) for each sampling site.

Site	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
1	0.501	−0.705	0.237	0.256	−1.246	0.464	0.103	−0.119
2	−1.312	−1.276	−1.687	0.057	−0.948	2.213	−0.048	−0.239
3	−0.642	3.246	0.990	−2.857	2.326	−0.370	−0.339	−1.219
4	−0.901	−1.123	0.024	−2.255	−1.086	0.836	2.285	−1.192
5	0.071	−0.217	−0.185	1.424	1.151	−2.688	−0.070	−0.085
6	1.302	0.198	−0.023	1.407	0.606	−2.588	−0.136	0.310
7	−0.628	−0.615	−2.040	−0.386	−0.601	0.007	−0.652	2.168
8	0.210	−0.813	−1.674	−0.934	−0.784	0.160	0.441	0.898
9	1.153	0.063	1.131	0.594	1.848	−2.769	0.074	−0.306
10	0.578	0.624	1.529	0.697	0.211	2.160	1.145	1.183
11	−3.421	0.365	−1.474	−0.491	−0.947	1.651	−2.166	−1.426
12	1.934	−0.238	1.729	1.338	0.048	−0.015	0.714	−0.492
13	1.156	0.491	1.443	1.148	−0.577	0.939	−1.350	0.521

Table 5
Summary of valid model parameter estimates for the diversity metrics (Ab: abundance, S: species richness, ^1D: species diversity of order 1, FRed: functional redundancy). The models are presented with the main component variables ordered according to their importance in the model from most to least important. The R^2 coefficient shows the reliability of the model. See table 3 for the weights of the explanatory variables in each PC.

Models	R^2
Ab = 1002.66–161.529*PC8 + 805.626*PC2433.215*PC3 + 92.5121 *PC7 + 80.1143*PC6 + 375.671*PC1-158.008*PC4	0.99
S = 89.3048–13.0704*PC3-8.2434*PC4 + 2.71623*PC6 + 14.7183*PC1-7.01239*PC8-7.5787*PC7	0.98
^1D = 27.4533 + 3.29823*PC2-3.05328*PC8 + 2.0175*PC7	0.92
FRed = 0.0413863 + 0.00590858*PC5-0.0015011*PC60.00284795* PC8 + 0.00256053*PC4-0.00326329*PC1	0.99

PCs; Table 5), the species diversity of order 1 (^1D) was affected by only three of them. However for both metrics, deadwood (PC2) and maximum temperature (PC8) were the most important explanatory variables (Tables 3, 5). Although species richness (S) was also affected by a large number of variables (six of the eight PCs; Table 5), the relevance among them of vegetation coverage and the presence of tree microhabitats (i.e. tree hollows and galleries of cerambycid beetles) were noteworthy (PC4; Tables 3, 5). Functional redundancy was affected mainly by all the variables related to the presence of tree microhabitats, with special importance attached to trunk excrescences (cankers) and tree decay (represented by the loss of more than half the tree canopy) (PC5; Tables 3, 5) and by abiotic factors like maximum temperature (PC8; Tables 3, 5).

3.1.1. Response of insect diversity to forest structure

The predictive model of the effect of the variation of the most significant environmental variables on the different diversity metrics showed several possible scenarios. Vegetation coverage revealed an important and negative effect on species richness and abundance (PC3; Table 5). Scrub coverage of about 20% in the study area could predict values of 1235 individuals and of 96.3 of species, which means increases over the meanvalues in the study area of 23.2% and 7.8% in these diversity metrics respectively (Figs. 3, 4). In contrast, tree density and tree diameter seemed to have a minor impact on the diversity metrics of the study area (PC1; Table 5). Differences were also found between the response of the taxonomic and functional metrics. While an increasing number of trees per ha led to a slight increase in species richness and abundance, the opposite occurred with functional redundancy with a slight decrease (Figs. 3, 4, 6).

The increase in deadwood on soil (DDW) had a strong effect on the species diversity of order 1 (^1D) and abundances, where an increase in DDW from the mean values in the study area (0.5 m^3/ha) to 20 m^3/ha would lead to values of 3120 individuals and 36.1 species. This implies an increase of 211.2% to 31.5% for both diversity metrics, respectively

(Figs. 3, 5).

3.1.2. Response of insect diversity to tree microhabitats

Tree microhabitats (tree hollows, trunk excrescences, *Cerambyx* galleries, tree dead branches, etc.) were especially important for species richness and functional redundancy, but not always in the same way (Figs. 4, 6). Although doubling the mean number of trees with *Cerambyx* galleries per hectare in the study area (i.e. increase from 10 to 20 trees/ha) could imply increases of 3.5% in species richness and 0.9% in functional redundancy, the same increase in tree hollows/ha would increase species richness by 7.4%, but would not ensure higher functional redundancy. What is more, this functional metric would lower at the same magnitude (Fig. 6). The presence of trunk excrescences and dead branches on trees would impact only functional redundancy (Fig. 6). So a decline of only five trees below the mean value in the study area (from 15 to 10 trees/ha) could imply a 4.5% decrease in functional redundancy.

3.1.3. Response of insect diversity to abiotic factors

Regarding the effect of the abiotic factors in the studied area, we noted that higher values of maximum temperature (TMax) mean a general decrease in all the studied diversity metrics, while higher TMean and TMin favour species richness and abundance at the same time, and negatively affect functional redundancy (PC6; Table 5). This allowed us to predict that an increase of 1℃ in the mean temperature (TMean) over 17.5 ℃, together with the subsequent decrease in the mean humidity, could favour increases of 4.8% in species abundances and 2.4% in species richness, but would imply a 3% decrease in functional redundancy (Figs. 3-4, 6). In contrast, an increase in 1℃ over the mean maximum temperatures could imply decreases of 3.2% in beetle abundance, 1.2% in species richness, 2.7% in the effective number of species and 1.8% in functional redundancy (Figs. 3-6).

4. Discussion

The results support the notion that abandonment of some traditional forest management in the Mediterranean Region may reduce saproxylic beetle diversity, and this may be further aggravated by climate change. Moreover, not all the diversity metrics are affected in the same way and degree by the distinct environmental variables, and the main differences appear between the response of the taxonomic metrics and that of functional redundancy (as a measure of community functional resilience; Pérez-Sánchez et al., 2021). Species richness and abundance are: the most widely used diversity metrics in the literature; the most direct ones in their interpretation; the most sensitive to variation in environmental variables in our case. However, their use combined with other metrics, such as the species diversity of order 1 and functional redundancy, provides information on communities' vulnerability and resilience.

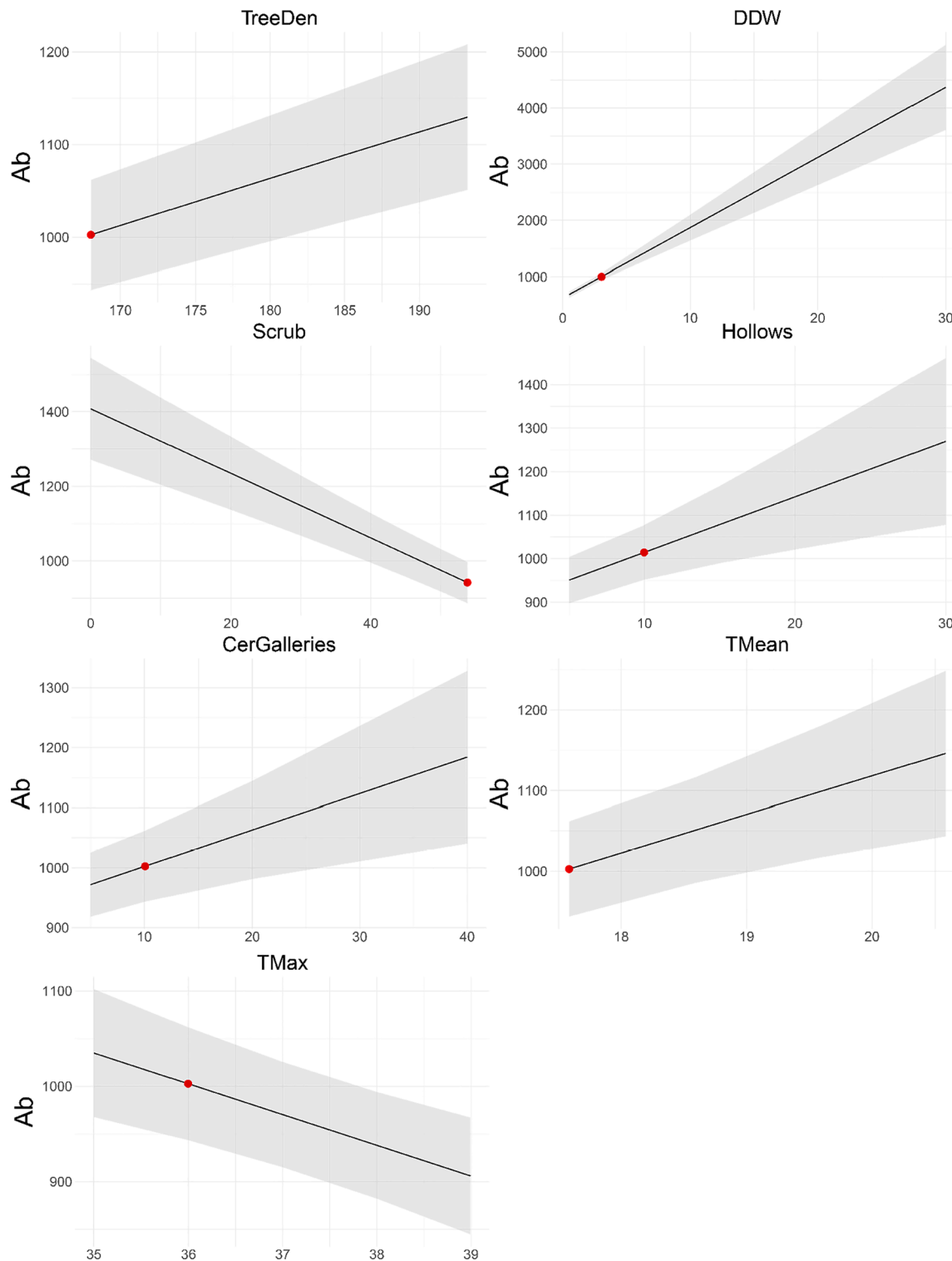Most of the variables describing forest structure and microhabitat

Fig. 3. Prediction of the response of species abundances to the environmental variables based on the obtained models in Table 5. TreeDen: number of trees per hectare, DDW: volume (m³) of fallen dead wood (≥7 cm in perimeter) per hectare, Scrub: percentage of total scrub coverage, Hollows: number of trees with tree hollows (≥10 cm in diameter) per hectare, CerGalleries: number of trees with visible damage caused by *Cerambyx* beetles per hectare, TMean: mean temperature (°C), TMax: maximum temperature (°C) (see Table 1). Red dots denote the medium value of each variable in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

availability are associated with traditional management (i.e., extensive livestock grazing, pollarding, firewood collection, forest thinning, etc.) or its abandonment. The analysis of the effect of these variables on biodiversity helped to provide guidelines to enhance diversity in different possible scenarios.

4.1. The dangers of bush encroachment and the deadwood gap

Scrub encroachment is one of the first effects of abandoning livestock grazing (Olea and San Miguel-Ayanz, 2006). Areas used for livestock grazing show little scrub coverage (5–25%), while the percentages of
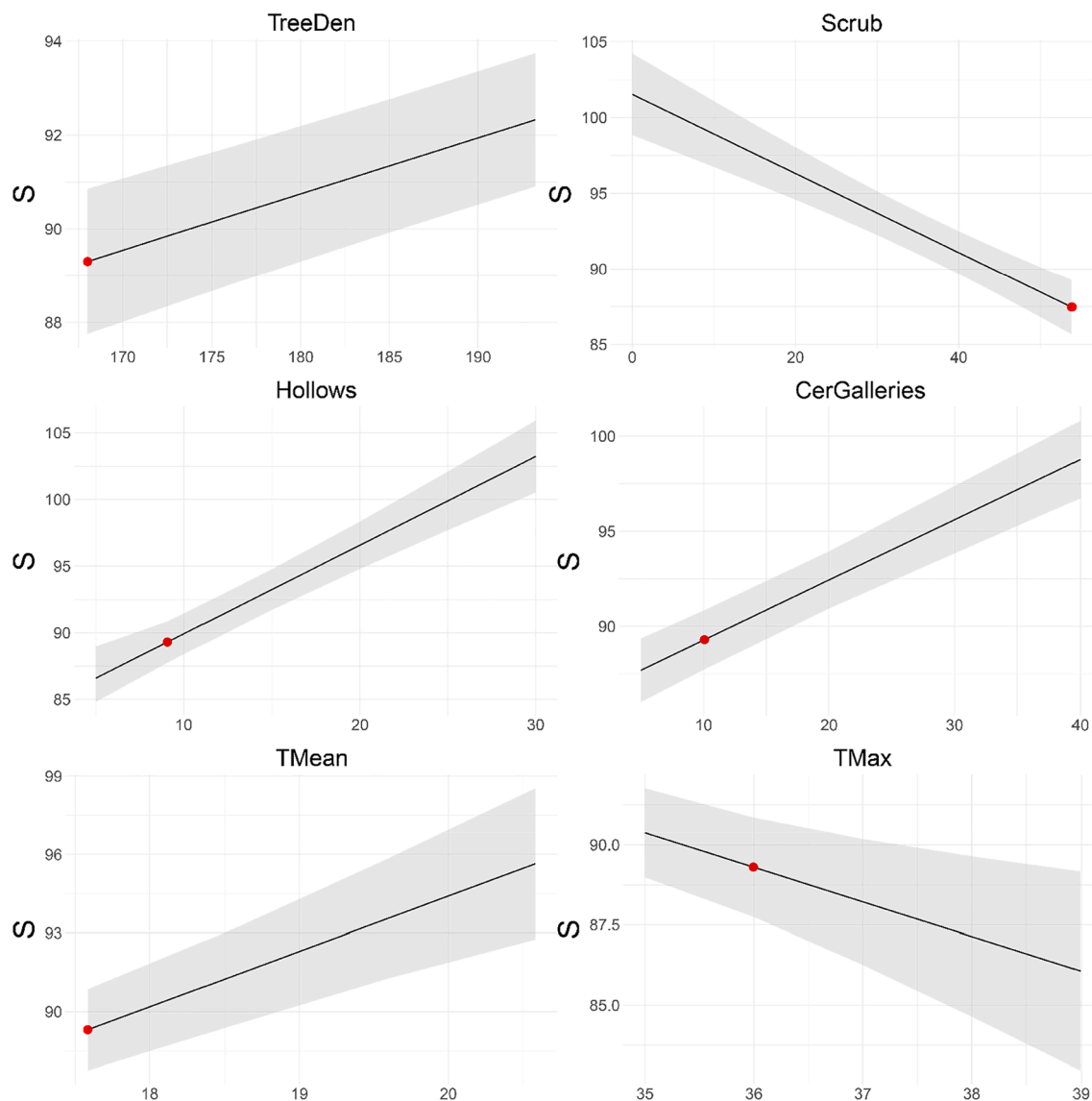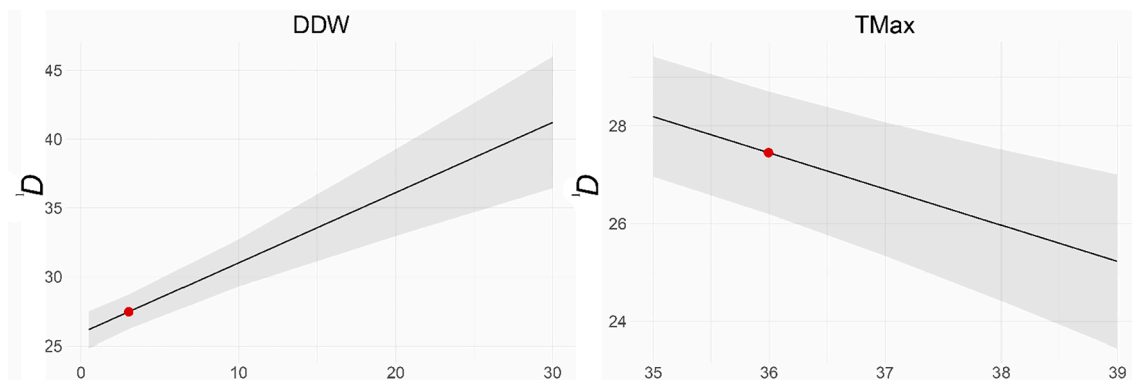
Fig. 4. Prediction of the response of species richness to the environmental variables based on the obtained models in Table 5. *TreeDen*: number of trees per hectare, *Scrub*: Percentage of total scrub coverage, Hollows: number of trees with tree hollows (≥10 cm in diameter) per hectare, CerGalleries: number of trees with visible damage caused by *Cerambyx* beetles per hectare, TMean: mean temperature (°C), TMax: maximum temperature (°C) (see Table 1). The red dot denotes the medium value of each variable in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)


Fig. 5. Prediction of the response of species diversity of order 1 (^1D) to the environmental variables based on the obtained models in Table 5. DDW: volume (m³) of fallen dead wood (≥7 cm in perimeter) per hectare, TMax: maximum temperature (°C) (see Table 1). The red dot denotes the medium value of each variable in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
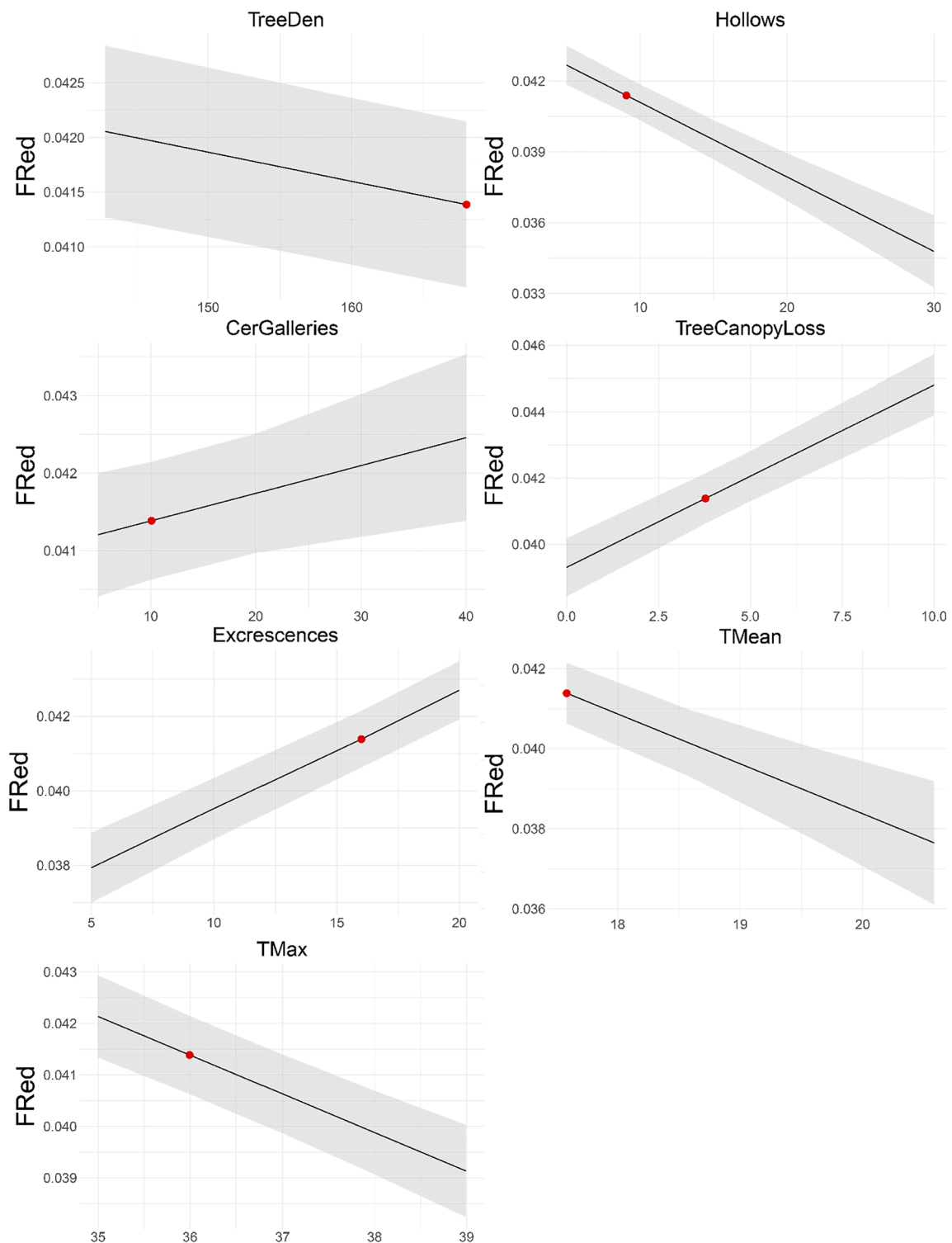
Fig. 6. Prediction of the response of functional redundancy to the environmental variables based on the obtained models in Table 5. TreeDen: number of trees per hectare, Hollows: Number of trees with tree hollows (≥10 cm in diameter) per hectare, CerGalleries: number of trees with visible damage caused by *Cerambyx* beetles per hectare, TreeCanopyLoss: number of trees with more than 50% of dead branches in the tree canopy per hectare, excrescences: number of trees with excrescences (burr and cankers) (≥10 cm in diameter) per hectare, TMean: mean temperature (°C), TMax: maximum temperature (°C) (see Table 1). The red dot denotes the medium value of each variable in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scrub cover in areas without livestock can exceed 90%. Nonetheless, the presence of flowering scrub can favour flower visitor insects in such managed ecosystems (nb: certain adult saproxylic beetles species depend on flower resources), which can broadly increase saproxylic beetle richness (Økland et al., 1996; Janssen et al., 2009; Ramírez-Hernández et al., 2014). Conversely, a dense scrub cover seems to negatively affect some saproxylic beetle diversity metrics, such as species richness and abundance. A real scenario in which scrub density coverage is maintained below 20% (the mean scrub coverage in our study area is about 40%) occurs in areas with livestock grazing, which

can help to increase beetle species richness and abundance by more than 7% and 23%, respectively (Figs. 3, 4).

While traditional forest management, which employs livestock grazing can, thus, favour saproxylic species richness and abundance by preventing forest encroachment, the virtual absence of DDW that characterises managed forests jeopardises saproxylic diversity, particularly species diversity (^1D) and abundance. The mean DDW values in such forests are very low (0.5 m³/ha) because it is used by citizens for firewood and deadwood volumes below 3.0 m³/ha have been classified as unsatisfactory for providing conditions for saproxylic organisms (see Karpiński et al., 2021). Several authors have indicated a deadwood threshold for saproxylic organisms at 20–50 m³, below which beetle species disappear and over which an increase in the number of species is not perceptible (Økland et al., 1996; Della Rocca et al., 2014; Müller & Bütler, 2010; Karpiński et al., 2021). In the study area, a real scenario of 20 m³ deadwood per ha would predict a major increase in species diversity (^1D) (more than 31.5% over the mean). Therefore, any activities that help to preserve or supply DDW at values above 20 m³/ha would secure good conditions for most saproxylic organisms and would contribute to the nutrient cycle in forests at the same time (Seibold et al., 2021).

4.2. More forest openness favours functional resilience over taxonomic diversity

Dehesa ecosystems are characterised by marked openness (fewer than 50 trees per hectare), which also favours tree growth and sun exposure. In central and northern European forests, openness has a positive effect on saproxylic species richness (Sverdrup-Thygeson & Birkemoe, 2009; Koch Widerberg et al., 2012). Conversely in the study area, increased tree density may favour species richness and abundance to some extent. In this way, tree density could dampen abiotic factors and affect saproxylic assemblages. However, this augmented species richness does not imply higher functional redundancy. Indeed functional redundancy slightly decreases with higher tree density. In areas with more scattered and bigger trees, such as *dehesa* ecosystems, this suggests that some kind of homogenisation resulting from tree and forest landscape management could favour functional redundancy and, to some extent, greater resilience to species loss (Pérez-Sánchez et al., 2021). However, following Micó et al. (2020), the functional space of saproxylic communities can be reduced with forest management.

4.3. Tree microhabitats are key for beetle taxonomic diversity and functional resilience

Tree management and forest openness can affect microhabitat diversity more or less directly because management can accelerate "veteranisation" of trees (Horák, 2017), and low tree density can favour the long-term formation of larger veteran trees. Tree-related microhabitats (tree hollows, trunk excrescences, insect galleries, canopy dead branches, etc.) are constantly evolving patchy substrates that host a wide variety of animals (mainly arthropods), plants and fungi (Larrieu et al., 2018; Winter & Möller, 2008; Speight, 1989; Dajoz, 2007). Moreover, the different types and characteristics of each microhabitat constrain species' functional traits and trophic guild distribution (Micó et al., 2020), which means that their presence and heterogeneity drive species diversity in different ways. Tree management (i.e., pollarding) promotes tree hollow formation, which are keystone elements for forest diversity, especially for arthropods (Müller et al., 2013; Micó, 2018; Hernández-Corral et al., 2021). The presence of tree hollows favours species richness, and doubling the mean number of tree hollows per hectare (from 10 to 20 trees) has been reported to increase species richness by more than 7%. However, an increase in both tree hollows and species richness has not involved higher functional redundancy because it actually decreased. Tree hollow assemblages are characterised by high functional diversity, which is driven by the niche

heterogeneity of tree hollows compared to other microhabitats (Micó et al., 2020). Therefore, it makes sense that the larger niche space offered by hollows allows them to host more species, but does not necessarily favour functional redundancy when species are specialised in using the different resources offered by this peculiar microhabitat (Mason et al., 2005; Pérez-Sánchez et al., 2021). In our case however, we cannot confirm a positive relation between the presence of tree hollows and functional richness because functional richness does not fit any model. In contrast, the presence of insect galleries in tree trunks not only favours species richness, but also functional redundancy. The positive effect of biotic variables, such as the presence of galleries made by big insects like *Cerambyx* species, has been previously demonstrated (Buse et al., 2008), and this kind of microhabitat favours mainly predator guilds that use such galleries for hunting (Micó et al., 2015). The presence of trees with *Cerambyx* galleries can be considered a sign of senescence, which increases saproxylic diversity (Larrieu et al., 2018; Buse et al., 2008), mostly of certain trophic guilds that confer the assemblage functional resilience. In the study area, the mean number of trees with galleries is 10 trees per hectare and although an increase to, for example 20 trees, can be perceived as a concern because it might threaten tree survival, it would mean an increase in species richness (3.5%) and functional redundancy (0.9%) (Fig. 6). In the same way, trees with trunk excrescences, which are discarded and not used in logging, provide a diversification of niches for saproxylic entomofauna, which implies increasing functional redundancy without necessarily increasing the number of species.

4.4. A possible increase in maximum temperatures could worsen saproxylic beetle diversity

One key question is whether diversity can worsen in the current climate change scene. It is assumed that the Mediterranean Basin is a region in which the impact of the global warming process is particularly strong (Lindner et al., 2010; Lozano-García et al., 2017). Morán-Ordoñez et al. (2021) show that by keeping the global mean temperature increase below 2℃ would secure the service provision and conservation of Mediterranean forests. Our results reveal that an increase in the mean and minimum temperatures (TMean and TMin) would be positively related to species richness and abundance. Along the same lines, some data from northern Europe indicate that an increase in the mean temperature could have a positive effect on saproxylic species richness (Kamboyi, 2019). In line with this, we predict that a rise of 1℃ in the mean temperature (TMean) over the mean of 17.5℃, together with the subsequent drop in the mean humidity, could favour an increase in both species abundance (4.8%) and species richness (2.4%). However, such an increase in TMean (and decreased humidity) would result in diminished functional redundancy (Fig. 6). This result highlights the vulnerability of these Mediterranean communities to climate warming. What is more, a rise in the maximum temperature (TMax) would mean the generally lowering of all the diversity metrics, including the functional one. In our study area, the mean of the maximum temperatures is 36 °C, and a rise of 1℃ could imply a decrease from 1.8% to 3.2% in all the metrics (Figs. 3-6). It is, thus, noticeable that the benefits on saproxylic diversity of an increase of 1℃ in the mean temperature are much less considerable than the negative impact (in all biodiversity metrics) of an increase in the mean maximum temperatures both qualitatively and quantitatively.

4.5. Guidelines to enhance saproxylic diversity in traditionally managed Mediterranean forests

Although there are many variables that influence saproxylic diversity, they are not all equally controllable in the short term. We suggest guidelines to boost saproxylic beetle diversity based on a combined assumption in real scenarios, which include the maintenance of scrub coverage and the density of trees with hollows at values of 20% and 20

trees per ha, respectively, and the retention/supply of deadwood on soil at 20 m³/ha. The two first are related to habitat and tree management, while retention or supply of deadwood is required to bridge a gap that is unfortunately common in traditionally managed forests.

This combined scenario would predict an increase in the studied taxonomic and ecological diversity metrics (Ab, S, ¹D) of 248.3%, 16.9%, and 31.5% respectively, over the current mean values in the study area. These minimal actions that address enhancing beetle diversity would not ensure higher functional redundancy. Instead, preserving trees affected by large borers and with excrescences is necessary to also confer the saproxylic system greater resilience.

CRediT authorship contribution statement

Estefanía Micó: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Funding acquisition. **Sandra Martínez-Pérez:** Conceptualization, Methodology, Measurement of functional traits and functional traits analysis, Statistical analysis, Reviewing and Editing. **Jorge Jordán-Núñez:** Statistical analysis, Modelling and prediction analysis, Reviewing. **Eduardo Galante:** Conceptualization, Reviewing, Funding acquisition. **Bàrbara Micó-Vicent:** Statistical analysis, Modelling and prediction analysis, Reviewing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120402.

References

Angelo, M.J., Slansky, F., 1984. Body building by insects: trade-offs in resource allocation with particular reference to migratory species. Fla. Entomol. 67, 22–41. https://doi.org/10.2307/3494102.

Barton, P.S., Gibb, H., Manning, A.D., Lindenmayer, D.B., Cunningham, S.A., 2011. Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage: morphological traits of beetles. Biol. J. Linn. Soc. 102, 301–310. https://doi.org/10.1111/j.1095-8312.2010.01580.x.

Bauer, T., 1981. Prey capture and structure of the visual space of an insect that hunts by sight on the litter layer (*Notiophilus biguttatus* F., Carabidae, Coleoptera). Behav. Ecol. Sociobiol. 8, 91–97. https://doi.org/10.1007/BF00300820.

Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zaragoza, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, S.A., Smith, A.B.T., 2011. Family-group names in Coleoptera (Insecta). Zookeys 1–972. https://doi.org/10.3897/zookeys.88.807.

Bouget, C., Brustel, H., Brin, A., Noblecourt, T., 2008. Sampling saproxylic beetles with window flight traps: methodological insights. Revue d'écologie 63, 13–24.

Bugalho, M.N., Caldeira, M.C., Pereira, J.S., Aronson, J., Pausas, J.G., 2011. Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. Front. Ecol. Environ. 9, 278–286. https://doi.org/10.1890/100084.

Buse, J., Ranius, T., Assmann, T., 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. Conserv. Biol. 22, 329–337. https://doi.org/10.1111/j.1523-1739.2007.00880.x.

Carmona, C.P., 2017. TPD: methods for measuring functional diversity based on trait probability density. R package version 1. https://CRAN.Rproject.org/package=TPD.

Carmona, C.P., 2014. Efectos de la intensificación y el abandono ganaderos en la composición, diversidad y funcionamiento de pastizales mediterráneos. Ecosistemas 23, 73–78. https://doi.org/10.7818/ECOS.2014.23-1.13.

Carmona, C.P., de Bello, F., Mason, N.W., Lepš, J., 2019. Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. Ecology 100, in press. https://doi.org/10.1002/ecy.2876.

Carmona, C.P., De Bello, F., Mason, N.W., Lepš, J., 2016a. Traits without borders: integrating functional diversity across scales. Trends Ecol. Evol. 31, 382–394. https://doi.org/10.1016/j.tree.2016.02.003.

Carmona, C.P., de Bello, F., Mason, N.W., Lepš, J., 2016b. The density awakens: a reply to Blonder. Trends Ecol. Evol. 31, 667–669.

Carmona, C.P., Mason, N.W., Azcárate, F.M., Peco, B., 2015. Inter-annual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance. J. Veg. Sci. 26, 538–551. https://doi.org/10.1111/jvs.12260.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547. https://doi.org/10.1890/11-1952.1.

Chao, A., Shen, T.J., 2010. Program SPADE (Species Prediction and Diversity estimation). Program and user's guide. http://chao. stat. nthu. edu. tw.

Cunningham, S.A., Murray, W., 2007. Average body length of arboreal and aerial beetle (Coleoptera) assemblages from remnant and plantation Eucalyptus forests in southwestern Australia. Oecologia 151, 303–312.

Dajoz, R., 2007. Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier. 2 è édition. Tec. et Doc. Lavoisier, Paris.

Dawson, T., Fry, R., 1998. Agriculture in nature's image. Trends Ecol. Evol. 2, 50–51.

Della Rocca, F., Stefanelli, S., Pasquaretta, C., Campanaro, A., Bogliani, G., 2014. Effect of deadwood management on saproxylic beetle richness in the floodplain forests of northern Italy: some measures for deadwood sustainable use. J. Insect Conserv. 18, 121–136. https://doi.org/10.1007/s10841-014-9620-1.

Díaz, M., Campos-Palacín, P., Pulido, F.J., 1997. The Spanish dehesas: a diversity in land use and wildlife. In: Pain, D.J., Pienkowski, M. (Eds.), Farming and birds in Europe: the common agricultural policy and its implications for bird conservation. Academic Press, London, UK, pp. 178–209.

Díaz, M., Pulido, F.J., Marañón, T., 2003. Diversidad biológica y sostenibilidad ecológica y económica de los sistemas adehesados. Ecosistemas 12.

FAO, 2018. Agriculture to Achieve the SDGs. 20 Interconnected Actions to Guide Decision-Makers. Food and Agriculture Organization of the United Nations: Rome, Italy.

Forsythe, T.G., 1983. Locomotion in ground beetles (Coleoptera carabidae): An interpretation of leg structure in functional terms. J. Zool. 200, 493–507. https://doi.org/10.1111/j.1469-7998.1983.tb02811.x.

Fountain-Jones, N.M., Jordan, G.J., Burridge, C.P., Wardlaw, T.J., Baker, T.P., Forster, L., Petersfield, M., Baker, S.C., 2017. Trophic position determines functional and phylogenetic recovery after disturbance within a community. Funct. Ecol. 31, 1441–1451. https://doi.org/10.1111/1365-2435.12845.

Galante, 2021. Dehesas y montados, ricos en historia y biodiversidad. In: Micó et al., (Eds) El bosque adehesado como refugio de una entomofauna muy diversa. Publicaciones Universidad de Alicante, pp. 13-30.

García Rodríguez, J.A., Puerto Martín, A., Rodríguez González, R., 1984. Aspectos ecológicos de la provincia de Salamanca (España). Centro Edafología y Biología aplicada Excma, Diputación provincial de Salamanca.

Gibb, H., Hjältén, J., Ball, J.P., Pettersson, R.B., Landin, J., Alvini, O., Danell, K., 2006. Wing loading and habitat selection in forest beetles: Are red-listed species poorer dispersers or more habitat-specific than common congenerics? Biol. Conserv. 132, 250–260. https://doi.org/10.1016/j.biocon.2006.04.017.

Gillespie, M.A.K., Birkemoe, T., Sverdrup-Thygeson, A., 2017. Interactions between body size, abundance, seasonality, and phenology in forest beetles. Ecol. Evol. 7, 1091–1100. https://doi.org/10.1002/ece3.2732.

Hernández-Corral, J., García López, A., Ferrández, M.Á., Micó, E., 2021. Physical and biotic factors driving the diversity of spider assemblages in tree hollows of Mediterranean Quercus forests. Insect Conservation and Diversity 14, 515–526. https://doi.org/10.1111/icad.12483.

Horák, J., 2017. Insect ecology and veteran trees. J. Insect Conserv. 21, 1–5. https://doi.org/10.1007/s10841-017-9953-7.

Janssen, P., Fortin, D., Hébert, C., 2009. Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. Ecography 32, 423–432. https://doi.org/10.1111/j.1600-0587.2008.05671.x.

Johansson, L.C., Engel, S., Baird, E., Dacke, M., Muijres, F.T., Hedenström, A., 2012. Elytra boost lift, but reduce aerodynamic efficiency in flying beetles. J. R. Soc. Interface 9, 2745–2748. https://doi.org/10.1098/rsif.2012.0053.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Kamboyi, C., 2019. Comparing the composition of saproxylic beetle fauna on old hollow oaks between two time periods. Linköping University. Ms Thesis.

Karpiński, L., Maákand, I., Wegierek, P., 2021. The role of nature reserves in preserving saproxylic biodiversity: using longhorn beetles (Coleoptera: Cerambycidae) as bioindicators. Eur. Zool. J. 88, 487–504. https://doi.org/10.1080/24750263.2021.1900427.

Koch Widerberg, M., Ranius, T., Drobyshev, I., Nilsson, U., Lindbladh, M., 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. Biodivers. Conserv. 21, 3035–3059. https://doi.org/10.1007/s10531-012-0353-8.

Kraus, D., et al., 2016. Catalogue of Tree Microhabitats – Reference Field List. Integrate+ Technical Paper. 16p.

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A. K., Regnery, B., Vandekerkhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. Ecol. Ind. 84, 194–207. https://doi.org/10.1016/j.ecolind.2017.08.051.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698–709. https://doi.org/10.1016/j.foreco.2009.09.023.

Llamas, O., Belinchón, G., Ramos, L.A., Albadalejo, P.V., 2011. El Rebollar. Tomero y Romillo Servicios Ambientales, León.

Löbl, I., Smetana, A., 2010. Catalogue of Palaearctic Coleoptera. Volume 6: Chrysomeloidea. Apollo books, Stenstrup, Denmark.

Löbl, I., Smetana, A., 2004. Catalogue of Palaearctic Coleoptera. Volume 2: Hydrophiloidea-Histeroidea-Staphylinoidea. Apollo books, Stenstrup, Denmark.

Lozano-García, B., Muñoz-Rojas, M., Parras-Alcántara, L., 2017. Climate and land use changes effects on soil organic carbon stocks in a Mediterranean semi-natural area. Sci. Total Environ. 579, 1249–1259. https://doi.org/10.1016/j.scitotenv.2016.11.111.

Manly, B.F.J., 1995. A note on the analysis of species co-occurrences. Ecology 76, 1109–1115.

Martín Vicente, Á., Fernández Alés, R., 2006. Long term persistence of dehesas. Evidences from history. Agroforest. Syst. 67, 19–28.

Martinez-Harms, M.J., Bryan, B.A., Figueroa, E., Pliscoff, P., Runting, R.K., Wilson, K.A., 2017. Scenarios for land use and ecosystem services under global change. Ecosyst. Serv. 25, 56–68. https://doi.org/10.1016/j.ecoser.2017.03.021.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x.

Micó, E., 2018. Saproxylic Insects in Tree Hollows. In: Ulyshen, M.D. (Ed.), Saproxylic Insects: Diversity, Ecology and Conservation, Zoological Monographs. Springer International Publishing, Cham, pp. 693–727. https://doi.org/10.1007/978-3-319-75937-1_21.

Micó, E., Marcos-García, M.A., Ramírez-Hernández, A., Galante, E., 2021. El Bosque adehesado como refugio de una entomofauna muy diversa. Publicaciones Universidad de Alicante. 141, pp.

Micó, E., García-López, A., Sánchez, A., Juárez, M., Galante, E., 2015. What can physical, biotic and chemical features of a tree hollow tell us about their associated diversity? J. Insect Conservat. 19, 141–153. https://doi.org/10.1007/s10841-015-9754-9.

Micó, E., Ramilo, P., Thorn, S., Müller, J., Galante, E., Carmona, C.P., 2020. Contrasting functional structure of saproxylic beetle assemblages associated to different microhabitats. Sci. Rep. 10, 1–11. https://doi.org/10.1038/s41598-020-58408-6.

Morán-Ordóñez, A., Ramsauer, J., Coll, L., Brotons, L., Ameztegui, A., 2021. Ecosystem services provision by Mediterranean forests will be compromised above 2°C warming. Glob. Change Biol. 27, 4210–4222. https://doi.org/10.1111/gcb.15745.

Moreno, G., Pulido, F.J., 2009. The functioning, management and persistance of Dehesas. In: Rigueiro-Rodríguez, et al. (Eds.), Agroforestry in Europe: Current Status and Future Prospects. Springer Science + Business Media B.V, pp. 127–170.

Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Ellers, J., Berg, M.P., 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Funct. Ecol. 31, 558–567. https://doi.org/10.1111/1365-2435.12776.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. Forest Res. 129, 981–992. https://doi.org/10.1007/s10342-010-0400-5.

Müller, J., Jarzabek-Müller, A., Bussler, H., Gossner, M.M., 2013. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. Anim. Conserv. 17, 154–162. https://doi.org/10.1111/acv.12075.

Norberg, U.M., 1990. Vertebrate flight Springer-Verlag. Berlin, Germany.

Økland, B., Bakke, A., Hågvar, S., Kvamme, T., 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers. Conserv. 5, 75–100. https://doi.org/10.1007/BF00056293.

Olea, L., San Miguel-Ayanz, A., 2006. The Spanish dehesa. A traditional Mediterranean silvopastoral system linking production and nature conservation. Grassland Science in Europe 11, 3–13.

Oliver-Moscardó, S., Luis-Calabuig, E., 1979. Factores termopluviométricos. In: Ballcells, E. (Ed.), Integrado y multidisciplinar de la dehesa salmantina. Centro Edafología y Biología Aplicada de Salamanca y Centro Pirenaico de Biología experimental, CSIC, Salamanca- Jaca, pp. 101–155.

Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., McNees, J., Akçakaya, H.R., 2014. Life history and spatial traits predict extinction risk due to climate change. Nat. Clim. Change 4, 217–221.

Pérez-Sánchez, D., Galante, E., Micó, E., 2020. Functional and taxonomic beta diversity of saproxylic beetles in Mediterranean forests: On what factors do they depend? Environ. Entomol. 49, 615–626. https://doi.org/10.1093/ee/nvaa045.

Pérez-Sánchez, D., Mason, N.W., Brustel, H., Galante, E., Micó, E., 2021. A higher taxonomic richness does not ensure the functional resilience of saproxylic beetle communities in evergreen Quercus forests. Ecol. Entomol. 46, 1215–1229. https://doi.org/10.1111/een.13069.

Plieninger, T., Wilbrand, C., 2001. Land use, biodiversity conservation, and rural development in the dehesas of Cuatro Lugares, Spain. Agrofor. Syst. 51, 23–34. https://doi.org/10.1023/A:1006462104555.

Plieninger, T., Pulido, F., Konold, W., 2003. Effects of land-use history on size structure of holm oak stands in Spanish dehesas: Implications for conservation and restoration. Environ. Conserv. 30, 61–70. https://doi.org/10.1017/S0376892903000055.

Quinto, J., Micó, E., Martínez-Falcón, A.P., Galante, E., Marcos-García, M.A., 2014. Influence of tree hollow characteristics on the diversity of saproxylic insect guilds in Iberian Mediterranean woodlands. J. Insect. Conserv. 18, 981–992. https://doi.org/10.1007/s10841-014-9705-x.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramilo, P., Martínez-Falcón, A.P., García-López, A., Brustel, H., Galante, E., Micó, E., 2017. Influence of traditional management and environmental variables on mediterranean saproxylic beetle assemblages. Environ. Entomol. 46, 1235–1242. https://doi.org/10.1093/ee/nvx140.

Ramírez-Hernández, A., Micó, E., Marcos-García, M.A., Brustel, H., Galante, E., 2014. The «dehesa», a key ecosystem in maintaining the diversity of Mediterranean saproxylic insects (Coleoptera and Diptera: Syrphidae). Biodivers. Conserv. 23, 2069–2086. https://doi.org/10.1007/s10531-014-0705-7.

Rathore, P., Roy, A., Karnatak, H., 2019. Assessing the vulnerability of Oak (Quercus) forest ecosystems under projected climate and land use land cover changes in Western Himalaya. Biodivers. Conserv. 28, 2275–2294. https://doi.org/10.1007/s10531-018-1679-7.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol. Ind. 34, 221–230. https://doi.org/10.1016/j.ecolind.2013.05.003.

Ribera, I., McCracken, D.I., Foster, G.N., Downie, I.S., Abernethy, V.J., 1999a. Morphological diversity of ground beetles (Coleoptera: Carabidae) in Scottish agricultural land. J. Zool. 247, 1–18.

Ribera, I., Foster, G.N., Downie, I.S., McCracken, D.I., Abernethy, V.J., 1999b. A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). Ann. Zool. Fenn. 36, 21–37.

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E., Pavoine, S., 2016. Measuring the functional redundancy of biological communities: a quantitative guide. Methods Ecol. Evol. 7, 1386–1395.

Sánchez Martínez, C., Peñil, B., de Enterría, S.G., Castro, I.B., Herrero, N.M., Ruiz, C.P., Sánchez, J.S., Agudo, J.A.S., de La Cruz, D.R., Galante, E., Marcos-García, M.A., Micó, E., 2012. Manual de Gestión Sostenible de Bosques Abiertos Mediterráneos. Castilla Tradicional, Salamanca.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8.

Speight, M.C.D., 1989. Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg, France.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge University Press.

Sverdrup-Thygeson, A., Birkemoe, T., 2009. What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees. J. Insect Conserv. 13, 183. https://doi.org/10.1007/s10841-008-9141-x.

Talarico, F., Brandmayr, P., Giglio, A., Massolo, A., Brandmayr, T.Z., 2011. Morphometry of eyes, antennae and wings in three species of Siagona(Coleoptera, Carabidae). Zookeys 203–214. https://doi.org/10.3897/zookeys.100.1528.

Ulyshen, M.D., Šobotník, J., 2018. An introduction to the Diversity, Ecology and Conservation of Saproxylic Insects. In: Ulyshen, M.D. (Ed.), Saproxylic Insects: Diversity, Ecology and Conservation, Zoological Monographs. Springer International Publishing, pp. 1–47. https://doi.org/10.1007/978-3-319-75937-1_1.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1.

Vogel, S., Gossner, M.M., Mergner, U., Müller, J., Thorn, S., 2020. Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. J. Appl. Ecol. 57, 2075–2085. https://doi.org/10.1111/1365-2664.13648.

Watts, C.H., Mason, N.W.H., 2015. If we build – they mostly come: partial functional recovery but persistent compositional differences in wetland beetle community restoration. Restor. Ecol. 23, 555–565. https://doi.org/10.1111/rec.12227.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manage. 255, 1241–1261.

Woodcock, B.A., Redhead, J., Vanbergen, A.J., Hulmes, L., Hulmes, S., Peyton, J., Nowakowski, M., Pywell, R.F., Heard, M.S., 2010. Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. Agric. Ecosyst. Environ. 139, 181–186. https://doi.org/10.1016/j.agee.2010.07.018.

Wootton, R.J., 1992. Functional Morphology of Insect Wings. Annu. Rev. Entomol. 37, 113–140. https://doi.org/10.1146/annurev.en.37.010192.000553.

Further reading

Fleming, P.A., Wentzel, J.J., Dundas, S.J., Kreplins, T.L., Craig, M.D., Hardy, G.E., St, J., 2021. Global meta-analysis of tree decline impacts on fauna. Biol. Rev. 96, 1744–1768. https://doi.org/10.1111/brv.12725.