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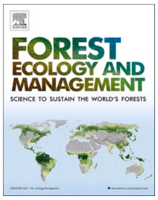

Environmental drivers shaping the macrofungal sporocarp community in Mediterranean *Quercus ilex* stands

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ABSTRACT

Holm oak is one of the most abundant tree-forming species in the Mediterranean area, hosting a great number of fungal species that are fundamental for the functioning of these forest ecosystems. However, the information about the fungal communities growing in *Quercus ilex* stands and the environmental drivers shaping their fruiting patterns is still scarce. This study aimed to characterize the productivity, diversity, and community composition of macrofungal sporocarps growing in Mediterranean *Quercus ilex* stands as shaped by key environmental drivers including meteorological and soil variables. We analysed a data set obtained from the autumn weekly sampling of all macrofungal sporocarps from 8 permanent plots over 13 consecutive years, and related weather and soil variables. We built up several linear mixed-effects models to describe productivity and richness changes over time, in addition to multivariate analyses aiming to describe the community composition variations. We identified 241 macrofungal species that were predominantly ectomycorrhizal, with Russulaceae and Cortinariaceae being the most abundant families. Agaricaceae and Tricholomataceae were the most abundant families of saprotrophic fungi. In addition, soil properties such as pH, organic matter and sand content played a significant role in sporocarp community composition. Our results highlight different drivers shaping different fungal fruiting processes, i.e., weather variables drive sporocarp productivity and sporocarp richness while soil characteristics may have a stronger influence on the aboveground fungal community composition. This study illustrates the high stochasticity of sporocarp occurrence and productivity, with species exhibiting higher values whenever the meteorological conditions were suitable for fungal fruiting.

1. Introduction

Holm oak woodlands (*Quercus ilex* L.) are one of the most widespread forest ecosystems in the Mediterranean basin and represent unique ecosystems with high mycological importance (Zotti and Pautasso, 2013). It is known that fungi are key organisms for forest ecosystem functioning (Hawksworth and Lücking, 2017), playing important roles as plant symbionts, pathogens, and decomposers (Saitta et al., 2018). In forest ecosystems, ectomycorrhizal fungi (ECM) provide their host plants with nitrogen and phosphorus (Smith and Read, 2008), and contribute in drier Mediterranean forests to water acquisition by trees (Allen, 2007; Querejeta, 2017). In addition, saprotrophs have an important effect on litter degradation (Baldrian et al., 2011), being essential for the functioning of the ecosystem, decomposing soil organic matter and nutrient release as well as nutrient uptake and production (Smith and Read, 2008).

Additionally, Mediterranean *Q. ilex* stands are characterised by a high fungal biodiversity with an abundance of rare species and with a predominance of ECM species, specifically those belonging to the genera *Russula* and *Cortinarius* (Richard et al., 2004; Zotti and Pautasso, 2013). Saprotrophs are less abundant in *Q. ilex* stands but share with the ECM community the high number of rare taxa (Richard et al., 2004).

Previous research focused on Mediterranean forests has shown that weather and soil variables influence both fungal sporocarps diversity

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Abbreviations: **AIC**, Akaike information criterion; **DCA**, Detrended correspondence analysis; **ECM**, Ectomycorrhizal; **GLMM**, Generalized linear mixed-effects model; **IUCN**, International Union for Conservation of Nature; **LC**, Least concern; **LMM**, Linear mixed-effects model; **NT**, Near threatened; **OM**, Organic matter.

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and productivity (Collado et al., 2018; Taye et al., 2016, Salerni et al., 2002). Therefore, predicted increasing drought impacts on Mediterranean forests may lead to a reduction of tree growth (Sardans and Peñuelas, 2013) and, consequently, may also entail a negative effect on ECM fungi in symbiosis with host trees and thus in fruiting patterns (Shi et al., 2002). On the other hand, saprotrophic fungi seem to be more associated with the substrate. In fact, many species show a preference for a specific tree or shrub litter (Boddy, 2016). In addition, some authors such as Primicia et al. (2016) and Salerni et al. (2002) found that saprotrophic fungi are also affected by weather variables. Moreover, there is a need for further research on environmental variables and soil characteristics driving fungal fruiting in water-limited Mediterranean *Q. ilex* ecosystems since soil water-retention properties are primarily determined by texture, structure, and organic matter content (Hudson, 1994). This background information suggests that fungal fruiting will be determined by the combination of soil properties that affect water retention, as well as by the local weather conditions.

Although numerous studies have analysed fungal communities in Mediterranean areas (Alday et al., 2017; Castaño et al., 2018; Collado et al., 2021), further information is needed in order to have a full understanding of the Mediterranean *Q. ilex* stands and their associated fungal species community. Most studies in Mediterranean areas in this field (Zotti and Pautasso, 2013; Richard et al., 2004) focus on qualitative diversity and community composition, without addressing fungal productivity in the form of sporocarp biomass (Richard et al., 2011; Saitta et al., 2018). Moreover, previous studies have largely focused on a single guild (ECM fungi) to the exclusion of others (Richard et al., 2011; Shahin et al., 2013), or employed DNA metabarcoding methods that preclude biomass estimates (Saitta et al., 2018; Shahin et al., 2013). Only a few studies have analysed the environmental drivers shaping the fungi growing in *Q. ilex* stands (Salerni et al., 2002; Saitta et al., 2018). The main aim of this study is to fill these knowledge gaps for key Mediterranean forest ecosystems by describing sporcarp productivity, diversity, and community composition in *Q. ilex* stands of the north-eastern Iberian Peninsula. Since our data set comprises sporocarps records from permanent plots sampled over 13 consecutive years, we analysed i) how macrofungal sporocarp productivity, diversity (sporocarps richness and evenness) and community composition of ECM and saprotrophic fungi change over time, and ii) how such changes are related to different potential environmental drivers including both weather and soil conditions.

2. Material and methods

2.1. Study area

The study area is located within the natural protected area of PNIN-Poblet (41° 21′ 6.4728″ E, 1° 02′ 25.8″ N), at the northern part of Prades mountains (Tarragona, Spain) between 400 and 1201 m a.s.l. The bedrock is mostly Palaeozoic phyllite with small amounts of metamorphic sandstones with micro-conglomerates and the soils are Inceptisols and Entisols (Ogaya et al., 2020) with a pH ranging from 5.3 to 7.0. The study area has a Mediterranean climate with continental trends with increasing altitude, characterized by dry summer seasons followed by wet autumns with a mean annual accumulated rainfall of 618 mm and temperature in a range of 0 °C in the colder months to 30 °C during the warmer summer months. The *Q. ilex* stands cover 76% of the whole study area and are characterised by an almost pure arboreal stratum of branched short-sized holm oaks (*Q. ilex* ssp. *ilex*) with the occasional presence of *Acer opalus, A. monspessulanum* and *Pinus pinaster*; the shrub stratum is composed of *Arbutus unedo*, *Calluna vulgaris*, *Erica arborea* and *Phillyrea latifolia*. Modelling data including sporocarp productivity and species richness, meteorological and soil variables in addition to altitude and slope of the plots are included in Table A.1 and Table A.2 in Appendix A.

2.2. Fieldwork and data collection

Eight *Q. ilex* stands with a range of altitudes (530–850 m.a.s.l.) and slopes (15–36%) were investigated (Table A.2 in Appendix A). In each stand, a 100 m^2 (10 × 10 m permanent sampling plot was randomly placed within the vegetation growing in the stand while maintaining sufficient distance to roads and between plots in order to avoid edge effects. In order to collect all epigeous sporocarps of ECM and saproteroph soil macrofungi fruiting in autumn, from 2008 to 2020, each plot was weekly surveyed from the beginning of September to the end of December with a total of 203 surveys and most of the yields being concentrated in October and November. Species forming microscopic, hypogeous, or resupinate sporocarps were not taken into account. Sporocarps of species fruiting directly on woody debris, fresh dungs, or living plants were also not considered. Sporocarps were taken to the laboratory for identification at the species level when it was possible following Bon (1987), Breitenbach and Kränzlin (1991), Moser (1983), Courtecuisse and Duhem (1994), and assigned to ECM or saprotrophs guilds according to Agerer (2006) and Tedersoo et al. (2014). Species nomenclature follows the CABI Bioscience Database of Fungal Names (as per May 2021). Sporocarp species richness was measured as the total number of species collected per plot and year. In addition, all sporocarps were counted and dry biomass was measured as described by Martínez de Aragón et al. (2007) and reported as fungal productivity (kg ha^{-1}). Finally, we checked The IUCN Red List of threatened species (IUCN, 2021) to analyse the current protection status of the gathered species.

2.3. Soil sampling and climate data

Soil samples were taken in all 8 plots in the Autumn of 2019 in order to analyse soil physicochemical properties. In each plot a soil core (20 × 20 × 20 cm) was taken using a cubic soil borer previously removing the litter layer but including humus and mineral soil profiles. In the laboratory, the soil samples were analysed using the methodology described in Alday et al. (2012). Each sample was air-dried and sieved (≤2 mm mesh) to separate the coarse elements fraction from the soil. Sand content was analysed using the Bouyoucos-method (Day, 1965). Soil pH was measured using a conductivity meter in a 1:2.5 soil: deionized water slurry (Allen,1989). Finally, total organic matter (OM) was analysed using the Walkley-Black method (Walkley, 1947).

Daily meteorological data for each plot, i.e. accumulated rainfall and temperature (minimum, maximum and average) were obtained from the weighted mean interpolation and altitudinal and slope correction of the daily meteorological records of the Spanish Meteorological Agency (1990–2011), and from both Catalan and Spanish Meteorological agencies stations (1990–2020), following the DAYMET methodology (Thornton and Running, 1999; Thornton et al., 2000) as implemented in the R package ‘meteoland’ (De Cáceres et al., 2018). From the obtained meteorological data, we developed the variables that will be tested in the data analysis. Variables were aggregated depending on the meaningful time scale to properly represent a given meteorological event. Some variables were aggregated monthly, such as monthly accumulated precipitation and mean temperature (min, mean and max) for August, September, October and November. Other variables represented a week or day of the year (DOY), such as: 1st 50 mm (Week / DOY), the moment of the year, from the 1st of August, in which 50 mm of precipitation are reached; 75% annual rainfall (Week / DOY), the moment of the year in which the 75% of the annual accumulated rainfall are reached; Cold 1st (Week / DOY), the moment of the year, from the 1st of August, in which 5 consecutive days with temperatures below 5 °C occurred; Frost 1st (Week / DOY), the moment of the year, from the 1st of August, in which the minimum temperature fell below 0 °C; Rainy Days (RD), number of rainy days from the 1st of August. Finally, Autumn accumulated rainfall (mm): accumulated rainfall in mm between the 1st of August and the first day in which temperatures fell below 0 °C (Table A.1 in Appendix A).

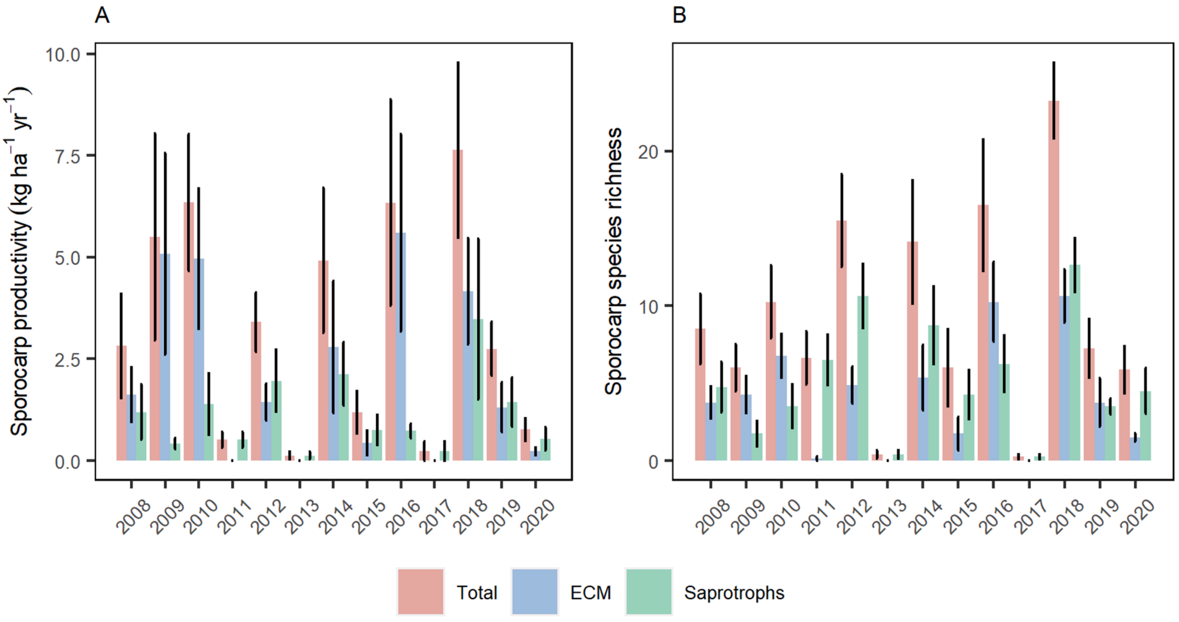

Fig. 1. Mean annual sporocarp productivity and sporocarp species richness variation along the study period (2008–2020). Sporocarp productivity in dry biomass (kg ha^{-1} yr^{-1}) (A) and sporocarp species richness (B) are split in total (i.e. considering all ectomycorrhizal and saprotrophic macrofungi), ectomycorrhizal (ECM), and saprotrophic fungal guilds. Error bars indicate ± Standard Error (SE) of the mean.

2.4. Data analysis

Statistical analyses were implemented in R software 4.0.2 (R Development Core Team, 2020) using the 'lme4' package (Bates et al., 2015) for generalized linear mixed-effects models (GLMM) and linear mixed-effects models (LMM) and 'vegan' package for multivariate analyses (Oksanen et al., 2020). We extracted the indicator species by using the 'indicspecies' package (de Cáceres et al., 2020). This package allows for analysing the relationships between species from our data set of sampled years and identifies those species that appeared more frequently in the data, taking into account both occurrence and abundance. The indicator species were extracted by setting 1 as the minimum number of occurrences for site and group combination. In addition, we did not apply any correction to the p-values with the purpose of describing all possible species with a special interest in conservation and management. To describe how annual sporocarp productivity and richness change over time, we fitted generalized linear mixed-effects models for both dependent variables separately. Sporocarp data were aggregated per plot and year, using different soil properties, topographic characteristics and meteorological variables as potential predictors (information on both dependent and independent variables is shown in Table A.1 in Appendix A). Random plot effects were considered on model interception to account for between- and within-plot random variation given that the same plots were re-sampled on multiple measurement occasions over time. Moreover, since a high occurrence of 'zero' values were found in the data due to strong dependence on certain weather conditions, limited plot sizes and the stochasticity of sporocarp emergence, we used a two-stage modelling approach to prevent statistical inconsistencies related to zero-inflation (de-Miguel et al., 2014; Hamilton and Brickell, 1983). The first stage estimated the probability of sporocarp occurrence using mixed-effects logistic regression with a logit link function (Eq. (1)) based on binomially distributed data indicating the absence or presence of sporocarps in a given plot. The second stage estimated sporocarp productivity or sporocarp species richness conditional on the probability of occurrence (Eq. (2)). Generalized linear mixed-effects models for sporocarp productivity were fitted using Gamma distribution, while a Poisson distribution was considered when modelling sporocarp species richness. Pielou's evenness index (Pielou, 1966) was obtained using the dry biomass values of different sporocarp species per plot and year. Evenness was modelled using linear mixed-effects models, with random plot effects on model interception and the environmental variables as fixed effects. Sporocarp productivity, species richness and evenness were analysed for the total fungal community as well as for two functional guilds, separately: ECM and saprotrophs.

Variable and model selection was based on the following criteria: statistical significance of model predictors (p-value ≤ 0.05), accordance with assumptions on error distribution, lack of multicollinearity (Variance Inflation Factor < 3, calculated using 'performance' package (Lüdecke et al., 2020)), Akaike's Information Criterion (AIC), and biological and ecological sense of model parameters according to existing scientific knowledge.

$$P(y=1|x)_{ij} = \pi(x) = \frac{1}{1+e^{-[(\alpha_0+a_{0i})+\alpha X_1]}} \qquad \text{Eq. 1}$$

$$(F_c)_{ij} = (\beta_0 + b_{0i}) + \beta X_2 + \varepsilon \qquad \text{Eq. 2}$$

Where $P(y=1|x)_{ij}$ is the probability of sporocarp occurrence in plot i and year j, $(F_c)_{ij}$ is the sporocarp productivity in dry biomass (kg ha^{-1} yr^{-1}) in the case of the productivity models or species number in the case of sporocarp species richness models conditional on the occurrence of sporocarps. X_1 and X_2 are vectors of model independent variables, α and β denote fixed-effects model parameters for each independent variable of X_1 and X_2, respectively, a_{0i} and b_{0i} denote the plot random-effects on the model intercept and ε is the residual.

Secondly, the autumn sporocarp community composition was described across plots and years by running a detrended correspondence analysis (DCA) using the sporocarp matrix of dry biomass. As a start, we build up three different DCAs, one with the entire community, another without rare species, and the third one without rare species plus logarithm. Rare species were described as those that did not reach the 10th percentile of the sum of sporocarp abundances. From the three different DCAs, we selected the one excluding rare species plus logarithm since it explained the greatest gradient lengths (GL) and it showed clearly how species were distributed. Since sporocarp productivity and richness in the years 2013 and 2017 were close to 0, both years were not considered in the multivariate analyses aiming at describing the community composition in order to avoid outlier effects. At the same time, one of the

Table 1

Significant parameter estimates for the selected models. The response variables tested are occurrence and sporocarp productivity and sporocarp richness divided in total, ectomycorrhizal (ECM), and saprotrophs fungi. In addition, the sporocarp evenness analysis for the total community is also included. Significance levels: p-value < 0.001 ‘***’, p-value < 0.01 ‘**’, p-value < 0.05 ‘*’. ECM and saprotrophs evenness models are not described in the table since no significant effect was found.

		Model												
		Productivity						Sporocarp species richness						Evenness
		Occurrence			Sporocarp productivity			Occurrence			Sporocarp richness			
		Total	ECM	Saprotrophs	Total	ECM	Saprotrophs	Total	ECM	Saprotrophs	Total	ECM	Saprotrophs	Total
Fixed effects	Intercept	+ 20.35***	+8.35	−19.53***	−3.76***	−4.76***	−1.61***	−6.76**	−4.78***	+3.65	+0.41	−0.67	−0.47	+1.27***
	September rain.	–	–	–	+ 0.02***	+0.01*	+0.01**	+0.14***	+0.07***	–	–	–	–	–
	October rain.	–	+0.01*	+0.06*	+ 0.01***	–	+0.01***	–	+0.02*	+0.04***	+0.001***	+0.001**	+0.01***	+0.001*
	November rain.	–	–	+0.03**	–	–	–	–	–	+0.03***	+0.001***	–	+0.01***	–
	1st 50 mm (DOY)	−0.08***	−0.07***	–	–	–	–	–	–	−0.08***	–	–	–	–
	75 % annual rainfall (DOY)	–	–	–	–	–	–	–	–	−0.02***	–	–	–	–
	Rainy days	–	–	+0.11*	+0.04***	+0.04**	–	–	–	–	+0.02***	+0.03***	–	–
	August min. temp.	–	–	–	–	–	–	–	–	–	–	–	–	−0.04*
	October min. temp.	–	–	–	–	+0.42***	–	–	–	–	+0.09*	+0.14*	–	–
	November min. temp.	+ 0.78**	–	–	–	–	+0.11***	+1.30***	+0.55**	–	–	–	–	–
	November mean temp.	–	–	–	–	–	–	–	–	–	–	–	+0.14**	–
	November max. temp.	–	–	+0.98**	–	–	–	–	–	–	–	–	–	–
	Cold 1st (Week)	–	–	–	+0.04***	–	–	–	–	–	–	–	–	–
	Cold 1st (DOY)	–	–	–	–	–	–	–	–	+0.07***	–	–	–	–
	Frost 1st (DOY)	–	+0.04*	–	–	–	–	–	–	–	–	–	–	–
Random effects	SD (intercept)	+0.51	0	+1.35	+0.69	0	+0.67	+0.69	+0.001	+0.75	+0.43	+0.43	+0.38	+0.08
	SD (residual)	–	–	–	+1.06	+1.17	+0.85	–	–	–	–	–	–	+0.15

Abbreviations: rain.: monthly accumulated rainfall (mm); 1st 50 mm (DOY): day of the year (from August 1st) when 50 mm of rainfall are reached; 75% annual rainfall (DOY): day of the year when 75% of the annual rainfall is reached; Rainy days: number of rainy days from the 1st of August until the first day in which temperatures fell below 0 °C; min. temp., mean temp. and max. temp.: mean monthly minimum, mean and maximum temperature (°C), respectively; Cold 1st (Week/DOY): first week or day of the year (from August 1st) in which 5 consecutive days with temperatures below 5 °C occurred; Frost 1st (DOY): first day of the year (from August 1st) in which the minimum temperature fell below 0 °C; SD: standard deviation.

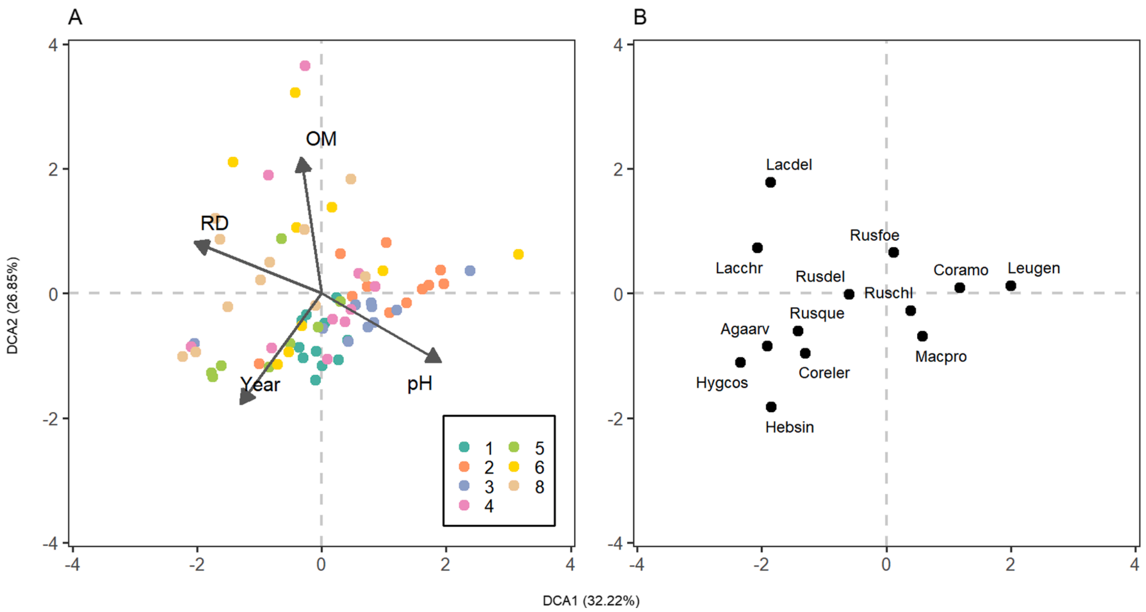

Fig. 2. Detrended correspondence analysis (DCA) of fungal sporocarp community composition across years in Mediterranean *Quercus ilex* stands. (A) Sites biplot with different dot colours indicating the belonging plots, and the significant environmental variables overlaid. (B) Species biplot of the most abundant sporocarps gathered during the study period. The percentage of variance explained by each DCA-axes is in parentheses. Abbreviations of fungal species shown in the DCA diagrams, Figs. 2-3: Agaarv – *Agaricus arvensis*, Agasa – *Agaricus sylvicola*, Agass – *Agaricus sylvaticus,* Bovplu – *Bovista plumbea,* Coppic - *Coprinopsis picacea*, Coramo – *Cortinarius amoenolens*, Coreler – *Cortinarius elegantior,* Gymdry – *Gymnopus dryophilus,* Hebsin – *Hebeloma sinapizans*, Hohpet – *Hohenbuehelia petaloides,* Hygcos – *Hygrophorus cossus*, Lacchr – *Lactarius chrysorrheus*, Lacdel – *Lactarius deliciosus*, Legbad – *Legaliana badia,* Leugen – *Leucopaxillus gentianeus*, Lycper – *Lycoperdon perlatum*, Macpro – *Macrolepiota procera,* Marper – *Marasmius peronatus*, Mycros – *Mycena rosella,* Rhobut – *Rhodocollybia butyracea,* Ruschl – *Russula chloroides*, Rusdel – *Russula delica*, Rusfoe – *Russula foetens*, Rusque – *Russula queletii*, Xerpud – *Xerula pudens.*

plots showed great differences concerning the rest of the plots conditioning the ordination space, thus we decided to eliminate it from the total community DCA to clearly identify the real effect of environmental variables over the compositional differences. These results are included and further discussed in Fig. A.1 in Appendix A.

We also tested whether autumn fungal sporocarp compositional differences were correlated with the environmental variables and soil characteristics using the passive fit of environmental variables over the DCA ordination. Only those variables that were significant in the models were described in the text (Year, September accumulated rainfall, September mean maximum temperature, Rainy days, OM content, pH and sand content). All tests were performed in three independent response data sets: (i) sporocarps biomass for the total community composition, (ii) sporocarps biomass for the ECM community composition and (iii) sporocarps biomass for the saprotroph community composition.

3. Results

3.1. *Fungal productivity and diversity*

As a result of 203 weekly surveys over 13 consecutive autumn fruiting seasons, we recorded a total of 4657 sporocarps, with an annual mean of 3.24 kg ha^{-1} yr^{-1} (median of 1.54) in dry biomass (Table A.1 in Appendix A). The ECM sporocarps community represented 66.57% of the total dry biomass, including families such as Russulaceae (30%), Cortinariaceae (19%), and Boletaceae (12%), showing peak productivity values in October and November. *Russula* was the most productive genus contributing to 22% of the total biomass. The saprotrophic sporocarps community represented 33.43% of the total including families such as Agaricaceae (19%), Tricholomataceae (5%) and Marasmiaceae (3%). Similar to the ECM sporocarp community, the highest productivity values of saprotrophic sporocarps occurred during October and November, being *Macrolepiota* the most productive genus, representing 15% of the total biomass.

We observed a high range of interannual variability in both total sporocarp species richness and productivity, e.g. with mean annual productivity values ranging from almost 0 to more than 7.5 kg ha^{-1} yr^{-1} (Fig. 1.A). When dividing the gathered data into fungal guilds, ECM fungal productivity values were higher compared with the saprotrophic community, but they followed the same interannual productivity trend during the study time (Fig. 1.A).

The 1st 50 mm (DOY) had a significant negative influence on total sporocarp occurrence and November mean minimum temperature had a significant positive influence on the same response variable. Total sporocarp productivity was significantly and positively influenced by September and October accumulated rainfall, Rainy days and Cold 1st (Week). ECM sporocarp occurrence was significantly positively influenced by October accumulated rainfall, and Frost 1st (DOY), while 1st 50 mm (DOY) had a significant negative influence on the same response variable. ECM sporocarp productivity was significantly positively influenced by September accumulated rainfall, Rainy days and October mean minimum temperature. On the other hand, saprotrophic sporocarp occurrence was positively influenced by October and November accumulated rainfall, Rainy days and November mean maximum temperature. Regarding saprotrophic sporocarp productivity, September and October accumulated rainfall had a significant positive effect in addition to November mean minimum temperatures (Table 1).

By contrast, when studying sporocarp species richness, a total of 241 species were found, including 123 ECM taxa and 118 taxa of saprotrophic fungi. In addition, we observed similar interannual trends between sporocarp species richness and productivity values; so that the years with higher sporocarp species richness were also those years with higher productivity values for total, ECM and saprotrophic functional guilds (Fig. 1.B). High interannual variability was also found, having years with near to 0 species fructifying, and others with maximums of 40 species (Table A.1 in Appendix A). When dividing the sporocarp species richness data set in functional guilds, we observed that the proportion between the number of ECM and saprotroph species varied during the study period, having years with more species of saprotrophs than ECM

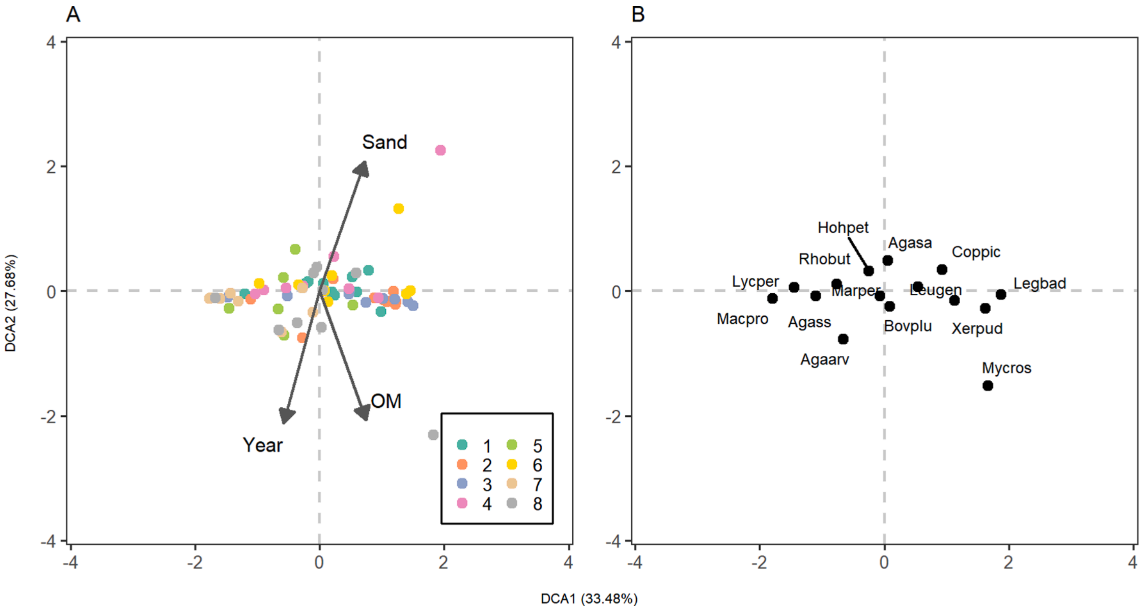

Fig. 3. Detrended correspondence analysis (DCA) of saprotrophic sporocarp fungal community composition across years in Mediterranean *Quercus ilex* stands. (A) Sites biplot with different dot colours indicating the belonging plots and the significant environmental variables overlaid (B) Species biplot of the most abundant sporocarps gathered during the study period. The percentage of variance explained by each DCA-axes is in parentheses. See Fig. 2 for species abbreviations.

and vice versa (Fig. 1.B).

Regarding the mixed-effects sporocarps richness models, the probability of occurrence of at least one fungal species was significantly and positively influenced by September accumulated rainfall and November mean minimum temperature. Total sporocarp species richness was significantly and positively influenced by October and November accumulated rainfall in addition to Rainy days and October mean minimum temperature. When referring to ECM species, the probability of fructification of at least one species was significantly and positively influenced by both September and October accumulated rainfall and November mean minimum temperature. Total ECM sporocarp species richness was significantly and positively influenced by October accumulated rainfall, rainy days and October mean minimum temperature. Regarding the fructification of at least one saprotrophic species, October and November accumulated rainfall and Cold 1st (DOY) exhibited a significant and positive effect. 1st 50 mm (DOY) and 75 % annual rainfall (DOY) were significantly and negatively influencing the fructification of at least one saprotrophic species. Saprotrophic sporocarp species richness was significantly and positively influenced by October and November accumulated rainfall and November mean temperature (Table 1).

Sporocarp evenness changed inter-annually as other variables did with minimums of 0.03 and 0.04, in the years 2015 and 2017, respectively, and reaching maximum values of 0.85 and 0.90 at years 2016 and 2020, although the average sporocarps evenness values for all the sequence was around 0.60. The evenness and environmental variable models showed that total sporocarps evenness positively correlated with October accumulated rainfall. In contrast, we found a negative influence on total sporocarps evenness with August mean minimum temperature. Evenness of both ECM and saprotrophic sporocarps was not significantly correlated with any of the tested environmental variables (Table 1).

3.2. *Fungal community composition*

From all ECM genera found, *Cortinarius* was the highest species-rich genus with 36 identified species and among all saprotroph genera, *Mycena* was the highest species-rich genus with 17 identified species fruiting in the study time.

The DCA ordination produced eigenvalues (λ) of 0.615, 0.415, 0.497 and 0.324, and GL of 5.400, 5.037, 4.356 and 4.281 for the first four axes respectively. The ordination showed that sporocarp composition varied slightly across plots with most of them located in the central area (Fig. 2.A). The DCA1 separated the 1, 2 and 3 plots at the positive-end with greater pH while plots as 5 and 8 had lower pH values (pH explained variation = 16%, $P = 0.017$). On the opposite side of the pH vector, the DCA1 separated the 8 and 5 plots at the left-end with a higher number of rainy days (RD) (explained variation = 19%, $P = 0.006$) from plots 1, 2 and 3 with a lower number of rainy days. The passive overlay of Year (explained variation = 21%, $P = 0.006$) showed that the year effect over sporocarps composition was mainly plot dependent since plots from the same years are located randomly across the ordination (Fig. 2.A). DCA2 clearly separates plots with lower OM and negative positions (plots 1, 3, 5) from a positive end with greater OM (explained variation = 15%, $P = 0.253$). The relative proportions of the total sporocarp community composition did not follow a clear trend during the study time (Fig. 2.A). Similarly, no clear trend was observed when dividing the overall species in ECM and saprotrophs.

Relative abundances of certain species such as *Russula foetens* (Rusfoe) were slightly related to higher OM values (Fig. 2.B). When regarding pH values, *Macrolepiota procera* (Macpro) was a species related to plots with lower pH values. Further, *Lactarius deliciosus* (Lacdel) and *Lactarius chrysorrheus* (Lacchr) were species related to a higher number of rainy days whereas other species preferred a lower number of rainy days as *Russula delica* (Rusdel) or *R. chloroides* (Ruschl) (Fig. 2.B). There were some differences in fungal community species between years, defined as indicator species for the years 2008: *Astraeus hygrometicus*; 2011: *Crepidotus variabilis*; 2012: *Peziza variabilis*, *Lepista castanea*, *Pseudosperma rimosum*; 2014: *Clitocybe squamulosa*; 2016: *Cortinarius fulgens*, *Russula delica*, *Russula foetens*; 2018: *Cortinarius evernius*, *Tricholoma atrosquamosum*, *Cortinarius elegantior*, *Entoloma sericeum*, *Hebeloma sinapizans*, *Mycena galericulata*, *Mycena galopus*, *Agaricus arvensis*, *Hygrophorus cossus*; 2019: *Cortinarius dicolor*, *Tricholomopsis rutilans*.

When dividing our data set into functional guilds, the ECM sporocarp ordination resembles the overall DCA ordination. Here, the relative abundance of ECM species was related to Year (explained variation = 36%, $P = 0.001$), September accumulated rainfall (explained variation = 27%, $P = 0.002$) and September mean maximum temperature (explained variation = 29%, $P = 0.002$). Relative abundance of some species such as *Russula chloroides* (Ruschl) were higher when September accumulated rainfall increased. By looking at September mean maximum temperature, we see a positive effect when increasing the temperature in species such as *Russula delica* (Rusdel) and *Cortinarius elegantior* (Coreler). We identified some differences in ECM fungal community species between years, defined as indicator species for the years 2008: *Astraeus hygrometicus*; 2012: *Pseudosperma rimosum*; 2016: *Cortinarius fulgens*, *Russula delica*, *Russula foetens*; 2018: *Cortinarius evernius*, *Tricholoma atrosquamosum*, *Cortinarius elegantior*, *Hebeloma sinapizans*, *Hygrophorus cossus*.

The saprotroph sporocarps DCA (eigenvalues (λ) of 0.687, 0.445, 0.438 and 0.433, and GL of 3.720, 4.556, 4.218, and 3.721) showed that only the passive overlaid OM content (explained variation = 12%, $P = 0.048$) and sand content (explained variation 20%, $P = 0.007$) were significant (Fig. 3.A). In contrast, there is no significant Year effect over saprotroph sporocarps composition (explained variation = 3%, $P = 0.425$). Relative abundances of *Mycena rosella* (Mycros) were related to higher OM content plots. Regarding sand content, species such as *Agaricus sylvicola* (Agasyl) and *Hohenbuehelia petaloides* (Hohpet) preferred soils with less sand content (Fig. 3.B). We found some differences in saprotrophs fungal community species between years, defined as indicator species for the years 2011: *Crepidotus variabilis*; 2012: *Peziza vesiculosa*, *Lepista castanea*; 2014: *Clitocybe squamulosa*; 2018: *Entoloma sericeum, Mycena galericulata*, *Agaricus arvensis*, *Mycena alcalina*; 2019: *Tricholomopsis rutilans*.

After comparing our data set with the IUCN Red List, we found *Cortinarius atrovirens* catalogued as near threatened (NT). Secondly, *Agaricus arvensis*, *A. sylvaticus*, *Lycoperdon perlatum* and *Russula aeruginea* were catalogued as least concern (LC). We observed that *C. atrovirens* was a scarce species found in 2016 and 2018, without clear trends of their ecological preferences when checking the DCA results since we did not find any significant relationship with the environmental variables tested. On the other hand, *A. arvensis* is a more frequent species that appeared in several years of the study period (2012, 2014, 2016 and 2018) and was related to higher September mean temperature values. *A. sylvaticus* occurred during most of the study time, even though the abundance was scarce since only 10 sporocarps were reported in 12 years. In addition, this species is related to September mean temperature. *L. perlatum* was a species found in a major part of the study time without a clear preference for the tested environmental variables. Finally, *R. aeruginea* was a rare species, with only one observation in 2012.

4. Discussion

4.1. Fungal productivity and diversity

In the current study, we found that sporocarp productivity changed interannually, with the ECM sporocarps contributing with higher productivity values to the total sporocarp in comparison with the saprotrophs sporocarps. This result seems logical since ECM species usually have larger sporocarps than saprotrophs (Bässler et al., 2015) and in our case represented most of the weight of total sporocarp (Table A.1 in Appendix A). This fact could mask the principal drivers of saprotrophs fruiting in the total community models and it is solved when analysing the database by trophic groups: ECM and saprotrophs. Regarding sporocarp species richness, we found 241 species in 13 consecutive years in a total area of 800 m^2 (8 plots of 100 m^2 each). Previous research on *Q. ilex* reported similar sporocarp species richness values although the survey methodology was different in terms of experiment length, frequency of the surveys and total studied area. Namely, Zotti and Pautasso (2013) recorded 246 species over 4 years in 7500 m^2; Richard et al. (2004) found 234 species in 2 years in a total area of 6400 m^2 and finally, Santos-Silva et al. (2011) recorded 123 species during 2 years in 6000 m^2 of the studied area.

Productivity and sporocarps richness showed similar trends in the way they were driven by weather conditions. That is, total, ECM and saprotrophs sporocarp productivity and richness responded to autumn meteorological variables. More specifically, increased rainfall amount and frequency (represented by monthly accumulated rainfall and number of rainy days) positively influence mushroom fruiting, while delayed rainfall (represented by the first 50 mm of rainfall after 1st of August and the date in which 75% of annual rainfall is reached) negatively influences mushroom fruiting. These results indicate that early, maintained rains during autumn will benefit mushroom fruiting, causing the end of summer drought and favouring sporocarp fructification during autumn as reported in Büntgen et al. (2015).

It is worth highlighting that years 2013 and 2017 were characterized by severe drought conditions and resulted in higher saprotrophic productivity and sporocarps richness compared to ECM fungi (Fig. 1.A – 1.B). This somehow could be related to the hypothesis that direct climate effects on fungi combine with indirect effects via host plants. Since ECM mycelium is associated with tree roots this trophic group relies more on host trees for phenological cues than direct experience with temperature and precipitation. On the other hand, since saprotrophs grow in superficial soil layers, can react more immediately to suitable temperature and rainfall conditions (Diez et al., 2013; Gange et al., 2007).

The analysis of the meteorological variables suggests an increase in fungal fruiting when prolonging autumn meteorological conditions. Thus, higher fungal fruiting would be benefited from the early onset of autumn rains and a delay in the onset of winter temperatures. We see this when variables as October mean minimum temperature and November mean minimum, mean and mean maximum temperatures positively influenced mushroom fruiting as documented by Hernández-Rodríguez et al. (2015), Karavani et al. (2018), specifically for mean minimum and mean maximum temperatures. In addition, the positive effect of variables as Cold 1st (variable indicating the moment of the year in which 5 consecutive days with temperatures below 5 °C occurred) and Frost 1st (variable indicating the moment of the year in which the minimum temperature, from the 1st of august, fell below 0 °C) point out to a higher fructification the late colder temperatures arrive. Overall, mushroom productivity and richness benefit when autumns begin earlier and end later, thus providing suitable fruiting conditions.

The low productivity values obtained in this study are expected since our *Q. ilex* plots are characterised by shallow soils, high stone content, and steep slopes in addition to high stem densities due to regeneration from coppice stands (Ibàñez et al., 1999). The latter leads to intense competition between trees and causes very low growth rates that may lead to an almost permanent state of stagnation (Gracia et al., 1999). In fact, Hagenbo et al. (2021) saw that the mycelial biomass of *Q. ilex* measured in the same plots remained relatively constant over the year. This is explained since holm-oak trees have better access to deep water reservoirs that could result in more stable conditions for associated ECM fungi.

In addition, we could not find significant effects of soil variables influencing sporocarps productivity or diversity. This might be due to two possible reasons: i) because of the high similarity between plots in soil characteristics, or ii) caused by the fact that soil extraction was done only once during the study time, which may have impaired the detection of slight changes in soil properties along the study period. The real cause was not disentangled, and further research on how soil characteristics influence fungal productivity and richness is needed.

Finally, the total sporocarp evenness was positively influenced by October accumulated rainfall, a very frequent variable in our sporocarp productivity and richness models, and negatively influenced by August mean minimum temperatures. A plausible explanation for these results may be that the community is well adapted to the current environmental conditions, and a major part of species would occur evenly whenever the meteorological conditions are suitable enough for fungal fruiting. While on the contrary, the meteorological variables that are not significantly positive in the productivity and sporocarp species richness and could affect negatively mushroom fructification (i.e., high August temperature variables) will result in evenness values lower than 0.25, since in those months the community will not be able to fructify equally.

4.2. Sporocarp community composition

When studying the sporocarp community composition, we found a high abundance of ECM species compared to saprotrophic species since ECM species contributed most of the weight in comparison with saprotroph species (Table A.1 in Appendix A). In addition, *Russula* and *Cortinarius* were the genera more frequently observed. We also found some species described as common to many Mediterranean holm oak forests as *Cortinarius callochrous, Laccaria laccata* and *Lactarius chrysorreus* (Zotti and Pautasso, 2013). When comparing our results with previous studies on Mediterranean dense *Q. ilex* forests (Zotti and Pautasso, 2013; Richard et al., 2004), we found a similar species richness, a similar proportion of functional guilds species (ECM and saprotrophs) and common species.

When studying sporocarp relative abundances and community composition in these stands, among the meteorological variables tested, only September meteorological conditions (September accumulated rainfall and September mean maximum temperature) and the number of rainy days had a significant effect on total and ECM sporocarp community composition. In addition, 2013 and 2017 exhibited near to zero sporocarps. This can be due to severe drought conditions (absence of rainfall) and could have resulted in not enough water availability for the mycelia and, consequently, in a strong negative impact on sporocarp formation. Similar results have been reported by Ogaya and Peñuelas (2015) since scarce moisture reduces sporocarp production.

We identified the ‘year’ factor largely affecting the total sporocarps community composition, remarking the high interannual variability of both productivity and sporocarp species richness (Fig. 1.A-1.B), ranging from a minimum of only one species to a maximum of 42 species identified per plot and year (Table A.1 in Appendix A). When dividing the data set by functional guilds, we found that ECM sporocarp community composition was significantly influenced by ‘year’, reflecting the stronger effect of the interannual variation in weather conditions on ECM fungal communities, compared with saprotrophic community composition. This is in accordance with our expectations since: i) ECM sporocarps had higher relative abundance values, contributing in greater quantity to the total biomass and, consequently, showing similar trends as for total community composition, and ii) the availability of carbohydrates for ECM fungi may vary with interannual weather variations that also affect host plants photosynthetic rates (Sato et al., 2012). These results indicate that the overall and ECM sporocarp fungal community are mostly constrained by the interannual climate fluctuations, whereas saprotrophs are more spatial-scale dependent since they obtain carbon directly by decomposing the organic matter, being, therefore, more dependent on the local site characteristics (Alday et al., 2017). With this, it is clear the high difficulty of characterizing sporocarps communities and how they are modelled by different weather variables with the increased hardship of dividing the data set in the two functional guilds analysed. Finally, we need to underline the importance of having long-term experimental designs, especially when studying both ECM and overall community composition since they are affected by interannual variations, in addition to multiple sampling points, especially when studying the saprotroph community composition since they are site dependent (Alday et al., 2017).

Soil variables also contributed to shaping sporocarps community composition. We found a pH effect on the sporocarp species composition, which has been also reported in similar research (Adamo et al., 2021; Taye et al., 2016; Tedersoo et al., 2020) in addition to other soil variables such as OM or sand content. In the case of ECM sporocarps composition, we did not appreciate a pH effect; this could be explained since the pH differences are low in our plots to produce changes in fructification trends. However, we expected a pH effect on the saprotroph community composition since they rely directly on plot-scale niche processes (Alday et al., 2017). Regarding OM content, we identified a positive correlation with the total and saprotrophic sporocarp species composition. The present findings seem to be consistent with previous research since OM is the direct energy resource for saprotrophs (Smith and Read, 2008), and increases soil water content (Hudson, 1994), being beneficial for both saprotroph and ECM species.

Although we observed interannual differences in the total sporocarp community composition, we did not observe a clear trend in the sporocarps composition of specific fungal guilds. This could be explained since the differences in temperature and rainfall between years were purely stochastic and did not follow a clear trend. In addition, those structural changes in the overall, ECM and saprotroph sporocarps community could be determined by the high inter- and intra-specific variability among fungi (total, ECM and saprotrophs) in their optimum conditions (i.e., soil physicochemical properties, rainfall, temperature) for growth and resource acquisition (Johnson et al., 2012). Concerning the species gathered in the study, both *Russula* and *Cortinarius* grew in different weather conditions and soil physicochemical properties, which could indicate the ability to fruit in different niches as reported for *R. cyanoxantha* or *C. cinnamomeus* (Sarrionandia et al., 2009) when *Q. ilex* is present. In contrast, species included in Russulaceae seemed to be more specific, growing in plots with high OM content and, consequently, with higher water retention capacity (Hudson, 1994) necessary for sporocarp occurrence.

Regarding the fungal species assessed by the IUCN, we could not find any relationship with the tested environmental variables. This is probably because these species occurred very rarely and without a temporal trend during the study time, which makes it difficult to find trends and significant relationships with potential environmental drivers. Further research needs to i) improve the background information about fungal species conservation status since only 5 out of 241 species growing in Mediterranean holm oak forest have been assessed and ii) deepen the focus on protected species to identify their key drivers to improve their conservation measures. For this purpose, combining sporocarp occurrence analysis with the evaluation of mycelium in soil using DNA sequencing techniques to profile the fungal communities is advisable to have a more accurate knowledge of the above- and below-ground fungal community composition. With all this, it would be possible to obtain a more adjusted knowledge of the presence/absence and current situation of target fungal species of special conservation interest growing in holm oak forests in the Mediterranean area. Finally, it is worth framing that this study has been carried out in a protected area so that regardless of the protection status of the fungal species, there is active protection and regulation of their habitat.

5. Conclusions

This study provides further insights into the environmental variables shaping the productivity and richness of the sporocarp fungal community growing on *Quercus ilex* stands in the Mediterranean area. Despite the low sporocarp productivity of the community, we have observed a high sporocarp species richness with the presence of species that occurred sporadically depending on the weather variables following interannual changes. In addition, we saw that fungal productivity and sporocarp species richness are modelled by mostly weather variables belonging to autumn, whereas the sporocarp community composition has as well predilection for specific soil physicochemical properties such as sand content, pH and OM. This study remarks the high stochasticity of sporocarp occurrence and productivity, with species fructifying in different periods during the year, depending on the environmental conditions. In addition, we heighten the necessity of studying fungal fructification and composition not just by ecological roles but by focusing on the intra-genera functional traits. This is crucial to have a deeper understanding of how fungal species create reproductive structures as well as how they interact and respond to different environmental drivers, and how they could cope within a climate change context.

CRediT authorship contribution statement

Ángel Ponce: Data curation, Formal analysis, Writing – original draft. **Josu G. Alday:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing – review & editing. **Juan Martínez de Aragón:** Conceptualization, Data curation, Investigation, Methodology, Validation, Writing – review & editing. **Eduardo Collado:** Data curation, Writing – review & editing. **Albert Morera:** Writing – review & editing, Data curation. **José Antonio Bonet:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Sergio de Miguel:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing – review & editing.

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.

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Appendix A

Explanation of all variables tested in the statistical analysis.

Table A.1
Modelling data summary (per year and plot) for the period 2008 to 2020 (n = 104).

	Min.	Mean	Median	Max.
Total productivity (dry biomass in kg ha^{-1})	0	3.24 ± 4.66	1.54	22.06
ECM productivity (dry biomass in kg ha^{-1})	0	2.16 ± 3.97	0.57	21.05
Saprotroph Productivity (dry biomass in kg ha^{-1})	0	1.08 ± 2.14	0.37	17.15
Total sporocarp species richness	0	9.25 ± 9.09	7	42
ECM sporocarp species richness	0	4.09 ± 4.95	2	24
Saprotroph sporocarp species richness	0	5.16 ± 5.42	4	23
August rainfall (mm)	0	16.11 ± 10.30	15.88	40.59
September rainfall (mm)	1.78	45.45 ± 26.41	39.76	95.66
October rainfall (mm)	11.76	72.38 ± 70.60	44.44	239.90
November rainfall (mm)	0.37	79.96 ± 56.80	82.48	185.78
1st 50 mm (Week)	35	39 ± 3	38	45
1st 50 mm (DOY)	247	274 ± 21	266	320
75% annual rainfall (Week)	24	40 ± 5	42	47
75% annual rainfall (DOY)	170	282 ± 36	295	330
Autumn rainfall (mm)	39.61	174.26 ± 81.02	178.88	380.65
Rainy days	6	30 ± 11	29	63
August min. temperature (°C)	12.5	15.32 ± 1.25	15.17	18.3
August mean temperature (°C)	19.41	23.28 ± 1.37	23.28	26.33
August max. temperature (°C)	23.26	28.45 ± 1.62	28.62	31.55
September min. temperature (°C)	8.8	11.64 ± 1.36	11.65	14.85
September mean temperature (°C)	16.24	19.17 ± 1.49	19.11	22.43
September max. temperature (°C)	20.49	24.06 ± 1.72	24.14	27.76
October min. temperature (°C)	5.29	8.22 ± 1.27	8.24	11.33
October mean temperature (°C)	12.24	14.88 ± 1.44	14.76	18.39
October max. temperature (°C)	16.22	19.20 ± 1.71	19.11	23.25
November min. temperature (°C)	0.39	3.83 ± 1.63	3.53	7.81
November mean temperature (°C)	5.97	9.33 ± 1.52	9.43	12.43
November max. temperature (°C)	8.52	12.91 ± 1.71	13.08	16
Cold 1st (Week)	42	45 ± 2	45	50
Cold 1st (DOY)	292	316 ± 13	316	347
Frost 1st (Week)	41	46 ± 3	46	52
Frost 1st (DOY)	288	321 ± 19	324	360

Total, ectomycorrhizal (ECM) and saprotroph productivity is the dry mushrooms biomass collected per hectare and year in each sampled plot; Total, ECM and saprotrophs sporocarp species richness is the number of species identified per hectare and year in each plot; August, September, October and November accumulated rainfall refers to the amount of rainfall per each month; 1st 50 mm (Week/DOY), variable indicating the week or the day of the year, from the 1st of August, in which 50 mm of rainfall are reached; 75% annual rainfall (Week/DOY), variable in weeks or days indicating the moment of the year in which the 75% of the annual accumulated rainfall are reached; Autumn rainfall (mm), accumulated rainfall between the 1st of August and the first day in which temperatures fell below 0 °C; Rainy Days, the number of rainy days from the 1st of August until the first day in which temperatures fell below 0 °C; Monthly (August, September, October and November) temperatures (minimum, mean and maximum) are referred to the mean monthly temperatures per plot and year; Cold 1st (Week/DOY), variable indicating the week or day of the year(from August 1st) in which 5 consecutive days with temperatures below 5 °C occurred; Frost 1st (Week/DOY), variable indicating the week or day of the year (from August 1st) in which the minimum temperature fell below 0 °C.

Table A.2
Summary of the descriptive data of the sampled plots (n = 8).

	Minimum	Mean	Median	Maximum
Altitude (m.a.s.l.)	530	730	765	850
Slope (%)	14	25	26	36
Sand content (%)	23.2	45.7	48	60.8
pH	5.3	6.3	6.2	7
Organic matter (%)	1.9	8	8.3	11.8

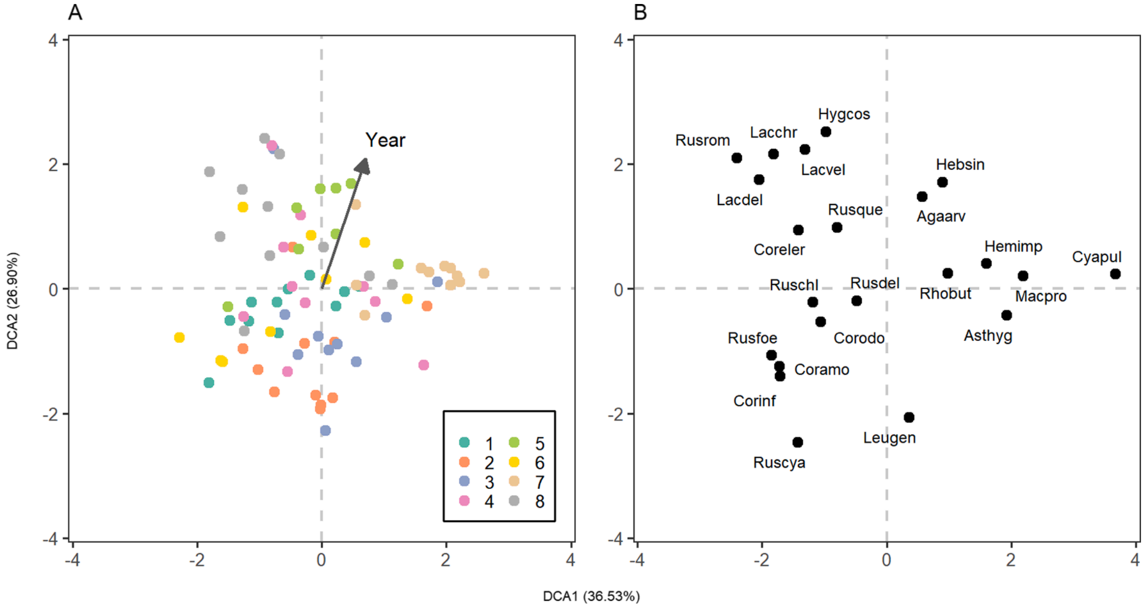

Fig. A.1. Detrended correspondence analysis (DCA) of fungal sporocarp community composition across years in Mediterranean *Quercus ilex* stands. (A) Sites biplot with different dot colours indicating the belonging plots, and the significant environmental variables overlaid. (B) Species biplot of the most abundant sporocarps gathered during the study period. The percentage of variance explained by each DCA-axes is in parentheses. Abbreviations of fungal species shown in the DCA diagrams. Agaarv – *Agaricus arvensis*, Asthyg – *Astraeus hygrometricus*, Coramo – *Cortinarius amoenolens*, Coreler – *Cortinarius elegantior*, Corinf – *Cortinarius infractus*, Corodo – *Cortinarius odorifer*, Cyapul – *Cyanoboletus pulverulentus,* Hebsin – *Hebeloma sinapizans*, Hemimp - *Hemileccinum impolitum*, Hygcos – *Hygrophorus cossus*, Lacchr – *Lactarius chrysorrheus*, Lacdel – *Lactarius deliciosus*, Lacvel – *Lactarius vellereus,* Leugen – *Leucopaxillus gentianeus*, Macpro – *Macrolepiota procera,* Rhobut – *Rhodocollybia butyracea,* Ruschl – *Russula chloroides*, Rusdel – *Russula delica*, Ruscya – *Russula cyanoxantha,* Rusfoe – *Russula foetens,* Rusque – *Russula queletii*, Rusrom – *Russula romellii.*

The DCA ordination of the fungal sporocarps showed that the main GL was conditioned by plot 7 with all points of different years situated at the right-end of the ordinations, with Year not having a significant effect (year explained variation = 8%, $P = 0.132$). Based on this we decided to eliminate plot 7 and redone the ordination that is presented in the main body of the manuscript.

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