DENDROBIOLOGY

2024, vol. 91, 16–31

https://doi.org/10.12657/denbio.091.002

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Biotic and abiotic factors influencing macrofungal diversity and biomass in Mediterranean forests with a focus on the Porcini group

Received: 4 March 2023; Accepted: 8 January 2024

Abstract: Macrofungi are among the most crucial ecological forest resources and essential components of terrestrial ecosystems. Despite growing socio-economic interest, knowledge of their production is not understood because of many factors that can affect their natural growth. The aim of this study is to analyze which biotic and abiotic factors can influence the diversity and biomass of macrofungal fruiting bodies, at small and large scales. We worked in broadleaf Mediterranean forests, with a special focus on wild edible species (Porcini). The mycological observations were focused on epigeous macrofungi. To investigate connections between the occurrence of *Boletus edulis* species distribution modeling was used. Contrary to previous studies, the results reveal that, at a small (local) scale, the soil properties and the geochemical content (traces and minor elements) are more strongly correlated with macrofungal communities than vegetation (tree richness, dead wood, and litter volume) and climatic parameters (air temperatures and rainfall). At large scale, both edaphic and climatic factors, are considered essential for fungal fruiting and distribution across landscapes. The quantity of precipitation of the driest month is the crucial climatic factor influencing the occurrence of Porcini. The different results highlight a high variability and site dependence of both biotic and abiotic factors. Further studies appear to be necessary to increase knowledge on which factors have the most influence on edible and non-edible mushroom yield in various habitats.

Keywords: mycobiota, biodiversity, deciduous forests, edible mushrooms, climate

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Introduction

Micro- and macrofungi play a crucial role in forest ecosystems functioning and they are key components in decomposition processes, nutrients cycling, symbiosis with plants and pathogenic interactions (Tedersoo et al., 2014, 2020). In addition, in many countries of the world, edible species are of socio-economic importance for both recreation and trade (Collado et al., 2018). Nowadays, more than

2000 fungal species are known to produce edible fruiting bodies (also called sporomata or sporocarps, Kirk et al., 2008), which are harvested and consumed in more than 85 countries (Boa, 2004; Sitta & Floriani, 2008; Ambrosio, 2015). Their market is rapidly expanding, and current estimations assign to wild edible mushrooms (e.g. *Boletus edulis* group; *Tuber magnatum* Pico) a market value of at least 2 billion US $ per year (Sitta & Davoli, 2012) and they are often more valuable than timber (Pettenella & Kloehn, 2007; Collado et al., 2018). Despite their ecological and economic importance, little information is available on their natural growing sites and on the main factors driving their growth.

Estimating wild epigeous and hypogeous mushroom production is a difficult task since many variables can affect the mycelium formation and then the growth of fruiting bodies. Moreover, it is well recognized that the fruit bodies formation is probably the most complicated stage in the life of fungi (e.g., primordia formation), being under the influence of a multitude of biotic (e.g., plants, animals and bacteria) and abiotic (e.g., air temperatures, sunlight and minerals) factors that complicate the completion of growth (Egli, 2011; Bünteng et al., 2012; Boddy et al., 2014).

Several studies have shown that the epigeous macrofungal growth can be influenced by different factors, such as habitat features (e.g., altitude and slope of sites; Bonet et al., 2004), stand structures (e.g. tree species, stand density, stand age; Gomez-Hernandez & Williams-Linera, 2011; Martínez-Peña et al., 2012a, 2012b; Ćosović et al., 2020), soil features (e.g., pH, CO_2 concentration; Bamford & Heath, 1989; Bécard & Piché, 1989) and climate (e.g. precipitation and air temperature; Lagana et al., 2002; Ambrosio & Feest, 2021; Pietras et al., 2021). Ferris et al. (2000) specifically, found a positive correlation between the species richness of ectomycorrhizal fungi and the number of trees in a site, and between the volume of dead wood and saprotrophic species. On the contrary, Ortega-Martínez et al. (2011) and Ágreda et al. (2014) observed that forest age-class is the main factor influencing fungal growth in Northern Spain Scots pine (*Pinus sylvestris* L.) sites, especially for edible species such as *Boletus edulis* and *Lactarius deliciosus*. Martínez-Peña et al. (2012a) developed an empirical model to predict the total annual yield of wild edible ectomycorrhizal mushrooms in conifer (*P. sylvestris*) forests in Spain. They found that precipitation, temperature and stand age are the strongest influencing factors for the fruiting bodies formation. More specifically, their proposed model showed that the tree basal area is a significant predictor for the *B. edulis* species occurrence.

In a recent paper, Baragatti et al. (2019) demonstrated that the two most important factors for hypogeous fungal – truffles – production in France were the precipitation from May to August and the number of cold days in the winter. Modelling tools have shown that precipitation in the coldest quarters (the total precipitation that prevails during the driest quarter), izothermality (quantifies the day-to-night temperatures fluctuations in relative to the summer to winter oscillations) and annual mean temperature are among decisive factors influencing the occurrence of edible suilloid fungi (Pietras et al., 2018; Pietras, 2019; Pietras & Kolanowska, 2019). Tomao et al. (2020), also observed that forests-stand structure (e.g. tree canopy cover, tree species diversity and density) can affect ectomycorrhizal fungi; whereas, the diversity and stage of decomposition of dead wood influence the wood-inhabiting fungal communities.

Some other studies also emphasized the influence of soil chemistry and physical properties on fungal diversity (Villeneuve et al., 1989; Humphrey et al., 2000; O'Hanlon, 2012; Ambrosio et al., 2019). Based on these studies, at small scale, the fruit body growth is correlated with the soil structure (e.g., pore space and aggregates) and the amount of organic matter. At a large scale instead, the soil type, the topography and the previous land use mainly influence the macrofungal community composition (O'Hanlon, 2012). Ferris et al. (2000) and Humphrey et al. (2000) also observed that soil pH and content of macronutrients (viz. K, Mg, and Ca) mainly affect the macrofungal diversity in conifers plantation of northern England.

Due to the extreme variability and the different impact that biological, physical, chemical and environmental variables might have on macrofungal communities, predicting the fruit bodies growth is still not straightforward. The large number of variables that can affect growth make it difficult to predict macrofungal yield, and this is even more complex for ectomycorrhizal species whose growth depends on plant interactions (Egli, 2011; Collado et al., 2018, 2019). Understanding the link between forests structure and dynamics, climate factors on macrofungal productivity can provide the baseline for monitoring responses to management and harvesting activities.

The primary aim of this study is to analyze, at small scale, the influence of biotic and abiotic factors on macrofungal diversity and biomass in broadleaf Mediterranean forests (NW Italy) with a special focus on wild edible species and *Boletus edulis* Bull. group, globally known as "Porcini" (that includes also *B. aereus* Bull., *B. reticulatus* Schaeff. and *B. pinophilus* Pilát & Dermek).

The second aim is to assess the connections between occurrence of *B. edulis* group at large scale (Europe) and climate factors. Porcini were chosen for this study because they are some of the most widely collected species in the world. In some Mediterranean countries, in Italy in particular, they are one

of the most harvested and consumed species (Boa, 2004; Sitta & Floriani, 2008; Sitta & Davoli, 2012; Ambrosio & Zotti, 2015). Dentinger et al. (2010) affirm that the economic value of Porcini is considerable, since 20.000–100.000 metric tons are estimated to be consumed annually and the median wholesale price (to harvesters) for fresh mushrooms is ca. US $10–55/kg, in exceptional circumstance $200/kg in the U.S. in 1991 (Hall et al., 1998). Since the availability of Porcini, as well as of many other wild edible species, depends on their natural and unpredictable growth, our study also aims to increase the knowledge on the favorable Porcini growing sites in Southern European Mediterranean broadleaf forests, being these habitats less investigated than North and Central European areas.

We postulated the following two hypotheses: H_1) biotic and abiotic factors differently influence macrofungal species richness and biomass in various broadleaf Mediterranean forests type, and H_2) climate factors mainly drive the occurrence of wild (edible) macrofungi (Porcini).

Materials and methods

Study areas

This study was carried out in three broadleaf forests located in Liguria (NW Italy) in the province of Savona (municipality of Sassello) (Fig. 1). Liguria is characterized by a significant level of macrofungal diversity and forests, that cover a remarkable percentage of the whole territory (ca. 62%, Mariotti, 2009) and are favorable habitats for the growth of wild fungi especially wild edible species (Onofri et al., 2005; Boccardo et al., 2008; Ambrosio & Zotti, 2015; Ambrosio et al., 2018).

- Site 1 is in the Locality Badani (44°27'56"N; 8°28'44"E) and is characterized by a young chestnut coppice of about 8.800 m^2. The altitude ranges from 420 to 450 m a.s.l. The tree layer is dominated by *Castanea sativa* Mill. A lower frequency of other woody species occurs on this site, such as *Sorbus torminalis* (L.) Crantz and *Populus tremula* L. The cover percentage of the shrub layer is very low (7%); whereas the herbaceous species are abundant (15%). The area is under the human intervention (i.e., by cutting and thinning) to remove the undergrowth vegetation and facilitate the collection of chestnuts.
- Site 2, in the Loc. La Maddalena (44°30'14"N; 8°29'17"E), is classified as high forest and covers a total area of about 7.500 m^2 with altitude of 340–380 m a.s.l. The whole area is dominated by *Quercus cerris* L.. Other woody species, such as *S. torminalis* and *P. tremula,* occur with a lower frequency in the site. The cover percentage of the shrub layer is very low (5%); whereas the herbaceous layer cover is very high (70%).
- Site 3, in the Loc. Veirera (44°27'3"N; 8°32'42"E), covers a total area of about 10.000 m^2 and it is also classified as high forest. The altitude is 1000 m a.s.l. The area is dominated by *Fagus sylvatica* L., followed by *S. torminalis* and *P. tremula* at lower frequency. The cover percentage of the shrub and herbaceous layer is very low (10% and 7%, respectively).

Geologically, sites 1 and 3 are characterized by soils developed mainly on Calceschists. Whereas site 2 lies in a complex area characterized by four different parent rocks: Serpentine schists, Calceschists, Chlorite–actinolite schists and Conglomerates.

The climate is ascribed to the Temperate Oceanic sub–Mediterranean type (Rivas-Martinez, 2008) for all the three sites.

Sampling design

The study sites were surveyed by following the same standardized procedure (Feest, 2006). Surveys were in 20 circular (4-m radius) plots selected in each study site along line-transects. Each plot was placed 20 m from the preceding one. The total sample area is of approximately 3000 m^2 (60 plots) per each site.

Data collection

Macrofungi

Macrofungal surveys were performed in each circular plot (60 in total) over three consecutive years (2012–2014), during the period of favorable fruiting bodies production (Apr–Jun and Sep–Nov) in the Mediterranean area, with a minimum sampling frequency of one per month, in a period of low fungal growth in spring, to a maximum of two times per month (every 12–15 days) in autumn. The qualitative (identification of species) and quantitative (number of fruiting bodies) mycological observations were focused on epigeous macrofungi, limiting the number of those with a certain determinate shape and which were visible to the naked eye (Kirk et al., 2008). Taxonomical identification was performed by analyzing the macro- and microscopical characteristics of the collected specimens. Systematic classification followed Hibbett et al. (2007) and Kirk (2008). Nomenclature was used in accordance with CABI (www.indexfungorum.org), CBS (www.cbs.knaw.nl) and IMA (www.mycobank.org).

The identified macrofungal species were split into functional groups after Tedersoo et al. (2010) based on their primary mode of nutrition: ECM (ectomycorrhizal), S (saprotrophs – soil (humus or litter) or wood decay) and P (parasites) species.

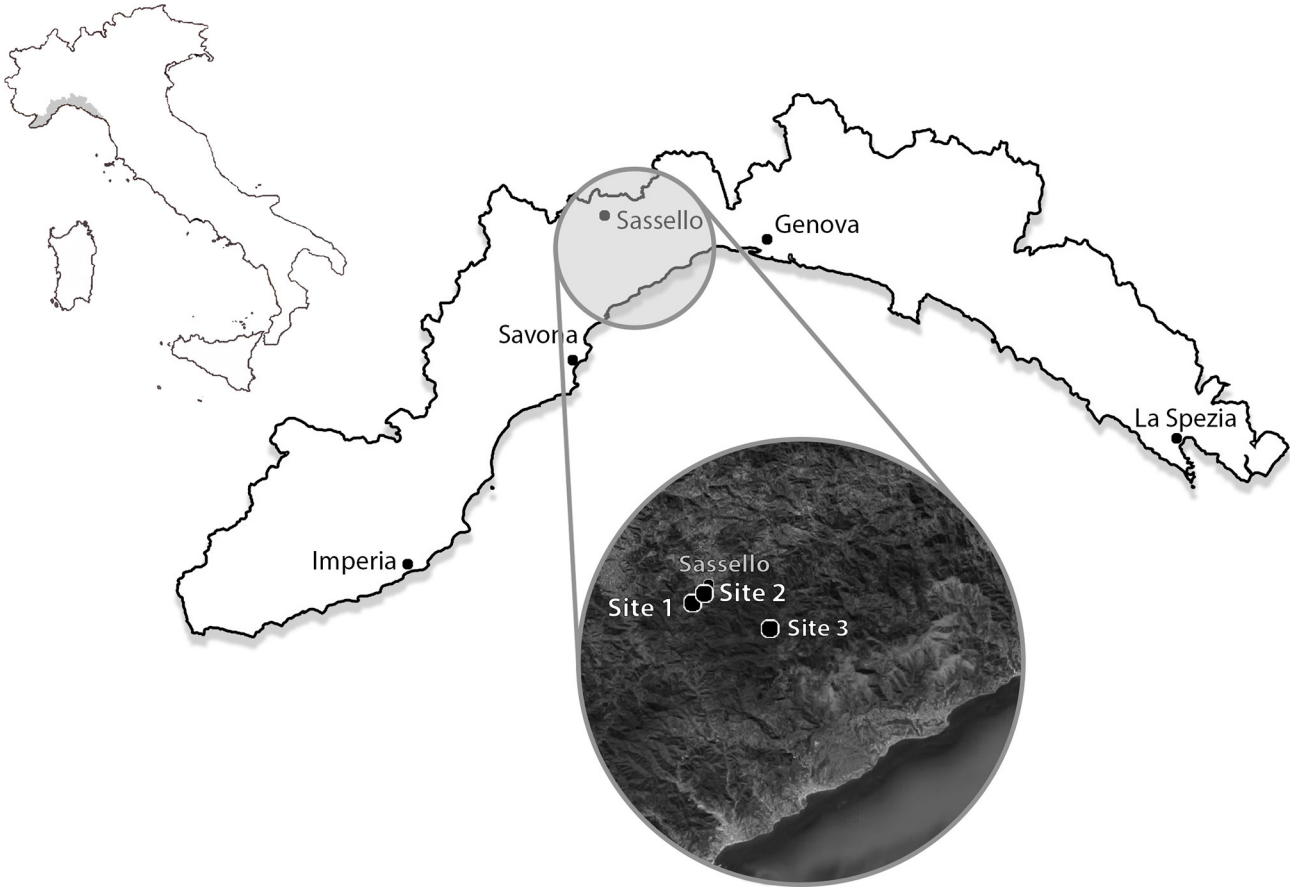

Fig. 1. Location of sites

The edibility status of macrofungi – "e" (edible) and "ne" (not-edible) in tables and appendices – was chosen in accordance with the consulted literature for the species identification and according to regional and national regulations. In Table 1 are listed all the macrofungal recorded variables.

Vegetation

The floristic and vegetation analysis in each plot of each site was performed during the late spring-early summer when the leaf canopy was well developed. In each selected plot, a set of vegetation variables, detailed in Table 1, were quantified.

Specifically, the measurement of vegetation canopy cover was taken by the calculation of Cover Index (CI) (O'Hanlon, 2012).

- Tree density was estimated by using number of trees recorded in each plot in relation with each plot surface (= 50.24 m^2).
- Tree diameter was measured at 1.30 m from the ground (at breast height-DBH).
- For the estimation of the volume of dead wood the number, length and diameter (midpoint) of each log and trunk recorded in each plot were used.
- Finally, litter depth was measured in each plot to calculate the total volume.

Chemical and physical soil parameters

During the period of maximum fruit body production (middle autumn) one soil sample of about 1 kg was collected in each plot (60 in total) near fruiting bodies (Porcini) samples. Samples were collected between 5 and 20 cm depth by preliminary removing the litter fraction >2 cm. The soil samples were successively used in laboratory (DISTAV, University of Genoa, Italy) to measure soil physical parameters and to determine the granulometry.

Chemical analyses of soils were performed on samples dried at 110°C in a stove (AG System, mod. G-therm) overnight. Each sample was sieved using 500 μm nylon mesh and then milled in an agate mortar. Portions of each sample were analyzed for macro-, micro- and trace elements by FUS-ICP mod. Varian Vista ICP, (0.2g of sample were mixed with a mixture of lithium metaborate/lithium tetraborate and fused in a graphite crucible. The molten mixture was then poured into a 5% nitric acid solution and shaken until dissolved), by ICP-OES mod. Varian Vista ICP (0.25 g of sample were digested with three acids beginning with hydrofluoric, followed by a mixture of nitric and

Table 1. List of biotic and abiotic variables recorded in each plot of studied sites. EMC – Ectomycorrhizal and S – Saprotrophs macrofungi

Dependent variables	Biotic and abiotic independent variables		
Macrofungi	Vegetation	Soil	Climate (at large scale – Europe)
Total number of species	Number of trees	pH	Annual Mean Temperature
Total number of ECM edible species	Tree layer coverage	Eh	Mean Diurnal Range
Total number of ECM non-edible species	Shrub layer coverage	Major elements content	Isothermality
Total number of species S edible species	Herbaceous layer coverage	Minor elements content	Temperature Seasonality
Total number of species S non-edible species	Density of trees	Traces content	Max Temperature of Warmest Month
Total number of Boletes (porcini) species	Trunk diameter	Sand content	BIO6 = Min Temperature of Coldest Month
Total abundance of fruiting bodies	Trunk basal area	Silt content	Temperature Annual Range
Total abundance of ECM edible fruiting bodies	Volume of dead wood	Clay content	Mean Temperature of Wettest Quarter
Total abundance of ECM non-edible fruiting bodies	Volume of litter		Mean Temperature of Driest Quarter
Total abundance of S edible fruiting bodies	Slope		Mean Temperature of Warmest Quarter
Total abundance of S non-edible fruiting bodies	Altitude		Mean Temperature of Coldest Quarter
Total abundance of Boletes (porcini) fruiting bodies	Climate (at small scale – Liguria)		Annual Precipitation
	Mean Annual Temperature 2012	Mean Annual Precipitation 2012	Precipitation of Wettest Month
	Mean Annual Temperature 2013	Mean Annual Precipitation 2013	Precipitation of Driest Month
	Mean Annual Temperature 2014	Mean Annual Precipitation 2014	Precipitation Seasonality
	Max Annual Temperature 2012	Max Annual precipitation 2012	Precipitation of Wettest Quarter
	Max Annual Temperature 2013	Max Annual precipitation 2013	Precipitation of Driest Quarter
	Max Annual Temperature 2014	Max Annual precipitation 2014	Precipitation of Warmest Quarter
	min Annual Temperature 2012	min Annual precipitation 2012	Precipitation of Coldest Quarter
	min Annual Temperature 2013	min Annual precipitation 2013	
	min Annual Temperature 2014	min Annual precipitation 2014	

perchloric acids) and INAA (1 g of sample was encapsulated in a polyethylene vial and irradiated with flux wires). The whole methodology is described in Hoffmann (1992). Employed standard reference materials were GBW 07113 (FluXana), GXR-4 (USGS) and BIR-1a (USGS).

The pH and Eh were measured by using the WTW 340i Multiline pH-meter equipped with the SenTix41 electrode after equilibrating of the soil fraction (<2 mm) in deionized water for 12–16 h.

The soil granulometry (wt.% of Gravel, Sand, Silt + Clay) was classified according to Folk et al. (1970).

Climate data at small scale (Liguria, Italy)

Climate datasets related to the period 2012–2014 were obtained from the ARPAL database (Table 1; https://www.arpal.liguria.it/; ARPAL 2020). Specifically, we selected daily data on mean daily temperatures (C) and mean daily precipitation (mm) for the studied sites (from Loc. Sassello weather station), for each year of survey. For statistical analyses we extrapolated mean, max and min temperature and rainfall (= precipitation) of each surveyed year (see details in Table 1).

Climate data at large scale (Europe) and a model for *Boletus edulis* group

To investigate connections between occurrence of *Boletus edulis* group at large scale, more detailed climatic conditions (see Table 1) species distribution modeling was used. The climatic niche preferences of *B. edulis* were described using MaxEnt 3.3.2 software (Phillips et al., 2006). This method gives an opportunity to determine the climatic variables linked with records of the particular organism. In this study data describing *B. edulis* occurrence in Europe were gathered based on records accessible in GBIF (GBIF.org (2 January 2018) modified), searching among observations and preserved specimens. Altogether the set of 2013 records of the fungus in Europe were generated as a basic input file. To create a model 19 climatic variables in 2.5 arc minutes (± 21.62 km^2 at the equator, Table 1; Hijmans et al., 2005) were also used in the MaxEnt analysis. The maximum iteration number was set to 10,000 and the convergence threshold to 0.00001. For each run, 10% of the data were used and set aside as test points. The "random seed" option was used, which provided a random test partition and background subset for each run. Each run was performed as a bootstrap with 1000 replicates, and the output was set to logistic. All operations on spatial data were carried out on ArcGis 9.3 (ESRI). The model was evaluated using basic metric – area under the curve (AUC), where values more than 0.9 indicate a high performance of the model.

Statistical analyses

A set of biodiversity indices (Magurran, 2004), based on the number of individuals (here fruiting bodies) that were present at the time of sampling in each study site, were computed as follows:

- The macrofungal species richness (SR) was computed by the number of species recorded. The SR expresses the alpha diversity and is the simplest measure of biodiversity albeit of low information value.
- The Shannon index (H') was computed to estimate the species diversity. This index assumes that individuals are randomly sampled and that all the species are represented in the sample. H' depends on the total number of species and their occurrence.
- Population abundance (A) referred to the number of individuals for each collected species.
- The Biomass was estimated using a non-destructive method (Tóth & Feest, 2007). Biomass is related directly to the size of the fruiting bodies calculated from the radius of the cap. More precisely, Biomass Index (BI) was computed from the biometrics of the species as dry weight (Feest 2006).
- Pearson's correlation (r) was used to interpret the relationships between mycobiota (macrofungal richness, abundance, diversity and biomass) and independent variables (biotic and abiotic factors). This coefficient indicates how well the two data set are interconnected. The positive and negative values denote respectively positive or negative linear correlation. If the coefficient is zero, there is no correlation between the two given variables. Specifically, all the recorded macrofungal species were split into functional groups and their richness (= number of species), abundance (= number of fruiting bodies), diversity and biomass were correlated with all the recorded biotic and abiotic factors using Pearson's coefficient (Legendre & Legendre, 1994; Magurran, 2004; Everitt & Hothorn, 2006). Since the chosen variables are expressed in different measurement scales they were transformed in logarithmic scale before performing Pearson's correlation.
- The effect of the abiotic and biotic factors on macrofungal communities was tested by the Multivariate technique of Principal Component Analysis (PCA) (Everitt & Hothorn, 2006). Since the environmental variables are expressed in different measurement scales, PCA was computed on the correlation matrix. The Euclidian distances were used to jointly display sites and variables in the PCA plot. Vector fitting was used to identify the significant variables onto ordination axes (PCA1 and PCA2).

All the statistical analyses were computed using Vegan and BiodiversityR packages in R system (version 4.1.2.; 2021).

Results

Macrofungi

After three years of intensive surveys a total of 1116, 1249, and 1474 fruiting bodies, belonging to 110 (site 1), 115 (site 2) and 122 (site 3) species respectively were collected in the three study areas (full list in Appendices A). In both site 1 and 2, the non-edible ectomycorrhizal group (ECM-ne) occurred with a high number (183 and 216 species, respectively), followed by non-edible saprotrophs (S-ne) (88 sp.- site 1 and 56 sp. – site 2). At low frequency were recorded edible ectomycorrhizal (ECM-e) and saprotrophs species (Table 2). Conversely, in the site 3 there were recorded 172 non-edible saprotrophs (S-ne) and 154 non-edible ectomycorrhizal species (ECM-ne). Edible ECM and saprotrophs occurred with 45 and 15 species, respectively (Appendices B–D).

Table 2. Summary of Species richness (SR), Abundance (A), Diversity (H') and Biomass (BI) values computed in each site. For each diversity index is given the sum, mean, standard deviation (sd), maximum and minimum value on 20 replicates (plots) in each site (60 in total). ECM= ectomycorrhizal; S= saprotrophs; e= edible; ne= not edible

		Site 1					Site 2					Site 3				
		Sum	mean	sd	Max	min	sum	mean	sd	Max	min	Sum	mean	Sd	Max	min
Species Richness (SR)	ECM-e	62	3.10	1.33	5	0	80	4.00	1.92	8	2	45	2.25	1.07	4	1
	ECM-ne	183	9.15	3.65	17	3	216	10.80	4.29	22	5	154	7.70	4.76	17	0
	S-e	13	0.65	0.59	2	0	36	1.80	1.06	4	1	8	0.40	0.60	2	0
	S-ne	88	4.40	2.28	8	0	56	2.80	2.17	9	0	172	8.60	3.94	16	1
	Porcini	1	0.55	0.51	1	0	2	0.75	0.55	2	0	2	0.75	0.64	2	0
Abundance (A)	ECM-e	181	9.05	6.33	29	0	264	13.20	7.64	28	3	134	6.70	5.22	20	1
	ECM-ne	403	20.15	10.44	41	6	665	33.25	20.24	94	13	394	19.70	18.62	65	0
	S-e	44	2.20	5.25	24	0	36	1.80	1.61	7	1	28	1.40	2.46	8	0
	S-ne	224	11.20	6.31	23	0	113	5.65	4.18	15	0	744	37.20	23.14	101	3
	Porcini	32	1.60	1.93	5	0	50	2.50	2.46	7	0	73	3.65	4.46	14	0
Diversity (H')	ECM-e	2.79	0.14	0.06	0.29	0	2.88	0.14	0.05	0.24	0.05	2.75	0.14	0.07	0.28	0.04
	ECM-ne	2.85	0.14	0.05	0.23	0.06	2.85	0.14	0.05	0.28	0.08	2.63	0.13	0.08	0.3	0
	S-e	1.74	0.09	0.09	0.33	0	1.45	0.07	0.07	0.24	0	1.78	0.09	0.13	0.36	0
	S-ne	2.82	0.14	0.06	0.23	0	2.58	0.13	0.08	0.27	0	2.82	0.14	0.06	0.27	0.02
	Porcini	2.23	0.11	0.12	0.29	0	2.46	0.12	0.10	0.28	0	2.32	0.12	0.11	0.32	0
Biomass (BI)	ECM-e	2841.7	142.09	99.36	455.3	0	4144.8	207.24	119.96	439.6	47.1	2103.8	105.19	81.99	314	15.7
	ECM-ne	5061.68	253.08	131.12	514.96	75.36	8352.4	417.62	254.25	1180.64	163.28	4948.64	247.43	233.81	816.4	0
	S-e	552.64	27.63	65.91	301.44	0	452.16	22.61	20.21	87.92	12.56	351.68	17.58	30.87	100.48	0
	S-ne	2461.76	123.09	69.38	252.77	0	1241.87	62.09	45.98	164.85	0	8176.56	408.83	254.33	1109.99	32.97
	Porcini	502.4	25.12	30.31	78.5	0	628	31.40	30.90	87.92	0	1146.1	57.31	70.08	219.8	0

The *Boletus edulis* group totally amounts to 32 (site 1), 50 (site 2) and 73 (site 3) fruiting bodies, respectively. Specifically, *B. edulis* was recorded in sites 1 and 3; *B. aereus* in site 2; and *B. reticulatus* in sites 2 and 3 (line "Porcini" in Table 2).

Several other edible species were recorded, such as: *Armillaria mellea*, *Cantharellus cibarius Craterellus cornucopioides*, *Hydnum repandum*, *H. rufescens*, *Macrolepiota procera*, *Russula cyanoxantha* and *Tricholoma acerbum* (Appendix A).

Vegetation

In Table 3 are displayed the data about vegetation, stand structure and climate of each site. The three sites are characterized by a different vegetation structure. Site 1 had a similar mean percentage of tree, shrub and herbaceous cover (18%, 16%, 24%, respectively). In site 2 the highest cover percentage was represented by herbaceous species (mean of 50%), followed by trees (27%) and shrubs (3%). Site 3 is mostly covered by shrubs (= 45%), then trees (15%) and herbs (<2%) (see full details in Appendices E–G).

The volume of litter had a similar value in all the sites whereas the lowest volume of dead wood was recorded in site 2 (Table 3).

Climate

At small scale, annual mean temperatures in the three study sites (Loc. Sassello, Liguria) ranged from −2.08 °C (Feb-2012) to 21.74 °C (Aug-2012); from 0.48 °C (Feb-2013) to 21.57 °C (Aug-2013); from 3.26 C (Jan-2014) to 20.06 C (Aug-2014). Mean rainfall, ranged from 1.8 mm (Jun-2012) to 348.8 mm (Nov-2012); from 29.8 mm (Jun-2013) to 416.8 mm (Dec-2014); from 50 mm (Sep-2014) to 676 (Nov-2014) (see Appendix H).

At large scale (Europe), MaxEnt analysis (Table 4) showed that the most important climatic (50.8% contribution) crucial for *Boletus edulis* group (Porcini) occurrence was the precipitation of the driest month. Less important factors were annual mean temperature and minimum temperature of coldest month, which reached 12.0% and 11.6% contributions, respectively. The models received high AUC scores (0.918), which indicates the reliable performance of this method. Moreover, the projection of distribution of *B. edulis* group occurrence overlaps with its records in Europe (data not shown), and additionally confirms the high quality of the model

Table 3. Summary of vegetation parameters, stand structure and climate variables (at local scale) of the Site 1–3. For each variable is given the mean, standard deviation, maximum and minimum value on 20 replicates (plots) in each site (60 in total).

	Site 1				Site 2				Site 3			
	Mean	sd	Max	min	Mean	sd	Max	min	Mean	sd	Max	min
Tree coverage (%)	17.50	12.62	40.00	0	27.25	18.24	70.00	5.00	14.50	8.72	40.00	5.00
Shrub coverage (%)	15.25	18.95	80.00	0	3.10	4.05	10.00	0	44.50	18.77	80.00	10.00
Herbaceous coverage (%)	24.00	20.75	80.00	5.00	49.50	23.95	80.00	10.00	1.50	2.35	5.00	0
Volume of litter (V/mq)	236.67	376.39	1500.00	0	203.47	71.93	351.68	100.48	233.62	69.68	401.92	100.48
Volume of dead wood (V/mq)	118.33	188.20	750.00	0	53.63	83.48	390.81	9.40	710.58	2064.40	9375.00	6.25
Number of trees	14.30	4.80	26.00	7.00	8.45	2.09	13.00	5.00	10.45	6.67	32.00	1.00
Density of trees	0.28	0.10	0.51	0.13	0.17	0.04	0.26	0.10	0.20	0.13	0.63	0.01
Trunk diameter (mean)	12.37	2.34	16.60	7.81	25.90	4.46	33.17	18.88	17.52	14.12	65.00	5.13
Trunk basal area (mean)	1068.39	3353.16	13031.00	6.13	20.33	3.50	26.04	14.82	3150.61	11570.56	51025.00	4.02
Slope (°)	12.75	2.55	15.00	10.00	2.70	3.26	10.00	0	11.45	5.00	20.00	5.00
Altitude (m)	423.60	4.13	431.00	419.00	321.25	5.46	330.00	315.00	1006.25	9.81	1023.00	1000.00
Temperature (°C-2012)	11.00	8.05	21.74	−2.08	11.00	8.05	21.74	−2.08	11.00	8.05	21.74	−2.08
Rainfall (mm-2012)	96.8	99.81	348.8	1.8	96.8	99.81	348.8	1.8	96.8	99.81	348.8	1.8
Temperature (°C-2013)	10.33	7.49	21.57	0.48	10.33	7.49	21.57	0.48	10.33	7.49	21.57	0.48
Rainfall (mm-2013)	138.9	113.21	416.8	29.8	138.9	113.21	416.8	29.8	138.9	113.21	416.8	29.8
Temperature (°C-2014)	11.51	6.29	20.06	3.26	11.51	6.29	20.06	3.26	11.51	6.29	20.06	3.26
Rainfall (mm-2014)	155.23	181.72	676.6	26.6	155.23	181.72	676.6	26.6	155.23	181.72	676.6	26.6

Soil

Geologically sites 1 and 3 are characterized by Calceschist. Only one selected plot in site 1 falls onto Alluvial deposits (Plot 10). Site 2 differs from site 1 and 3 because it is characterized by a high level of geo-diversity. The parent rock consists of Siliciclastic conglomerate, Serpentine schist and Calceschist (Appendices I–K).

Table 4. Codes of climatic variables developed by Hijmans et al. (2005) and their importance for Boletus edulis occurrence in Europe. The most important variables in bold

Code	Description	Percent contribution
bio1	Annual Mean Temperature	12
bio2	Mean Diurnal Range = Mean of monthly (max temp − min temp)	7.5
bio3	Isothermality (bio2/bio7) * 100	0.5
bio4	Temperature Seasonality (standard deviation * 100)	2.0
bio5	Max Temperature of Warmest Month	0.3
bio6	Min Temperature of Coldest Month	11.6
bio7	Temperature Annual Range (bio5 − bio6)	2.0
bio8	Mean Temperature of Wettest Quarter	0.5
bio9	Mean Temperature of Driest Quarter	0.3
bio10	Mean Temperature of Warmest Quarter	3.7
bio11	Mean Temperature of Coldest Quarter	8.4
bio12	Annual Precipitation	0
bio13	Precipitation of Wettest Month	0
bio14	Precipitation of Driest Month	50.8
bio15	Precipitation Seasonality (Coefficient of Variation) 0.1	0.1
bio16	Precipitation of Wettest Quarter	0.1
bio17	Precipitation of Driest Quarter	0
bio18	bio18 Precipitation of Warmest Quarter	0.2
bio19	Precipitation of Coldest Quarter	0

The three sites have shown variable pH values (4.38–5.83) according to the parent rock (Table 5). The lowest pH value corresponds to Siliciclastic conglomerate; whereas the highest values were found on Calceschist and Serpentine schist (see Appendices I–K). Eh values are quite homogeneous with values from (min) 226.6 to (Max) 331.7 mV (Table 5).

According to the grain size analyses (the percentage of sand, silt and clay; Folk et al., 1970) soil texture was classified as: sandy gravel to muddy sand for site 1; gravelly sand to muddy gravel for site 2; and sandy gravel to gravelly mud for site 3 (Table 5; Appendices I–K).

The three sites have shown a different soil chemistry. The distribution of major, minor and trace elements (e.g., Al, K, Rb) in soil of sites 1 and 3 were homogeneous in accordance with the presence of only one type of parent rock (Calceschist). An exception was observed for Plot 10 in site 1. This soil sample was the only one taken on a soil profile formed from a different parent rock (Alluvial conglomerate). The content of minor elements differs in fact, from the other samples. Specifically, concentration of Ni, Co, Cr, Zn were higher than that measured on Calceschist. Therefore, this high level of toxic elements (e.g., Cr) can be due to the natural pedo-geochemical signature rather than to anthropogenic contamination (Table 5).

Table 5. Summary of soil parameters recorded in Site 1–3. For each variable is given the mean, standard deviation, maximum and minimum value on 20 replicates (plots) in each site (60 in total)

	Site 1				Site 2				Site 3			
	mean	sd	Max	min	mean	sd	Max	min	Mean	dev	Max	min
pH	4.91	0.18	5.32	4.54	5.18	0.39	5.83	4.27	4.61	0.19	4.90	4.20
Eh (V)	109.78	36.32	216.00	66.10	78.91	23.29	133.50	35.20	268.76	11.32	301.30	252.70
Sand (%)	13.31	4.34	25.55	4.75	21.86	6.69	35.64	4.80	25.38	28.18	7.56	41.56
Silt (%)	38.29	7.05	51.81	18.60	28.37	5.03	35.07	16.31	19.81	18.09	45321.00	25.66
Clay (%)	48.40	10.37	76.65	22.63	49.77	9.35	72.05	29.94	17.90	10.32	55.33	4.88
Si (%)	50.33	1.14	51.52	47.66	48.28	3.59	54.57	39.83	49.01	3.31	58.47	42.68
Ti (%)	1.01	0.09	1.16	0.84	1.60	0.46	2.86	1.02	1.38	0.22	1.84	1.09
Al (%)	19.72	1.23	22.03	17.10	15.10	1.72	19.87	12.69	16.45	1.78	18.94	11.93
Fe (%)	8.77	0.87	10.83	7.38	10.69	1.75	15.83	8.49	10.37	1.70	12.78	6.94
Mn (%)	0.12	0.03	0.19	0.07	0.16	0.06	0.40	0.10	0.18	0.12	0.43	0.06
Mg (%)	3.42	0.65	4.52	2.54	8.36	2.60	13.20	3.09	6.03	1.67	11.43	4.45
Ca (%)	0.72	0.26	1.51	0.38	2.53	0.70	5.15	1.90	1.56	0.42	2.49	1.03
K (%)	3.26	0.56	4.30	2.14	1.00	0.25	1.62	0.69	1.90	0.65	3.19	0.82
S (ppm)	2017.60	169.71	2368.00	1692.00	1280.70	294.51	2023.00	827.00	2070.85	762.76	4502.00	1012.00
V (ppm)	164.15	28.18	232.00	112.00	153.30	31.90	223.00	99.00	178.85	20.52	213.00	146.00
Cr (ppm)	111.95	27.11	183.00	81.00	549.10	556.71	1871.00	75.00	219.40	49.61	323.00	146.00
Co (ppm)	51.35	13.89	103.00	36.00	83.80	38.20	219.00	41.00	59.00	16.44	86.00	28.00
Ni (ppm)	176.40	107.73	491.00	85.00	644.75	224.07	1371.00	257.00	153.70	70.12	309.00	30.00
Cu (ppm)	70.35	34.79	185.00	42.00	50.60	17.10	103.00	28.00	32.20	11.33	59.00	13.00
Zn (ppm)	94.95	7.47	117.00	88.00	81.20	8.24	96.00	65.00	90.10	20.60	117.00	41.00
Rb (ppm)	205.35	39.47	279.00	118.00	48.35	13.70	69.00	17.00	116.55	35.67	202.00	62.00
Sr (ppm)	101.30	18.94	133.00	54.00	93.25	27.54	186.00	60.00	116.05	17.83	155.00	90.00
Zr (ppm)	187.85	38.93	273.00	143.00	187.20	46.62	305.00	97.00	204.60	39.34	275.00	137.00
Nb (ppm)	74.50	9.98	100.00	62.00	46.18	8.01	60.00	35.00	84.10	30.29	175.00	51.00
Mo (ppm)	42.46	12.57	62.00	23.00	45.90	8.20	60.00	37.00	45.40	32.51	131.00	0.00
Cd (ppm)	27.95	3.59	36.00	21.00	31.90	4.04	39.00	26.00	28.40	4.64	37.00	17.00
Sn (ppm)	35.45	7.07	51.00	23.00	43.75	6.87	58.00	31.00	40.85	9.87	58.00	27.00
Ba (ppm)	232.90	23.03	284.00	189.00	30.08	3.09	35.00	26.00	153.50	30.10	239.00	103.00
Pb (ppm)	49.45	6.35	61.00	38.00	153.00	31.78	215.00	79.00	62.45	15.18	97.00	38.00

The major elements soil composition of site 2 was homogeneous despite the presence of various rock types (Appendices I–K). Conversely, the concentration of some trace elements differs considerably and varies according to the different parental rock. Specifically, high content of Ni and Cr were found in soil derived from serpentine schist parental rocks. These elements are in fact, typically present in very high concentration within ultrabasic rock. Hence, as observed for site 1 and 3, the very high content both of Ni and Cr (e.g., Cr: 782–1871 ppm; Ni: 567–1371 ppm), even if over the legal limits (D. Lgs 152/2006), are influenced by the presence of parent rock rather that anthropogenic factors and must be considered as the natural background of the area.

Statistical analyses

By Pearson's correlation values obtained (see full details in Appendices L-Q) it is possible to observe that "strong" positive correlations exist among macrofungal ecological groups and the vegetation site's structure. The highest value (r=0.81) was observed between the shrub coverage and the total abundance of fruiting bodies recorded (e.g., in site 1). Some moderate correlations exist among volume of dead wood/litter, number/density of trees, trunk diameter/basal area and macrofungi. Climate factors (viz. mean annual temperatures and precipitations) at small scale, are not strongly correlated despite being positive.

Conversely, geological variables have shown more correlation with each single macrofungal group. A higher number of positive values were observed between minor, trace elements and the mycobiota (Appendices L-Q).

The PCA results are shown in figure 2. The first two axes (PCA1 and PCA2) account for 53% (Fig. 2A), 54% (Fig. 2B), 53% (Fig. 2C), 49% (Fig. 2D), 44% (Fig. 2E), 51% (Fig. 2F) of the data variability for each ordination, respectively. In Supplementary Tables S1 and S2 instead, are summarized results of vector fitting. The significant variables are indicated with a specific code (see caption of each table). Each variable showed a different effect on macrofungal communities in each site. Among vegetation variables, the volume of litter and wood, as well as the number and size of trees (diameter and basal area) are more influential than forest structure (e.g.,

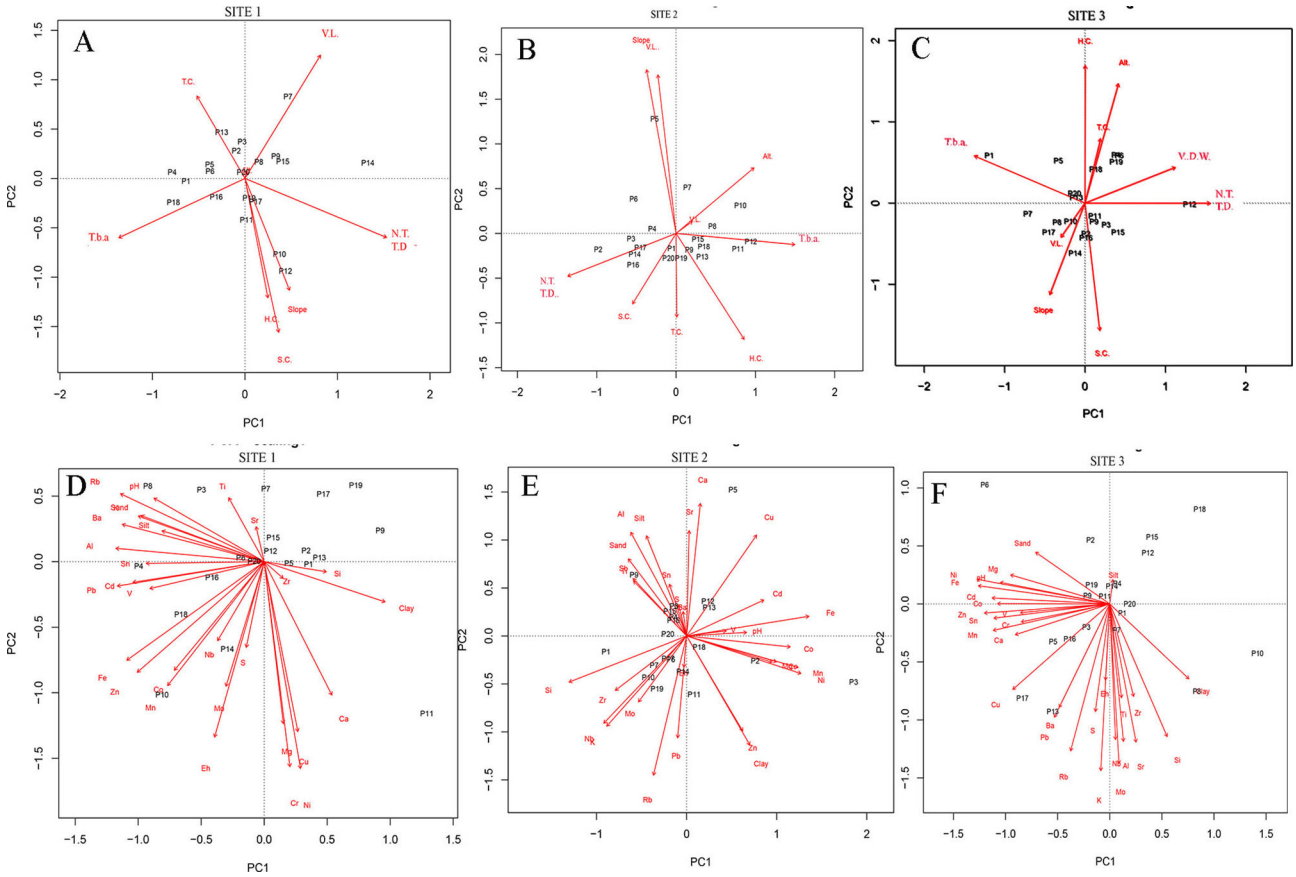

Fig. 2. PCA biplot of macrofungal communities recorded in site 1–3. Variables relative to vegetation, climatic (A–C) and geological (D-F) data are indicated by vectors whose length is proportional to the significance of the same variable. N.T. – Number of Trees; T.C.: Tree layer Coverage; S.C. – Shrub layer Coverage; H.C. – Herbaceous layer Coverage; T.D. – Density of Trees; T.d. – Trunk diameter; T.b.a. – Trunk basal area; V.D.W. – Volume of Dead Wood; V.L. – Volume of Litter; Alt – Altitude; Slope; pH; Eh; Sand – Sand content; Silt – Silt content; Clay – Clay content; Si – Silicon; Ti – Titanium; Al – Aluminium; Fe – Iron; Mn – Manganese; Mg – Magnesium; Ca – Calcium; K – Potassium; S – Sulfur: V – Vanadium; Cr – Chromium; Co – Cobalt; Ni – Nickel; Cu – Copper; Zn – Zinc; Rb – Rabidium; Sr – Strontium; Zr – Zirconium; Nb – Niobium; Mo – Molybdenum; Cd – Cadmium; Sn – Tin; Ba – Barium; Pb – Lead

vegetation coverage). Among the geological parameters, the concentration of minor and traces elements (e.g., Cr, Co, Ni, Cu, Zn, Rb) are more significant than soil proprieties (e.g., pH, Eh) and major elements content. Climate variables were not statistically significant at small scale.

Discussion

It is well recognized that wild edible mushrooms are the most valuable non-timber forest products whose trade and exploitation are becoming an important complementary activity for many countries and regions in the world (Boa, 2004; Pettenella & Kloehn, 2007; Collado et al., 2018). Predicting fungal yield, it is not an easy task because of a wide range of factors have been known to influence fruiting bodies formation (Boddy et al., 2014; Egli, 2011). The results obtained by several studies have revealed that there is not sufficient information to optimize forest conditions for mushrooms production since biotic and abiotic factors are often site- or species-dependent (Bonet et al., 2004; Ortega-Martínez & Martínez-Peña, 2008; Martinez-Pena et al., 2012a, 2012b). By the results of some long-term monitoring inventories, it has been observed that a strong positive correlation between the amount of rainfall (precipitation), air temperature and mushroom yield (Straatsma et al., 2001; Laganà et al., 2002; Straatsma & Krisai-Greilhuber, 2003; Krebs et al., 2008; Martinez-Pena et al., 2012). Some other studies emphasized the influence of forest structures, mainly the stand age, on fruiting bodies biomass (Smith et al., 2002; Bonet et al., 2004; Ortega-Martínez et al., 2011; Martinez-Pena et al., 2012a, 2012b; Ágreda et al., 2014). More recent papers (Collado et al., 2019; Tomao et al., 2020) analyze the relationships between fungal productivity, forest structure and management and climatic conditions across Mediterranean, temperate and boreal forests in Europe. They observed that there were no consistent relationships across the different biomes.

Moreover, Collado et al. (2019) found significant synchronies between mushroom yield and climatic (i.e., summer and autumn rainfall) and dendrochronological variables, mostly in Mediterranean sites. They observed few or no significant correlations in the boreal and temperate regions.

Despite these studies, very little information is available on Southern European Mediterranean forests, especially for broadleaves (that are very favorable and productive edible fungal habitats). The above-mentioned researches were in fact, mainly carried out in coniferous stands.

The contribution of this study is twofold. First it has been performed in three different (and 60 plots) Mediterranean broadleaf forest types which represent much of the Italian territory, and these are well known for being very productive for many wild edible mushrooms (Sitta & Floriani, 2008; Ambrosio & Zotti, 2015). Secondly a novel aspect concerns the recording of a wide set of biotic and abiotic factors: 12 dependent and 36 independent variables, respectively, at small scale; and 19 climatic variables for modeling of *Boletus edulis* group occurrence, at large (European) scale (see Table 1).

Based on the results obtained by statistical analyses (see Table S1-S2) it is possible to affirm that, at small scale, vegetation, soil and climate parameters differently affect macrofungal communities (supporting H_1). In broad terms, for all the three sites soil variables are a more significant influence than vegetation and climate factors (viz. mean annual rainfall and temperature).

Among vegetation factors, tree species richness and dimension (e.g., trunk basal area), as well as the presence of dead wood and high volume of litter, were found to be more correlated with macrofungi than stand characteristics (e.g., vegetation cover) and environmental variables (e.g. slope and climate).

This result corresponds to a recent study published by Leski et al. (2019) who have found that above- and belowground ectomycorrhizal communities of Scots pine are significantly correlated with total number of trees, and number of trees thicker than 10 cm breast diameter. The relationship between fungal diversity and the presence of large trees has been also suggested by other studies (Kutszegi et al., 2015; Spake et al., 2016; Tomao et al., 2020), in which the density of large trees and tree trunk basal area were important drivers of fungal diversity. The production of sporocarps is known to require a large amounts of resources, in case of ectomycorrhizal fungi provided by the tree partner (Högberg et al., 1999; Kuikka et al., 2003). Therefore, the assumption can be put forward, that large trees with higher photosynthates production (Bond, 2000) are able to assemble a larger and more diverse community of symbiotic fungi.

In our study macrofungal communities were also connected with the presence of dead wood and a high volume of litter. At general a high volume of dead wood is regarded as a key feature for natural forests, and wood inhabiting fungi are often use as good indicators of high value ecosystems (Blaschke et al., 2009). The deadwood provides specific ecological niches that allow fungi, including ectomycorrhizal taxa belonging (i.e., to telephoroid fungi) to develop and form sporocarps. In this study ectomycorrhizal, and saprotrophic fungi were considered, thus a correlation between species diversity and amount of dead wood and high volume of litter seems to be clear. Similarly, to results obtained in this study Leski et al. (2019) showed that the taxa composition of belowground communities was correlated with total volume of wood debris, especially coarse debris thicker than 10 cm in diameter. Wood debris are crucial element for the nutrient cycle influencing chemical and physical properties of forest soil (Lasota et al., 2022; Piaszczyk et al., 2019). By nutrients delivered to the soil during wood debris decomposition and changes in soil bulk density, moisture, porosity, and air capacity forest soil become more suitable environment for growth of mycelium of fungi. A large body of literature has shown that forests characterized by a greater volume of deadwood are often exhibit higher biodiversity and the same are more valuable for conservation and can be assigned as protected areas. In a review paper published recently by Tamao et al. (2020) they confirmed that fungal diversity can be conserved in managed forests if deadwood amount and diversity is promoted. The Liguria forests analyzed in this study should be regarded as highly valuable ecosystems, having great importance for fungal biodiversity protection.

Soil chemistry content has shown highly significant correlation values. Specifically, minor and traces element concentrations have a strong influence on macrofungal communities, particularly Cr, Ni, Zn and Rb. These elements in fact, are recognized for being key markers due to their spoor mobility in soil (Kabata-Pendians & Pendias, 2001; Ambrosio et al., 2019). Among major elements the concentrations of Si, Al, Ca and Mn are more influential than other elements, in accordance with the parent rock type (mostly ophiolitic soil). Contrary to other European studies (Ferris et al., 2000; Humphrey et al., 2000), low significant values were observed between soil properties, such as pH, sand, silt and clay content and fungal communities in the Ligurian sites, as well as climate parameters.

Pearson's correlation results show it is possible to observe that few strong correlations exist among all the selected variables and each single fungal group recorded. This result might be due to the "dimension" (mainly for species richness and abundance of

fruiting bodies) of each fungal samples/group (viz. Ectomycorrhizal edible fungi; edible Saprotrophs; Porcini). Despite the idea that the impact of mushrooms harvesting on fruiting bodies biomass is insignificant (Bünteng et al., 2011), for the Ligurian sites there might be hypothesized a different scenario. All the three studied woods were intensely visited by harvesters for all the duration of this work (Ambrosio & Zotti, 2015; Ambrosio et al., 2018). Hence, the percentage, number and biomass of edible species, especially Porcini, were strongly affected by the gathering rate.

At larger scale, both edaphic and climatic factors, are considered essential for fungi fruiting and fungal species distribution across landscapes (Eveling et al., 1990). Here, a maximum entropy approach implemented in MaxEnt was used to assess the most important climatic factors linked with occurrence of the most desirable Porcini – *B. edulis* group – in Europe. The crucial climatic factor influencing the occurrence of Porcini is the precipitation of the driest month (50.8% of the contribution) (supporting H_2). This result is not surprising. Occurrence of fungi is mostly related to high precipitation because, fungi have a preference for humid conditions (Krebs et al., 2008). Most climatic factors connected with precipitation, especially precipitation of driest month/quarter and/or coldest month/quarter were major drivers of the occurrence of different fungi (Pietras et al., 2016; Pietras et al., 2018; Pietras, 2019; Pietras & Kolanowska, 2019), including boletoid species (Banasiak et al., 2019). Observations of other authors have shown that the productivity of fungi is linked to annual climate conditions, such as the average monthly or annual precipitation (Eveling et al., 1990; Krebs et al., 2008). Moreover, seasonal changes in precipitation represented the main weather-related driver affecting sporocarps production (Ambrosio & Feest, 2021). Salerni et al. (2014) showed that appearance of truffle ascocarps is positively correlated with the rainfall of the previous three months and, in general, with those of the autumn months prior to collection. Therefore, amount of precipitation, especially during dry seasons, should be regarded as a main factor for the productivity of Porcini. More recent research (Ambrosio & Feest, 2021) explained that at small scale, in Mediterranean forests, inter- and intra-annual temperatures and rainfall fluctuations affected the formation of fungal fruiting bodies (sporocarps) and consequently the dynamics of communities.

Conclusions

The results of this work are a contribution to the knowledge of which biotic and abiotic factors that mostly affect macrofungal diversity and biomass in broadleaf Mediterranean forests. Contrary to previous studies, these results have revealed that soil properties, especially geochemical content (traces and minor elements) are more strongly correlated with macrofungal communities than vegetation and climatic parameters, mainly at small (local) scale. More specifically vegetation expressed by tree species richness and composition, presence of dead wood and high volume of litter, were the most decisive factors correlated with macrofungi communities in contrast to other environmental variables, like slope and climate conditions.

The different correlation values observed among Ligurian broadleaf woods, and some European conifer stands highlight that a high variability and site-dependence of both biotic and abiotic factors exists. Identifying which factors mainly influence the growth of fungi and estimating their production is an essential task from both an ecological and economic point of view. Analyzing favorable habitats will help us improve the management of productive forest fungi sites, aiming to maintain high amount of wood debris, keep the structurally diverse forest ecosystems and to mitigate negative effect of climate change on forests.

Acknowledgements

This study was partly carried out in the framework of a PhD project in Applied Botany to the Agriculture and the Environment, University of Genoa, Italy and by Institute of Dendrology Polish Academy of Sciences within statutory activity. Elia Ambrosio was supported by MIUR (Ministry of Education, Universities and Research−Italy) doctoral fellowship (2012–2014). Authors would like to thank all the people from University of Genoa who contributed to field surveys and anonymous reviews for their useful comments.

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