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Effects of fuel reduction treatments on the sporocarp production and richness of a *Quercus*/*Cistus* mixed system

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ABSTRACT

Wildfire is a recurrent factor that shapes and influences Mediterranean ecosystems where mixed oak (*Quercus*) forests with a rockrose (*Cistus*) understory are broadly represented. These ecosystems are also associated with large and diverse fungal communities. These fungal communities play essential ecological roles for the survival of vascular plant, such as the mineral and water uptaking or resistance against pathogens carried out by mycorrhizal fungi, as the saprotrophic fungi are a key factor for the recycling of the dead matter. In addition, edible fungi, such as *Boletus edulis*, provide a source of income for the nearby rural population. Fuel reduction treatments are applied to reduce the risk of wildfire; however, their potential impact on fungal communities is unclear. Thus, the aim of this work was to investigate the effect of different fuel reduction treatments on fungi associated with *Quercus* and *Cistus*. This aim is accompanied by the management-driven objective to obtain data from fuel reduction treatments that will enable managers to find solutions with a balanced approach to maintaining productive areas of edible mushroom production while reducing fire risks across the landscape. Sporocarps were sampled over a five-year period in stands dominated by mature or coppiced *Quercus pyrenaica* and accompanied by *Cistus ladanifer* understory. These stands had been subjected to different fuel reduction treatment levels involving moderate- or high-intensity thinning, for *Q. pyrenaica,* or clearing, for *C. ladanifer.* The goal was to determine sporocarp production, species richness, and taxonomic composition. Sporocarp production and fungal richness were drastically affected by the fuel reduction treatments but only when *C. ladanifer* is included in the treatment. Taxa composition was strongly correlated with the treatments applied to the rockrose understory. This was probably due to the large range of associated ectomycorrhizal fungi of *C. ladanifer* and their high capacity to recolonize an area after disturbances. Based on our results, we conclude that the implementation of moderate-/high-intensity fuel reduction treatments is compatible with the conservation of the fungal community present in these systems. In addition, the creation of a multi-stage mosaic of stands through mechanical management could enable fire prevention to be managed in an effective way while maintaining fungal diversity and sporocarp production, favoring the use of non-wood resources in rural areas and conserving a healthier forest ecosystem.

1. Introduction

Fire is an ecological and anthropological force that has drastically influenced Mediterranean ecosystems for millions of years. The composition and structure of Mediterranean vegetation depends on climate, fire intensity, and frequency; however, the vegetation characteristics also determine the fire intensity and frequency (Trabaud, 1994). For example, in recent decades, summers have been dryer, making it easier for the climatic threshold to be exceeded, which can lead to intense fire in areas where fuel availability is high, such as those in the Mediterranean basin, modifying the vegetation and the ecosystem drastically (Pausas and Paula, 2012).

Various oaks (*Quercus* spp.) are common in Mediterranean ecosystems, which are adapted to a recurrent fire regime. Oak woodlands around the Mediterranean basin are commonly accompanied by an understory of rockroses (*Cistus* sp.). These scrublands are known to be

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pyrophytic and are frequently affected by wildfires. Furthermore, the high density of *Cistus ladanifer* plants in mature stands increases the intensity of a potential wildfire (Hernández-Rodríguez et al., 2015). Also, *C. ladanifer* contains aromatic compounds which make easier the possibility of ignition (Keeley et al., 2011). These scrublands, despite being considered as ecologically unimportant and economically unproductive, host a huge fungal community, including highly valued edible species (Oria-de-Rueda et al., 2008). This means that these scrublands are a source of non-wood forest products, together with the products obtained from *Quecus sp*., generating complementary incomes for the local rural economy (Hernández-Rodríguez et al., 2015; Lázaro García, 2008). About 200 fungal species belonging to 40 genera are known to form an ectomycorrhizal association with *Cistus* species (Comandini et al., 2006), some of which, such as *Boletus edulis*, have a high economic and culinary value. In the study area, *B. edulis* is known as "zamoranitos" due to its small size, and is collected by local families, enabling them to earn thousands of euros annually as a supplementary income (Comandini et al., 2006; Oria-de-Rueda et al., 2008). Principally, forest wildfires are the major disturbance affecting these ecosystems (Martín-Pinto et al., 2006). Fires not only have a big impact on the vegetation but also disturb the associated fungal communities (Cairney and Bastias, 2007).

Forest management is necessary to prevent deforestation and ecosystem loss due to uncontrollable and severe fires. Thinning not only induces a growth response in *Q. pyrenaica* stands but also reduces losses due to mortality, which reduces the amount of deadwood and, hence, reduces the amount of fuel available (Moreno-Fernández et al., 2020). Clearing, here used as removal of the understory, can act as a safe way of improving biodiversity by enabling new seedlings to colonize and by changing microclimatic conditions favoring variability, as well as reducing the amount of biomass susceptible to burning (Santana et al., 2018). Furthermore, mechanical clearing has been shown to improve the fructification of fungi as well as decreasing the amount of biomass that can act as a fuel (Hernández-Rodríguez et al., 2015; Mediavilla et al., 2019). Given the need for fuel reduction strategies in these *Quercus/Cistus* scrublands, the effect of fuel reduction treatments on fungal communities also needs to be assessed. In particular, the impact of these treatments on *Boletus* spp. due to their commercial importance. A balanced fuel reduction plan must be designed to avoid a negative impact on mushroom production and diversity. To achieve this, we need to identify the best combination of management treatments for both oak and rockroses.

In light of all this, we expect to find a negative effect of silvicultural treatments (i.e., high- and moderate intensity thinning and clearing treatments) on sporocarp biomass levels (Egli et al., 2010; Hernández-Rodríguez et al., 2015; Pilz et al., 2006) in response to physio-photosynthetic changes. However, we predict that no effects will be seen on fungal richness (Castaño et al., 2018) because it has already been seen that mycelium should not be affected by mechanical management treatments in short terms, with all species able to produce a minimal amount of sporocarps. We also expect to see a drastic decrease in the production of *Boletus* due to the elimination or injury of its hosts (Mediavilla et al., 2017). Furthermore, we expect to find differences between treatments, related to ecological guilds as saprotrophic and ECM fungi and edible or inedible fungi. We expect a lower sporocarp production levels in plots that receive the high-intensity thinning treatment due to the reduction in host photosynthesis (Bonet et al., 2012; Collado et al., 2018; Hernández-Rodríguez et al., 2015; Kucuker and Baskent, 2017; Salerni et al., 2020). Finally, we expect that fungal composition will be affected by treatments (Jones et al., 2003; Salerni et al., 2020; Santos-Silva et al., 2011; Tomao et al., 2020), particularly in plots where *Cistus* has been totally cleared. This could be due to the wide range of ECM fungi that form an association with *Cistus*, and their dependence from the host which will be removed (Comandini et al., 2006; Martín-Pinto et al., 2006). To verify these hypotheses, our overall aim was to analyze the effect of fuel reduction treatments on fruitbody production and diversity of macrofungi associated with mixed *Quercus/Cistus* systems. Specifically we want to investigate the effects of fuel reduction treatments on: (i) the sporocarp production and species diversity of the macrofungus community and functional groups (ectomycorrhizal, saprotrophic) of the study area; (ii) the sporocarp production levels of *B. edulis*, the most appreciated edible mushroom species marketed from the study area; and (iii) the macrofungus community composition.

2. Material and methods

2.1. Study site

The study area was located in NW Spain (X 728.081 and Y 4.623.845, ETRS89 / UTM zone 29 N), between 820 and 840 m a.s.L. with a SW aspect. This area is characterized by a sub-Mediterranean climate, with a dry season lasting three months in summer and low temperatures and frosts in winter. The mean annual precipitation is 705 mm and the mean temperature is 11.4 °C. These climatic data were provided by the closest meteorological station (Villardeciervos, 6°17′22’ W longitude, 41°56′32’’ N latitude, 850 m a.s.L., Spanish Meteorological Agency). The soil is characterized by a mixture of inceptisol and entisol, with inceptisol predominating, a moderately acidic pH (5,0–5,5) and a scarcity of calcium and phosphorus, and variable levels of nitrogen and potassium richness. The study area is characterized by forest dominated by *Quercus pyrenaica* that has been affected by wildfire during the past decades. In addition, there is a dense undergrowth dominated by *Cistus ladanifer*.

2.2. Sampling design

The study case was located in a representative area of 186 ha. This is a representative forest structure which dominates thousands of hectares in this Region, where *Quercus* stands were affected by wild fires in the last decades. Fires affect more than 2000 ha per year in Castilla and León Autonomous community, most of them are located in the NW of this Region where the study area was selected to combine the priority of fire prevention with the production and conservation of wild mushrooms. The treatments specifically affected a surface of one ha (five ha in total). Three 2 m × 50 m plots per treatment were established for sampling. The plots were localized randomly, using aleatory direction and distance from a reference point, in representative areas corresponding to each treatment. The fuel reduction treatments were applied in 2010 by the Autonomous Community Forest Service. A total of fifteen 2 m × 50 m plots were established to compare the effects of different fuel reduction treatments on the fungal community associated with either mature oak stands (M) or coppiced oak stands (R). Oak stands were either subjected to high-intensity thinning (50% of trees, with a distance between trees of half of the original thinned oak height, Q) or moderate thinning (25% of trees, with a distance between trees of a quarter of the original thinned oak height, q) and rockroses, which were uniform with a coverture near to 100%, were either partially cleared, plants between 1 and 1,5 m of separation (50%), (c) or totally cleared (C). Clearing was manually done, removing the whole plants without altering soil layers. In total, four different fuel reduction treatments (MCQ, Mcq, RCQ, and RCq) were

Table 1
Management treatment type applied per each plot.

Plots	Origin	TreatmentCistus	Treatment Quercus
1 2 3	M	c	q
4 5 6	M	C	Q
7 8 9	R	C	q
10 11 12	R	C	Q
13 14 15		Control	

M: mature oak stands; R: coppice oak stands; C: total clearing; c: partial clearing; Q: high intensity thinning; q: moderate thinning.

established in the 15 studied plots, plus controls, and are showed in Table 1. Controls are represented by a canopy cover for mature trees that varied between the 40–60%. Total vegetation coverture varied from 85 to 95% which is complemented by young oaks and shrubs. Trees and shrubs distribution was irregular but homogeneous. The mature trees survived a wildfire 18 years ago with an age between 60 and 80 years. The coppice vegetation with regenerated *Cistus* came from year of the fire (18 years) with an average *Quercus* sp. height of 4–6 m and an average *Cistus* sp. height of 1.8–2.5 m.

2.3. Sporocarps sampling, identification and classification

We collected sporocarps on a weekly basis during the autumn mushroom season from late October to late December from 2012 to 2016. Sampling began the first autumn production season after the treatments had been implemented. As the average duration of fruiting bodies varies among species from 4 to 20 days (Vogt, 1992) it is difficult to choose a sampling frequency that suits all species and does not distort production. Weekly sampling frequency has been used by several authors in previous works (Ohenoja and Koistinen, 1984). Fungal sporocarps were harvested, transported to the laboratory and stored at 4 °C. Sporocarps were stored at 4 °C until they were processed and identified, before 24 h. Fresh weight biomass (kg ha^{-1}) was recorded. The sporocarps were identified at species level whenever possible. As in previous works (Bonet et al., 2004; Martín-Pinto et al., 2006) samples that could only be identified to genus level were grouped into genus taxa. Fungal taxa names and authors were obtained from the Index Fungorum database (www.indexfungorum.org). Taxa were classified according to their trophic group (saprotrophic/mycorrhizal) for further statistical analysis according to (Põlme et al., 2020). Species traditionally consumed in the study region and those classified as edible in most of the literature consulted were listed as edible (Gassibe et al., 2015; Martínez de Aragón et al., 2007).

2.4. Data analysis

Sporocarps were identified at species level whenever possible and then categorized on the basis of their nutritional strategy as either mycorrhizal (ECM) or saprophytic (S), and as either edible (E) or inedible (IE). Fungi with scarce culinary value were categorized as inedible. Mean annual fresh weight sporocarp production and richness values were calculated for mycorrhizal and saprophytic fungi (ECM/S), edible and inedible fungi (E/IE), as well as for the total sporocarp production under each treatment. In addition, the fresh weight production of *B. edulis* was also calculated because of its high commercial value worldwide and because *B. edulis* fruiting bodies are processed and marketed by several companies in the area.

We compared total fungal fresh weight and richness as well for mycorrhizal, saprophytic and *Boletus edulis* among the treatments by using Linear Mixed Effects models (LME, $P \leq 0.05$), developed by using the package Nlme (Pinheiro et al., 2016) and Tukey's HSD test. We implemented for all these statistical analyses the R software environment (version 3.5.3; R Development Core Team 2019). To analyze differences in taxa composition, non-metric multidimensional scaling (NMDS) was performed using CANOCO version 5.0 (Smilauer and Lepš, 2014). Analysis was performed on the full dataset (111 taxa and 15 plots) based on fresh weight data. Hellinger transformed matrix for fungal community and scaled matrix for environmental variables were used. A fitted Generalized Additive Model (GAM) for the intensity of *Cistus* treatments was included.

3. Results

3.1. General information

Over the five-year sampling period, 3,690 sporocarps were collected, representing 111 taxa belonging to 39 different genera. Ninety-two of these taxa were identified down to species level. Based on their trophic level, 76% of taxa were mycorrhizal taxa and 24% were saprotrophic. However, only 38% of taxa were edible (83% of which were ectomycorrhizal taxa, Table 2).

3.2. Effect of fuel reduction treatments on fungal production and richness

The average fresh weight production of sporocarps was 70.3 kg ha^{-1} $year^{-1}$. In total, 52.74 kg of sporocarps were collected over the five-year sampling period. Mushroom production in all plots that received a fuel reduction treatment was significantly lower than in control plots (LME Test; $p < 0.001$) (Fig. 1A). However, contrary to what we expected, production levels did not differ significantly among treatments (Tukey test; $p > 1$). The same pattern was observed only in terms of the thinning intensity applied to the oaks ($p < 0.005$) and to the rockroses ($p < 0.005$). In terms of overall fungal richness, treatment plots and control plots were not significantly different (Fig. 1B). Furthermore, neither the saprophytic fungal richness ($p = 0.184$) nor the ectomycorrhizal fungal richness ($p = 0.07$) of the treatment plots differed significantly from the richness values of the control plots. ECM fungal species showed an expected but no significant trend with higher values observed in the low intensity *Quercus* thinned plots.

In terms of the intensity of the *Quercus* thinning treatment, saprophytic taxa were not significantly influenced by thinning treatments ($p = 0.09$) and the Tukey test revealed that none of the groups were affected by the moderate intensity thinning treatment when compared to control and low-intensity thinning ($p > 0.1$). However, Tukey tests did reveal significantly lower levels of mycorrhizal richness ($p = 0.02$) and total fungal richness in high intensity thinning when is compared to moderate intensity thinning ($p = 0.02$) (Fig. 1C). Furthermore, edible fungi ($p = 0.02$) and total fungal species ($p = 0.01$) showed also significantly differences when *Quercus* had been subjected to high-intensity thinning against control plots. Whether treatments took place in stands of coppiced or mature *Quercus* trees, it did not influence fungal richness or sporocarp production ($p > 0.1$).

3.3. Effect of fuel reduction treatments on Boletus edulis production

B. edulis sporocarp production was dramatically lower in plots subjected to fuel reduction treatments than in control plots ($p < 0.001$) (Fig. 2). However, the type of fuel reduction treatment did not significantly affect the level of *B. edulis* sporocarp production ($p > 0.05$).

3.4. Effect of fuel reduction treatments on the composition of fungal taxa

The ordination analyses for the total taxa found showed that samples were grouped according to their stand type and to the fuel reduction treatment received. Control were located appart, together to the Coppice stand type. Our NMDS (Fig. 3) revealed a large value for the first eigenvalue (0.5132) so a greater variability among stand type in terms of fungal species composition could be explained by the gradient associated with axis 1. According to the treatment, the ordination of composition, according to the fitted generalized additive model (GAM), is driven significantly by the intensity of the *Cistus* treatment, showing a strong effect on the species composition between control and moderate treated plots and high intensity treated plots. The cluster of fungi collected from plots of thinned coppiced *Quercus* (R), were in a large contraposition against the mature *Quercus* (M), while in terms of origin effect, have more similarities with Control plots. This means that the type of *Quercus* stand (R or M) had a strong effect on fungal composition. Control plots were observed to have a specific fungal composition, including *B. edulis*, which was different from that presented in the treated plots. Model test of the effect of partial or complete clearance of *Cistus* on fungal composition revealed an adjusted p-value < 0.005 with a contribution of 33.15% in axis 1. We observed a strong influence of

Table 2
List of total taxa collected in the plots according to their trophic group, edibility and treatment.

	Guild	Edibility	Treatment				Control
			M cq	M CQ	R Cq	R CQ	
Amanita citrina Pers.	ECM	IE	x	x	x	x	x
Amanita excelsa (Fr.) Bertill.	ECM	E	x				
Amanita gemmata Quél.	ECM	IE			x		
Amanita mairei Foley	ECM	E					x
Amanita muscaria (L.) Lam.	ECM	IE	x	x			x
Amanita pantherina (Dc.) Krombh.	ECM	IE	x		x		x
Amanita rubescens Pers.	ECM	E	x	x	x	x	x
Bolbitius titubans (Bull.) Fr	S	IE	x				
Boletopsis leucomelaena (Pers.) Fayod	ECM	E	x				
Boletus aereus Bull.	ECM	E	x				
Boletus edulis Bull.	ECM	E	x	x	x	x	x
Boletus ferrugineus Schaeff.	ECM	E			x		x
Boletus reticulatus Schaeff.	ECM	E	x		x	x	x
Boletus sp. L., Fr	ECM	IE	x	x			
Boletus spretus Bertéa.	ECM	E			x		
Cantharellus sp. Adans. ex Fr.	ECM	IE					x
Clitocybe cistophila Bon & Contu.	S	IE	x			x	
Clitocybe leucodiatreta Bon.	S	IE		x		x	
Clitocybe metachroa (Fr.) P. Kumm.	S	IE					x
Clitocybe nebularis (Batsch) P. Kumm	S	E					x
Clitocybe sp. *(Fr.) Staude*	S	IE					x
Collybia sp. *(Fr.) Staude*	MP	IE	x				
Cortinarius cinnamomeoluteus P. D. Orton	ECM	IE	x	x	x		
Cortinarius cinnamomeus (L.) Gray	ECM	IE			x		
Cortinarius elegantissimus Rob. Henry	ECM	IE			x		
Cortinarius infractus (Pers.) Fr.	ECM	IE			x		
Cortinarius purpurascens Fr.	ECM	E			x		
Cortinarius sec. *caerulescens* (Schaeff.) Fr.	ECM	IE				x	x
Cortinarius sec. *sanguineus* (Wulfen) Gray	ECM	IE					x
Cortinarius sp. (Pers.) Gray	ECM	IE	x	x	x		x
Cortinarius splendens Rob. Henry	ECM	IE			x		
Cortinarius trivialis J.E. Lange	ECM	IE	x	x	x	x	x
Cuphophyllus pratensis (Fr.) Bon.	S	E				x	
Entoloma sericeum (Bull.) Quél.	S	IE					x
Fistulina hepatica (Schaeff.) With.	PP	E	x		x	x	x
Gymnopus dryophilus (Bull.) Murrill.	S	E		x	x	x	x
Gymnopus erythropus (Pers.) Antonín, Halling & Noordel.	S	IE					x
Hebeloma cistophilum Maire	ECM	IE	x				
Hebeloma hiemale Bres.	ECM	IE		x			
Hebeloma sp. (Fr.) P. Kumm.	ECM	IE			x	x	
Hydnum repandum L.	ECM	E	x	x	x		x
Hygrophorus chrysodon (Batsch) Fr.	ECM	E	x				
Hygrophorus nemoreus (Pers.) Fr.	ECM	E	x				
Hygrophorus pseudodiscoideus (Maire) Malençon & Bertault	ECM	IE	x				
Hypholoma fasciculare (Huds., Fr.) P. Kumm.	S	IE	x				
Inocybe sp. (Fr.) Fr	ECM	IE	x	x			
Laccaria amethystina Cooke	ECM	E		x			
Laccaria bicolor (Maire) P.D. Orton	ECM	E		x	x		
Laccaria laccata (Scop.) Cooke	ECM	E	x	x	x	x	x
Laccaria sp. Berk. & Broome	ECM	IE					x
Lactarius acerrimus Britzelm.	ECM	IE					x
Lactarius chrysorrheus Fr.	ECM	IE	x	x	x	x	x
Lactarius cistophilus Bon & Trimbach	ECM	IE				x	x
Lactarius hepaticus Plowr.	ECM	IE	x		x		x
Lactarius mairei Malençon	ECM	IE			x		
Lactarius quietus (Fr.) Fr.	ECM	IE				x	
Lactarius sp. Pers.	ECM	IE				x	x
Lactarius subumbonatus Lindgr.	ECM	IE					x
Lactarius tesquorum Malençon	ECM	IE	x	x	x	x	
Lactifluus piperatus (L.) Roussel	ECM	IE				x	
Leccinum sp. Gray.	ECM	IE	x				
Leccinellum corsicum (Rolland) Bresinsky & Manfr. Binder	ECM	E	x		x		
Lichenomphalia meridionalis (Contu & La Rocca) P.A. Moreau & Courtec.	L	IE	x				
Lycoperdon perlatum Pers.	S	E		x			
Lyophyllum decastes (Fr.) Singer	ECM	E		x			
Lyophyllum infumatum (Bres.) Kühner	ECM	E			x		
Lyophyllum semitale (Fr.) Kühner	ECM	E				x	
Lyophyllum sp. P. Karst.	ECM	IE				x	
Lyophyllum transforme (Sacc.) Singer	ECM	E				x	
Melanoleuca sp. Pat.	S	IE					x
Mycena aetites (Fr.) Quél.	S	IE					x
Mycena epipterygia (Scop.) Gray	S	IE	x	x			x
Mycena epipterygia var. *pelliculosa* (Quél.) Maas Geest.	S	IE		x			
Mycena maculata P. Karst.	S	IE			x		

(*continued on next page*)

Table 2 (*continued*)

	Guild	Edibility	Treatment				Control
			M cq	M CQ	R Cq	R CQ	
Mycena polygramma (Bull.) Gray	S	IE			x		
Neoboletus erythropus (Pers.) C. Hahn	ECM	E	x	x	x	x	x
Paxillus involutus (Batsch.) Fr.	ECM	IE	x	x	x	x	x
Protostropharia semiglobata (Batsch) Redhead, Moncalvo & Vilgalys.	S	IE	x				x
Psathyrella candolleana (Fr.) Maire	S	IE	x				
Psathyrella sp. (Fr.) Quél.	S	IE	x				
Ramaria sp. Fr. ex Bonord.	ECM	IE	x				
Rheubarbariboletus armeniacus (Quél.) Vizzini, Simonini & Gelardi.	ECM	E		x			
Rhodocollybia butyracea (Bull.) Lennox	S	E	x		x	x	x
Ripartites sp. P. Karst.	S	IE		x			
Russula adusta (Pers.) Fr.	ECM	E	x	x	x	x	x
Russula cyanoxantha (Schaeff.) Fr.	ECM	E	x	x	x	x	
Russula cyanoxantha f. *peltereaui* Singer.	ECM	IE				x	
Russula densifolia Secr. ex Gillet	ECM	E	x				x
Russula foetens Pers.	ECM	IE	x				
Russula heterophylla (Fr.) Fr.	ECM	E	x				
Russula insignis Quél.	ECM	IE			x		
Russula rosea Pers.	ECM	E			x		
Russula rubroalba (Singer) Romagn.	ECM	E			x		
Russula sp. Pers.	ECM	IE	x	x	x	x	x
Russula subfoetens W.G. Sm.	ECM	IE	x	x			
Russula tinctipes J. Blum ex Bon	ECM	IE			x		
Stereum hirsutum (Willd.) Pers.	S	IE			x		
Tremella mesenterica Retz.	MP	E			x		
Tricholoma acerbum (Bull.) Quél.	ECM	E		x	x	x	x
Tricholoma albobrunneum (Pers.) P. Kumm.	ECM	IE	x				
Tricholoma columbetta (Fr.) P. Kumm.	ECM	E	x	x	x	x	x
Tricholoma josserandii Bon.	ECM	IE	x				
Tricholoma portentosum (Fr.) Quél.	ECM	E	x	x	x	x	x
Tricholoma roseoacerbum A. Riva.	ECM	IE	x	x	x	x	x
Tricholoma saponaceum (Fr.) P. Kumm.	ECM	IE	x	x	x	x	x
Tricholoma sp. (Fr.) Staude	ECM	IE	x	x			x
Tubaria sp. (W.G. Sm.) Gillet	S	IE	x	x	x	x	x
Xerocomellus chrysenteron (Bull.) Šutara.	ECM	E	x	x	x	x	x
Xerocomus sp. Quél..	ECM	IE	x	x	x	x	x
Xerocomus subtomentosus (L.) Quél.	ECM	E				x	
Total ECM			42	31	41	30	34
Total S			9	7	6	6	12
Total E			20	17	25	18	18
Total IE			35	22	26	20	30
Total sporocarps			56	39	51	38	48

Guild: ECM, mycorrhizal; S, saprotrophic; MP, Mycoparasite; PP, Plant Pathogen; L, Lichenized Edibility: E, edible; IE, inedible. Fuel reduction treatments: Mcq, mature *Quercus* stands subjected to moderate thinning and partial clearing of *Cistus*; MCQ, mature *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; RCq, coppiced *Quercus* stands subjected to moderate thinning and total clearance of *Cistus*; RCQ, coppiced *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; Control, mature *Quercus* stands with an understory of *Cistus*.

Cistus treatment on fungal community association, with the community in the control plots clearly differentiated from those in the treated plots. A relatively separated community was observed in plots of mature *Quercus* between those that were subjected to moderate thinning and partial clearing of *Cistus* (Mcq) in comparison to those with a high intensity treatment. Once again, *B. edulis* showed the opposite tendency to fungi associated with a fuel reduction treatment and was localized in control plots.

4. Discussion

To our knowledge, this is the first study providing empirical data from the effect of mixed fire prevention treatments on fungal communities associated with *Quercus/Cistus* forests, widely distributed in Mediterranean systems. Although our analysis were based on mushroom fresh weights, and this could lead to variation due to the environmental humidity conditions, as we expected, we could observe a negative effect of the fire prevention treatments on the sporocarps production. But surprisingly although we expected to find lower sporocarp production in the plots receiving high-intensity treatments, we could not find significant differences among these treatments, related to saprotrophic and ECM fungi and specifically for the appreciated species *Boletus edulis*. Finally, as we hypothesized fungal composition was significantly affected by treatments particularly in plots where *Cistus* has been totally cleared.

4.1. Fresh weight production and richness

Sporocarp production following a moderate- or high-intensity thinning treatment was considerably lower than in control plots, which supports the findings observed by Luoma et al. (2004). This decrease in sporocarp production following thinning can be easily explained because the loss of the green parts of a plant will reduce photosynthetic productivity and, hence, less fixed carbon will be available to symbionts, which reduces their ability to form new structures such as sporocarps (Högberg et al., 2001; Kuikka et al., 2003; Lamhamedi et al., 1994; Last et al., 1979). In addition, the chemical composition of soils can be altered by thinning, which can also influence sporocarp production (Colgan et al., 1999). Most of the sporocarps collected in our study were produced by mycorrhizal fungi, which suggests that these species play a key role as a carbon sink (Li et al., 2002). The loss of some parts of a plant or plant clones is known to stimulate in resprouter species, such as *Q. pyrenaica*, the movement of reserved fixed carbon, such as sugars, to areas that have suffered loss (Calvo et al., 2003). This stimulates tree regrowth; however, this means that less fixed carbon is allocated to the roots (Shaw et al., 2003) and, therefore, less carbon is available to the mycorrhiza associated with the roots (Egli et al., 2010; Godbold et al., 2015; Hacskaylo, 1983). Another explanation for higher sporocarp

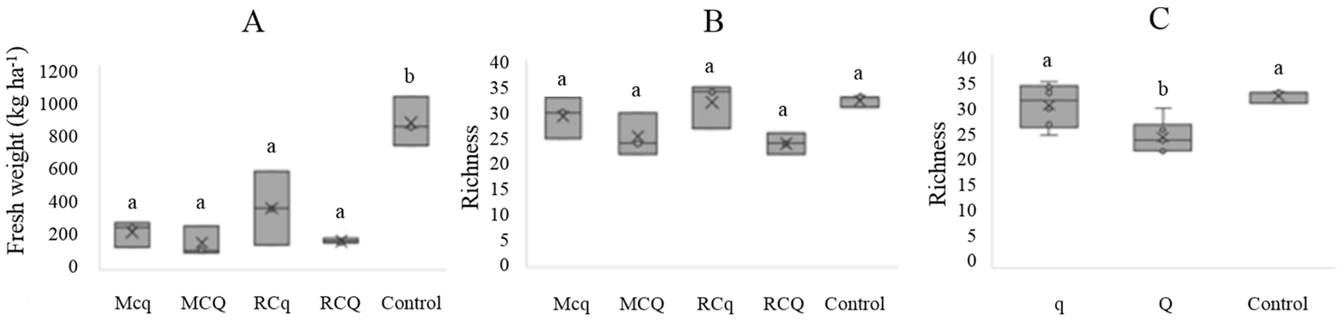

Fig. 1. (A) Effect of fuel reduction treatments on sporocarp total fresh weight production and (B) richness. (C) Effect of *Quercus* thinning intensity, i.e., high-intensity (Q) or moderate thinning (q), on fungal richness. Values with the same letter are not significantly different (Tukey test; $p \leq 0.05$). Fuel reduction treatments: Mcq, mature *Quercus* stands subjected to moderate thinning and partial clearing of *Cistus*; MCQ, mature *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; RCq, coppiced *Quercus* stands subjected to moderate thinning and total clearance of *Cistus*; RCQ, coppiced *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; Control, control plots. Fresh weight: in the total fresh weight collected during the study period.

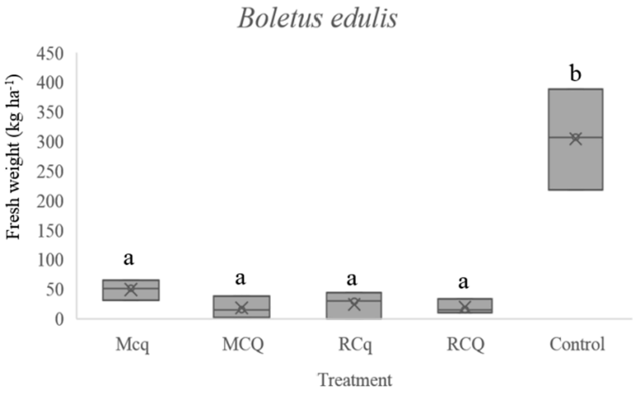

Fig. 2. Effect of fuel reduction treatments on the total fresh weight production of *Boletus edulis* sporocarps. Values with the same letter are not significantly different (Tukey test; $p < 0.05$). Fuel reduction treatments: Mcq, mature *Quercus* stands subjected to moderate thinning and partial clearing of *Cistus*; MCQ, mature *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; RCq, coppiced *Quercus* stands subjected to moderate thinning and total clearance of *Cistus*; RCQ, coppiced *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; Control, mature *Quercus* stands with an understory of *Cistus*. Fresh weight: in the total fresh weight collected during the study period.

production levels in control plots than in treatment plots could be that the tree canopy and shrub layer provide more cover than they do in treatment plots, creating greater protection from solar incidence and, hence, greater retention of soil moisture, which prevents the delay of fructification and the subsequent overlapping of the fructification with frozen seasons which inhibit or reduce the sporocarp production (Kropp and Albee, 1996; Maghnia et al., 2017; Pilz et al., 2006; Savoie and Largeteau, 2011; Tomao et al., 2020). Moreover, our study investigated the impact of applying silvicultural treatments to both trees and shrubs rather than to only one of the host species separately, which could influence more drastically the overall stand capacity of driving fixed photosynthetic carbon to their symbionts. Our results agreed with those observed by Pilz et al. (2006); however, they showed a different pattern to those presented by Hernández-Rodríguez et al. (2015), who investigated sporocarp production following fire-reduction treatments on *Cistus* at a study site like ours. They showed that lighter thinning treatments resulted in a less critical decrease in the fresh weight production of sporocarps while in our study the intensity degree was not a differentiating factor in terms of sporocarp production. Following this assumption, only the amount of fuel removed should prevail as a differential factor for applying any treatment (Moreno-Fernández et al., 2020).

Regarding fungal richness, in total, 111 fungal taxa were collected from the study area over a five-year sampling period. This level of fungal richness was much higher than the 21 taxa recorded in *Q. pyrenaica* plots over a single season by Oria-de-Rueda et al. (2010), and similar to the 157 taxa recorded by a similar study in the same region involving a monospecific stand of *C. ladanifer* that was sampled over a four-year period (Hernández-Rodríguez et al., 2015). The number of taxa recorded in this study, characterized by a low-nutrient soil, is comparable to the number obtained in other studies of different tree species and in more productive soils. For example, Gassibe et al. (2015) found 193 taxa in a *Pinus pinaster*-dominated forest, Egli et al. (2010) collected 191 taxa in an old-growth forest mixed with deciduous and coniferous trees and Martínez-Peña et al. (2012) collected 119 taxa during a ten-year study of a *Pinus sylvestris* stand. Variations in the species range observed each year due to different factors are normally seen, and changes in composition and sporocarp production in the years following a silvicultural treatment have been observed in other studies (Pilz et al., 2006). This study represents the wide systematic research providing noticeable contribution to the knowledge of fungal communities in the Mediterranean oak forests in Western Spain and their relationship with fire prevention. The work helps in broadening management objectives for NTFPs in the Mediterranean oak forests. However, the results should be regarded as a preliminary indication due to sampling limitations.

The fungal richness did not appear to have been critically influenced by these sylvicultural treatments when compared to the richness of the control plots. Similar findings have rarely been reported in similar studies (Castaño et al., 2018; Egli et al., 2010; Kranabetter and Kroeger, 2001). Thinning, clearing or any treatment that result in the loss of photosynthetic tree organs are considered to lead to a reduction in fungal richness (Hernández-Rodríguez et al., 2015; Kuikka et al., 2003; Luoma et al., 2004) but this was not what our results showed in a global overview (Fig. 1B), which is in contradiction with other studies (Buée et al., 2011; Colgan et al., 1999; Hernández-Rodríguez et al., 2015; Kropp and Albee, 1996). By contrast, just focusing on the trees treatment, the richness values of plots in which oak trees had been less intensively thinned were not significantly different to those of the control plots, as the ones with high intensity thinning were significantly less rich (Fig. 1E). Richness results seen in the literature show inconsistent conclusions (Egli, 2011); however, it is possible, that the reduced photosynthetic activity of hosts following high-intensity thinning just triggers a trade-off between mycelia and sporocarps, reducing the carbon allocation for fruiting and, hence, the appearance of differences in richness compared with control plots (Kuikka et al., 2003). A readjustment of host–symbiont associations following high-intensity thinning due to the decreased photosynthetic activity and redirection of carbon flow (Saikkonen et al., 1999) could create a competitive scenario between ECM species. In addition, it is important to consider that perturbations, particularly physical perturbations (Hernández-Rodríguez et al., 2017), can increase the growth of different specific taxa

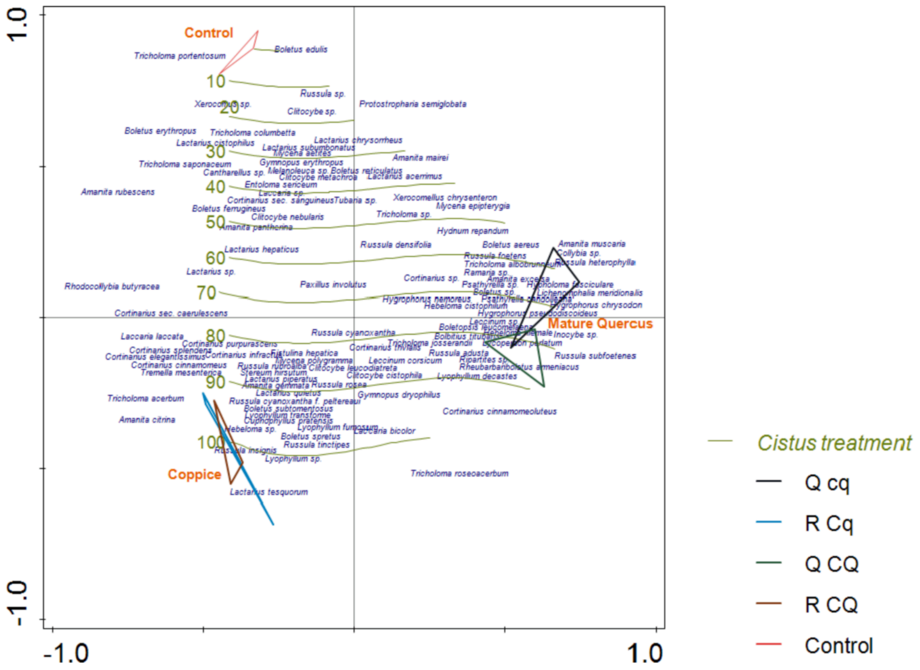

Fig. 3. Non-metric multidimensional scaling (NMDS) of fungal taxa produced following different fuel reduction treatments. Fuel reduction treatments: Mcq, mature *Quercus* stands subjected to moderate thinning and partial clearing of *Cistus*; MCQ, mature *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; RCq, coppiced *Quercus* stands subjected to moderate thinning and total clearance of *Cistus*; RCQ, coppiced *Quercus* stands subjected to high-intensity thinning and total clearance of *Cistus*; Control, mature *Quercus* stands with an understory of *Cistus*. A fitted Generalized Additive Model for the intensity of *Cistus* treatments was included.

(Kranabetter and Kroeger, 2001; Salerni et al., 2020; Savoie and Largeteau, 2011) and that bacterial renovations of the soil provide better conditions for some profitable edible taxa (Barbato et al., 2019; Mediavilla et al., 2019). Following our results, the intensity applied over the tree stands has an influence in the richness of fungi observed. So, in contrast to what was maintained regarding sporocarps production, the intensity degree may be evaluated and if the purpose is to maintain a richer fungal population, moderate intensity treatment over trees should be applied. Supporting this idea, fungal richness is an important issue because its influence on the conservation of mycophagous animals as well their predators (Luoma et al., 2004). The integration of an analysis of priority on fire prevention areas should be helpful to generate a geographical ordination of areas. High intensity treatments can be applied in highly flammable areas while neighborhood areas with less fire risk can be moderately treated to maintain more diversity (Alcasena et al., 2019). A mosaic landscape is a well-considered management by the local inhabitants, as provides a balance of ecosystem services such as multifunctionality, habitat diversity and ecological resilience and ecological connectivity among different succession stages (Martínez-Sastre et al., 2017). Also, the presence of non-thinned areas, as are the most productive stands, it is interesting in a socio-economical point of view due to the growing interest in mushroom picking. In regions as Castilla y León a 54 % of the population enjoy this activity, reaching 15.000 tons of marketable mushrooms production (García-Bustamante et al., 2021), which can be an economical source for rural areas in both direct or indirect way with permits sales or through mycotourism development (Martínez-Ibarra et al., 2019).

Saprophytic sporocarp production was, like mycorrhizal sporocarp production, much lower in plots subjected to fuel reduction treatments than in control plots. However, the sylvicultural treatments did not affect the richness of saprophytic fungi, probably because of their lack of dependence on hosts. In addition, mechanical treatments should not affect the chemistry of the substrate (Castaño et al., 2018) and, therefore, soil physical alterations are not a determinant factor that can be used to explain differences in sporocarp production between control and treated plots. These differences may are due to changes in the forest environment, soil moisture (Lin et al., 2015; Maghnia et al., 2017), and changes in the amount of biomass available for decomposition. This could be interestingly approached by the use of livestock for fire prevention, which appears to have more social approval (Martínez-Sastre et al, 2017). It has been seen that large landscapes with an intermediate human management as grazing creating new niches and microhabitat diversity (Blondel, 2006; García-Llorente et al., 2012) as can introduce nutrient input through dung benefiting specific guilds of decomposers fungi.

The type of stand is normally a determinant variable regarding production and richness (Bonet et al., 2004; Hernández-Rodríguez et al., 2015; Mediavilla et al., 2014, 2019; Savoie and Largeteau, 2011). However, our study showed that, in terms of stand type, i.e., mature or coppiced oaks, no differences were found between the treatments. Some studies have argued that sporocarp productivity and diversity does not rely on the original characteristics of the stand before treatment, such as stand age (Danell and Camacho, 1997), but on the carbon flux of photosynthates (Högberg et al., 2001; Lamhamedi et al., 1994; Yamada et al., 2001). Thus, the determinant factor for sporocarp production was probably an undisturbed photosynthetic rate, enabling fixed carbon to be allocated to the roots, meaning that the pre-existence of a coppiced forest or a mature forest is not as crucial as the treatment itself.

4.2. Effect of fuel reduction treatments on Boletus edulis

Boletus sporocarp production has been shown to decrease due to thinning treatments, with more intense thinning treatments causing proportionally larger decreases in sporocarp production. The highest levels of sporocarp production have been recorded in control old stands (Hernández-Rodríguez et al., 2015; Kropp and Albee, 1996; Ortega-Martínez et al., 2011; Salerni and Perini, 2004). This is understandable because *Boletus* species are strictly host-dependent ECM and late-stage fungi, so the elimination of the host means a reduction in *Boletus* sporocarp production (Mediavilla et al., 2017). Furthermore, *Cistus* shrubs can also develop a symbiotic relationship with *Boletus* (Águeda et al., 2008; Albuquerque-Martins et al., 2019; Comandini et al., 2006; Hernández-Rodríguez et al., 2015, 2017; Martín-Pinto et al., 2006; Mediavilla et al., 2017, 2019; Oria-de-Rueda et al., 2008) and the understory clearing can affect negatively due to its host dependance. The absence of phenoloxidases makes Boletales a group of strictly host-dependent mycorrhizal symbionts (Agerer, 2001). In addition, soil moisture and a punctual shock of low temperature are indispensable factors for sporocarp production (Savoie and Largeteau, 2011). In this regard, cover provided by the tree canopy and understory vegetation enables soil moisture to be maintained, which favors fructification, prevents solar incidence and permits colder areas (Mediavilla et al., 2019). Our results are in accordance with all those mentioned above; however, fructification was not significantly affected by the intensity of the thinning treatment. It is possible that there are other determinant influences derived from the interaction of tree–shrub management and the fungal community that have not already been considered. What is clear is that sporocarp production levels following moderate- or high-intensity clearing, and thinning treatments did not differ significantly in our study in short term, taking into account the fact that only one partial clearing have been applied. Based on this assumption more intensive thinning treatments seems to be a good management option in, to reduce the maximum amount of fuel biomass while, showing no differences in terms of *Boletus* production when comparing with lower intensity treatments.

4.3. Taxa composition

When the supply of fixed carbon to the roots is reduced by sylvicultural treatments, ECM fungi with lower demands for fixed carbon are favored (Colgan et al., 1999; Jones et al., 2003; Kuikka et al., 2003; Saikkonen et al., 1999). Furthermore, 'early-stage fungi' that form associations with trees during the early stages of succession are highly dependent on tree photosynthate, especially during fructification, while tree photosynthesis itself is dependent on the nutrients provided by ECM fungi (Nara et al., 2003). However, some ECM fungi are also able to obtain carbon from their surroundings by producing extracellular enzymes that breakdown organic matter (Agerer, 2001). This suggests that the different stages of fungal succession are driven mainly by the nutrient demand of fungi (Savoie and Largeteau, 2011). Our results support the idea that silvicultural treatments drive the development of the fungal community, particularly regarding ECM species which, indeed, make up the majority of the community. In our ordination analysis, the fungal population associated with control stands, which included *B. edulis*, was clearly distinguishable. The presence of *B. edulis* in control stands was expected because this species is only found in association with its host due to an inability to process lignin (Agerer, 2001) and because it is a 'late-stage species' that requires a longer time to establish a population before producing sporocarps than an early-stage fungus (Albuquerque-Martins et al., 2019). *Cistus* host many ECM fungi (Comandini et al., 2006) that act as early-stage fungi when associated with *Cistus* (Savoie and Largeteau, 2011). This explains the strong influence of shrub clearance on fungal composition meaning that many of the fungal species lost their specific host and leads to a higher competence among the remaining *Quercus* ECM taxa. In the case of *B. edulis*, because it acts as a late-stage fungus, but is a strict symbiont, a reduction in the density of its host should drastically decrease its capacity for fructification. The observed effect of stand type (i.e., mature or coppiced oak) and the similarity in the fungal composition of coppiced stands and control stands may be due to the composition of their soil bacterial communities, which are considered by some studies as more defining of the fungal community than vegetation (Barbato et al., 2019). Furthermore, it is possible that due to the presence of some coppiced areas in our control plots, combined with the effect of *Cistus* clearing, may have had an effect on the microbial population of the stands and in determining their fungal community (Mediavilla et al., 2019). The NMDS revealed that species considered as late-stage fungi, such as *Boletus*, *Xerocomus, Russula*, and *Lactarius* (Hernández-Rodríguez et al., 2015), clustered with controls stands even they are more associated with coppice stands. The NMDS suggests that cross-taxa congruence in compositions is due to complex interactions between biotic and environmental factors, such as the different interactions that fungi may have with *Quercus* or *Cistus*, or the influences that disturbances in one of these forest units could have over the other one.

5. Conclusions

After applying the different fuel reduction treatments, there was no significant difference in sporocarp fresh weight values among treatments, reducing all of them dramatically the sporocarp production. This means that higher intensities of thinning and clearing could result in the same level of sporocarp production as lower intensities but provide a better scenario in terms of fuel reduction and wildfire-prevention management. Furthermore, this could help the renovation of microbiological soil diversity because thinning and clearing treatments trigger the appearance of new heliophilous species or early-stage fungi with a high colonization capacity. In addition, fungal richness seems to be significantly affected by high-intensity thinning of *Quercus* and altering the density of *Cistus* seemed to have a drastic effect on the composition of the fungal community. Consideration of these factors from a socioeconomic point of view is also important. Maintaining as many commercial and edible species in forests as possible would have a positive effect on the rural economy and this would also have a positive an ecological impact by providing more food resources for all the mycophagous fauna associated with these forests. Considering the discussed results of this work, heavy intensity treatments are a proper option if the aims of the management is principally to reduce the risk of wildfire by removing biomass. As we could observe, in a productive way, none of the global treatments made a difference, reducing widely the sporocarp production. Although, if the purpose is to maintain a larger richness, moderate thinning should be a proper option in order of keeping a wider diversity by the time wildfire risk is reduced.

Finally, mosaic management could be an efficient method of managing areas like the one in this study. It would be helpful to restrain wildfire propagation by eliminating fuel biomass in some priority areas, with higher levels of fungal richness and variations in fungal community composition in other areas associated with more dense and mature vegetation. Senescent shrubs could also act as a source of propagules for adjacent areas. Risk priority analysis with local participation and different ways of fire prevention methods such as livestock grazing should be considered in the future in order to improve the ecosystem services balanced. This forest structure should mean that economic benefits for rural communities and biodiversity conservation can be combined with efficient management for wildfire prevention, always considering previous socioeconomical and environmental constraints. Exploiting new ways of economic income as permits commercialization or the development of a mycological touristic framework and services, apart of the commercialization of the mushrooms itself, may become an interesting economic improvement for rural areas. Furthermore, more analysis related to the trade-offs between extensive fire which should reduce drastically the mushroom production and the shifting mosaic management with short-term reduction associated in sporocarp production should be done.

CRediT authorship contribution statement

Ignacio Sanz-Benito: . **Olaya Mediavilla:** Methodology, Supervision. **Adriana Casas:** Investigation, Data curation. **Juan Andrés Oria-de-Rueda:** Supervision. **Pablo Martín-Pinto:** Conceptualization, Methodology, Investigation, Supervision, Formal analysis, Project administration.

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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