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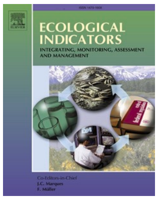

Mosaic forest management at landscape scale to enhance fungal diversity and production, in a context of forest fire-prevention in Mediterranean ecosystems

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ABSTRACT

Landscapes of oak (*Quercus*) forests alternated with extensive fields dominated by rockroses (*Cistus*) are widespread throughout the Mediterranean Basin. Due to the recurrency of fires and the mycological potential of both *Quercus* forests and *Cistus* fields, adequate management of this landscape is a key forest management objective. Although both *Quercus* and *Cistus* species are considered super-productive in terms of fungal production and diversity, fungal diversity and productivity vary depending on the stand age and structure. The aim of this study was to assess the complementary mycological potential of these ecosystems by studying sporocarp production, diversity, and community composition to elucidate management practices that would enhance fungal diversity and productivity within a fire management framework. We collected sporocarps over a period of four consecutive years (2012–2015) in young *Cistus* plots (1-m tall *Cistus*), old *Cistus* plots (2-m tall *Cistus*), and *Quercus* Forest plots. Our analyses showed that age as well as dominant vegetation influences sporocarp production, diversity, and richness, with young *Cistus* stands most suited to high levels of sporocarp productivity and diversity. In addition, a progressive restructuring of the fungal community was observed from a large, diverse community in *Cistus* early-stage stands to a smaller, less diverse but well-defined community in *Quercus* stands, transiting through an intermediate composition in old *Cistus* fields. Based on our findings, we suggest that a management process that not only favors stand rejuvenation would achieve greater sporocarp production and richness, including edible commercial species, while reducing the amount of fuel. In addition, the differentiated diversity of the *Quercus* stands plays an important role in terms of landscape diversity, being necessary the recommendation of a rejuvenation management in order to protect this stands associated diversity. We propose that these goals could be best achieved with a mosaic landscape model to connect the different stages of succession, enabling greater interconnectivity and, hence, allowing the presence of different "fungal stages" at the landscape level.

1. Introduction

Oak (*Quercus*) forests alternated with extended rockrose (*Cistus*) scrublands are the dominant landscape in Mediterranean ecosystems (Frazão et al., 2018). Both of these ecosystems are associated with high levels of mycological production and diversity (Moricca and Ragazzi, 2008; Richard et al., 2005, 2004; Saitta et al., 2018). The fungal communities associated with *Quercus* systems not only have a large taxonomic variability, but also a large functional variability due to the wide range of environmental conditions that can be found in these forests (Maghnia et al., 2017), or even due to their land-use history (Martín-Pinto et al., 2021; Orgiazzi et al., 2012). In addition, edible fungal sporocarps, both ectomycorrhizal and saprophytic, are harvested for recreational and commercial purposes in *Quercus* forests and *Cistus* scrublands, therefore these ecosystems are also an important economic resource (Górriz-Mifsud et al., 2017; Martínez de Aragón et al., 2011).

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Indeed, the economic value of many sporocarps in the Mediterranean region exceeds the market value of the timber, particularly in the case of mycorrhizal species (Herrero et al., 2019; Honrubia et al., 2008). Fifty-four percent of the population of Castilla y León collect edible mushrooms, with up to 15,000 tons of edible marketable mushrooms collected annually (García-Bustamante et al., 2021). According to Oria-de-Rueda et al. (2008), although *Cistus* fields have been traditionally considered as ecologically and economically unproductive, they can host a highly diverse fungal community, including highly sort after and marketable edible species (Comandini et al., 2006).

However, these systems are seriously threatened by potential wildfires owing to the presence of high fuel loads, the increasingly frequent extreme weather conditions, the flammability of *Cistus ladanifer* due to its aromatic compounds, and *Cistus* invading abandoned fields following depopulation of rural aeras (Hernández-Rodríguez et al., 2015; Keeley et al., 2011; Tárrega et al., 2009). This wildfire risk was exemplified during the summer of 2022, with more than 450,000 ha affected by wildfires in Spain, which was the largest area burnt in three decades. In the province of Zamora, where we conducted our study, more than 70,000 ha were affected by two mega-wildfires. The information reported by the satellite Copernicus showed that the Losacio mega-wildfire affected 36,000 ha—the largest fire reported in Spain in the 21st century (eldiario.es). The other mega-wildfire affected more than 30,000 ha, including a large area of the Sierra de la Culebra Natural Park, one of the most important ecological hotspots in the region (Muñoz et al., 2018). The affected areas were mainly dominated by *Quercus* forests and *Cistus* scrublands, and are the manifestation of how a fire-prone Mediterranean area (Keeley et al., 2011), unmanaged and encroached by scrubland (Rivest et al., 2011; Rolo and Moreno, 2012) can provide the conditions for this new phenomenon of a mega-fire (Stephens et al., 2014). In this context, forest management becomes a necessary but recurrent alteration in these Mediterranean landscapes in order to prevent deforestation and ecosystem loss due to wildfires. Nevertheless, some wildfire prevention treatments, such as removing the biomass susceptible to becoming fuel, have been reported to promote fungal diversity (Santana et al., 2018) and/or the fructification of some highly sort after fungal taxa (Hernández-Rodríguez et al., 2015; Mediavilla et al., 2019). More information about the optimal management of these ubiquitous landscapes is needed to determine how best to protect these productive and ecologically relevant areas (Fernandes, 2013).

Given that no landscape-level studies have been performed to evaluate the combined mycological potential of *Quercus*- and *Cistus*-dominated systems, it would be interesting to investigate how the fungal communities associated with these systems, particularly sporocarp productivity and diversity, are affected by stand age, forest structure, and hosting species (Bonet et al., 2004; Martín-Pinto et al., 2022; Saitta et al., 2018; Tomao et al., 2020). This would provide a scientific baseline to optimize the management of these widespread landscapes, already under wildfire prevention treatments, to foster mycological resources. Therefore, the overall aim of this study was to analyze the mycological production and diversity in landscapes dominated by a mosaic of *Quercus* and *Cistus* forests. In addition, we analyzed the effect of stand age on the fungal community. We expected that a stand with an age-related structure that provides suitable conditions for the fructification of fungi would have greater fungal richness and biodiversity values than stands that are less favorable for fructification. Most fungal species are associated with closed canopies where shade is maintained (Nordén et al., 2013; Senn-Irlet & Bieri, 1999). Factors that can affect the stand microclimate include vegetation and its openness (Pouska et al., 2016). Furthermore, comparisons of young and old *Picea abies* stands revealed that sporocarp production in young stands was nearly double that of older stands; however, sporocarp richness was higher in mature closed-canopy stands. As the stand develops, only those taxa that can adapt to the changing conditions of the stand are present (Greeshma et al., 2016). Species present at the primary succession stage have a lower specificity (Richard et al., 2009) and produce a greater amount of sporocarps than species present at later successional stages (Peay et al., 2011). Consequently, we expect fungal production to be greater and also more diverse at the early successional stages. To test these hypotheses, we analyzed the effect of stand age on the total macrofungal production and diversity associated with *Cistus* and *Quercus*, and the effect on ectomycorrhizal and saprophytic fungi. In addition, we analyzed the effect of host species (*Cistus* or *Quercus*) and the developmental stage of the stand (young *Cistus*, old *Cistus* and *Quercus*) on fungal communities. Given that shrubs are known to facilitate the recruitment of tree seedlings (Livne-Luzon et al., 2021) and are related to regressive and secondary succession stages (Simões et al., 2009), we hypothesized that a progressive restructuring of the fungal community would be found. Based on our findings, we conclude that forest management practices to create a mosaic landscape model would enhance fungal richness and communities diversity as well as forest succession, helping as well in reducing fuel biomass (Sanz-Benito et al., 2022).

2. Material and methods

2.1. Study site

The study was developed at the central-west part of Spain, in the province of Zamora. Frosts and snow are common during the winter, with temperatures ranging from −8 to 13 °C in winter. There is a dry season of at least two months in the summer, with most of the precipitation falling between October and February at all sampling sites. The mean annual precipitation is 464 mm and the mean annual temperature is 11.3 °C. Tertiary sands are the predominant soil type in this landscape. The study area comprised by: 1) high forest stands of *Quercus pyrenaica* (closed canopy timber wood), characterized as fuel model type 9 in Rothermel classification, with between 85 and 100% canopy cover that have received some silvicultural management in the past 15 years, 2) *Cistus ladanifer* fields with a dense, almost monospecific stand of rockroses covering 90–100% of these fields. The different stand ages within these fields can be distinguished based on the height of the plants: old *Cistus* stands are approximately 2 m in height, corresponding with the fuel model type 4 (35–40 t/ha) in Rothermel classification and young stands are between 0,6–1 m in height, corresponding with fuel model 6 (10–15 t/ha). Both with a high intensity fire propagation (Rothermel, 1972).

2.2. Sampling design, identification, and classification

Aleatory directions and distances were followed by a reference point in order to stablish randomly plots for every stand type in representative areas, establishing three plots per forest type, (except for *Cistus* young which included three more as this is more frequent found in the studied landscapes). Following Ohenoja and Koistinen (1984) sporocarps were collected every week all along the autumn mushroom season (from late October to late December) from 2012 until 2015. Once the sporocarps were harvested, they were taken to the laboratory and kept at 4 °C until the processing, identification within the next 24 h. Besides, fresh weight biomass (kg ha-1 was obtained). Identification was carried until species level whenever it was possible, grouping in genus taxa those which genus level was only achieved. The Index Fungorum database (https://www.indexfungorum.org) was used for this task. The trophic guild (saprotrophic or ectomycorrhizal) was identified based on Põlme et al. (2020) as edibility was stated consulting the work of Gassibe et al. (2015).

2.3. Data analysis

Total community, ectomycorrhizal and saprotrophic production, understood as mean annual sporocarp production, and richness were calculated for the three stand types. Linear mixed models (LME, $p \leq$

0.05) were used for studying the stand type effect over the mentioned variables through the Tukey's HSD test, using the "nlme" package (Pinheiro et al., 2007) in the R software environment (version 3.5.3; R Development Core Team 2019). A permutational multivariate ANOVA (PerMANOVA) based on 999 permutations was carried out in order to check the effects of the stand type over the fungal community using the adonis function found in the vegan package. Forest type influence over fungal composition was represented through a non-metric multidimensional scaling (NMDS) based on a Hellinger-transformed fungal matrix. Correlation between NMDS axes scores and the explanatory variables was evaluated through the envfit function in R software environment.

3. Results

3.1. *Effects on fungal production and richness*

During the four-year sampling period (from 2012 to 2015), 1867 sporocarps belonging to 163 different taxa were collected, 63.37% of which were ectomycorrhizal taxa and 36.63% were saprotrophic.

The total fresh weight of sporocarps collected was 990.17 kg ha^{-1}, with an average of 247.54 kg $ha^{-1}year^{-1}$. Sporocarp production was significantly higher in *Cistus* plots, particularly in young stands, which accounted for 62.88% of the total sporocarp production and 62.12% of the ectomycorrhizal and 74.14% of the saprotrophic taxa production. A Tukey test for total sporocarp fresh weight showed that *Quercus* and old *Cistus* stands did not differ significantly from each other ($p = 0.14$), whereas plots of young *Cistus* stands differed markedly from both of these stand types ($p < 0.05$) (Fig. 1A). Old *Cistus* plots accounted for only 14.35% of ectomycorrhizal taxa production and *Quercus* plots for 23.53%. The most significant difference in the production of ectomycorrhizal species was found between the young and old *Cistus* stands ($p < 0.01$), with a greater similitude of these young and old *Cistus* stands with those of *Quercus* ($p = 0.16$ and $p = 0.14$, respectively) (Fig. 1B). In the case of saprotrophic taxa, fresh weight production was also significantly higher in young *Cistus* plots than in *Quercus* plots, accounting for 74.12% of saprotrophic taxa production, compared with 5.52% in

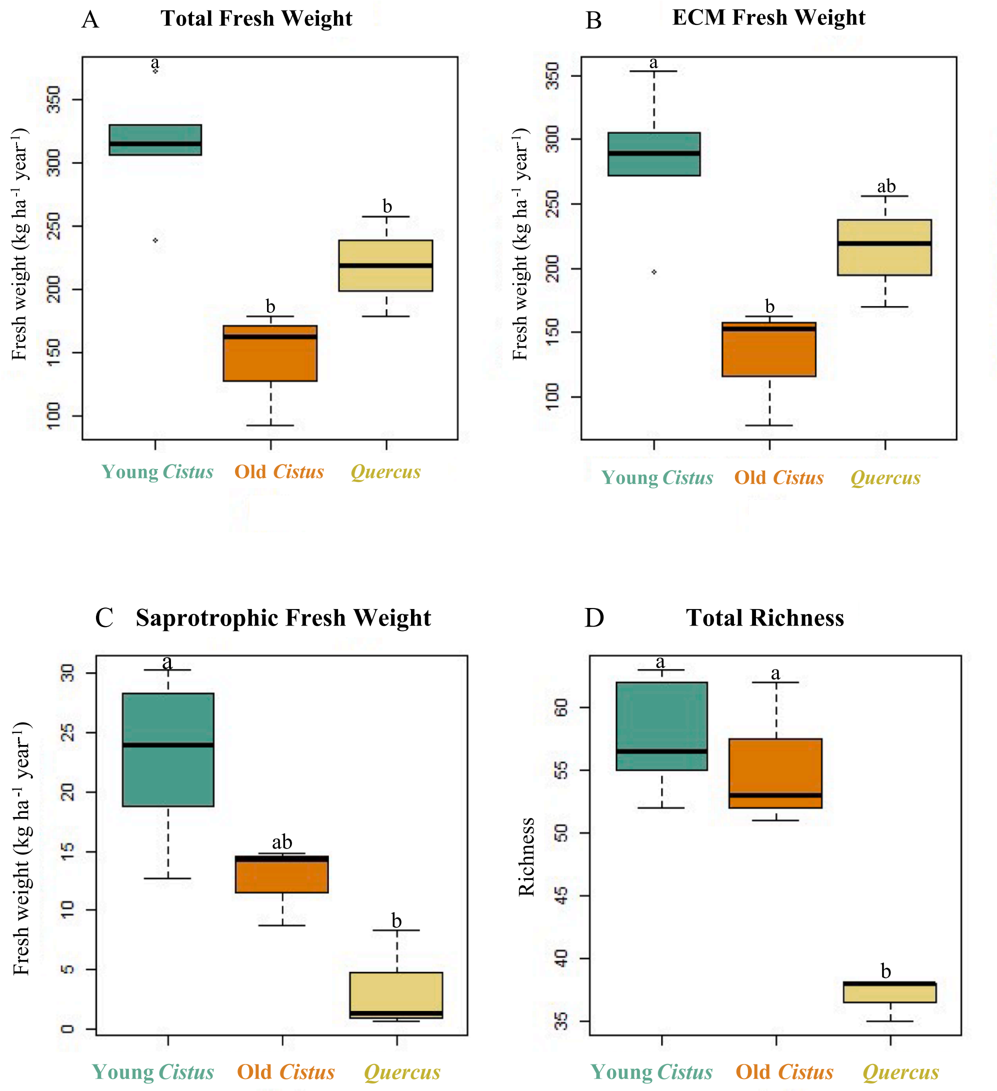

Fig. 1. Sporocarp production, richness, and diversity in young Cistus, old Cistus, and Quercus stands. Annual fresh weight production of: (A) total sporocarps; (B) ectomycorrhizal (ECM) fungal sporocarps; and (C) saprotrophic sporocarps. (D) Total richness. (E) Shannon Index for total sporocarp production. (F) Shannon Index for ectomycorrhizal sporocarp production. (G) Shannon Index for saprotrophic sporocarp production. Different letters above bars indicate a significant difference between stand types ($p > 0.05$).

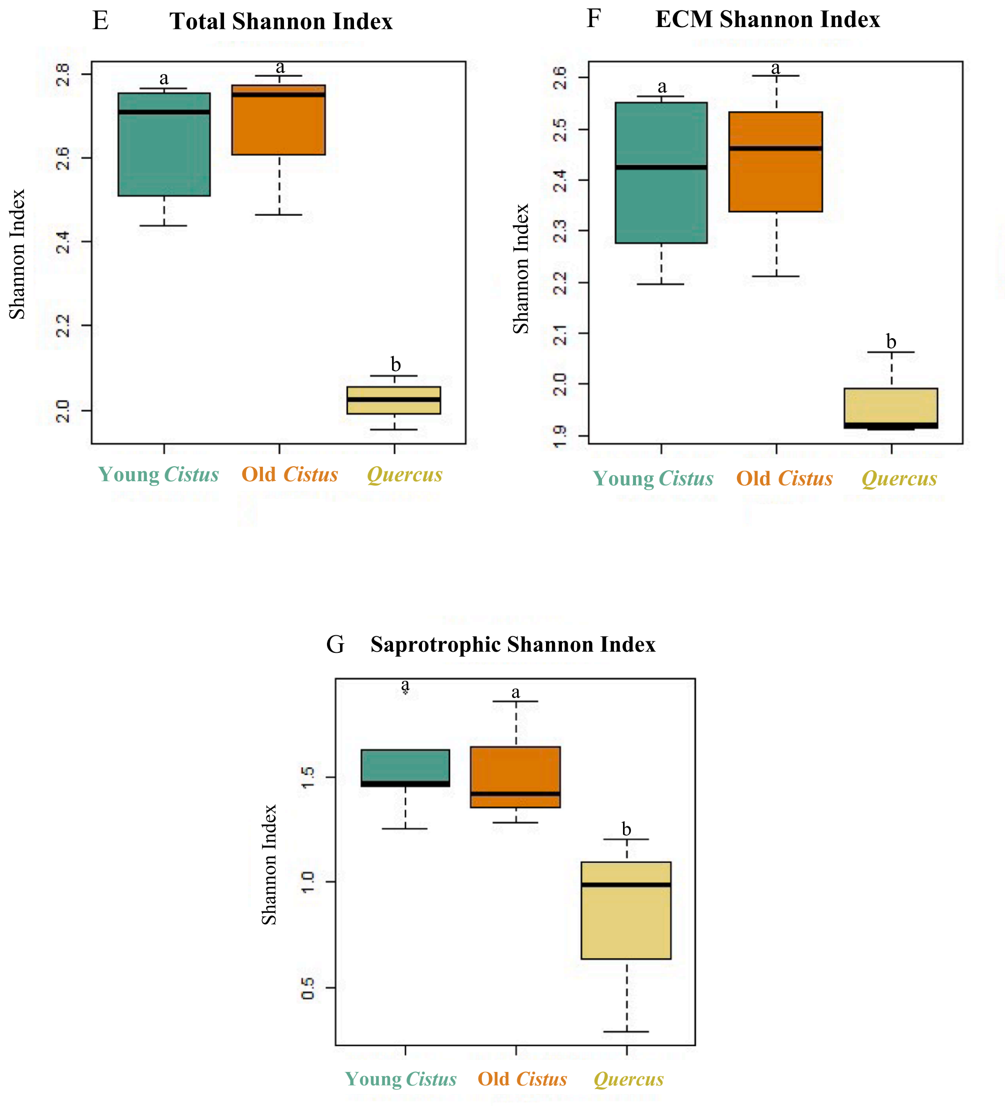

Fig. 1. (*continued*).

Quercus plots and 20.34% in old *Cistus* plots. Saprotrophic fresh weight production in old rockrose plots did not differ significantly from that of young rockrose or oak plots ($p = 0.15$) (Fig. 1C).

Total fungal richness was significantly higher in stands of young or old rockroses than in oak plots ($p < 0.01$; Fig. 1D). However, the Tukey test revealed that the fungal richness of young and old rockrose stands did not differ significantly ($p = 0.75$).

Shannon Index values for total fungal diversity and ectomycorrhizal fungal diversity in young and old *Cistus* plots showed a similar trend; however, the Shannon Index values for these plots were markedly different to those for *Quercus* plots ($p < 0.01$) (Fig. 1E,F). However, in the case of saprophytic fungal diversity (Fig. 1G), the Shannon Index values for young and old *Cistus* and *Quercus* did not differ significantly ($p = 0.06$).

3.2. *Influence of the host on the composition of fungal taxa*

A Non-metric Multidimensional Scaling (Fig. 2A) was carried out to observe the influence of the host on fungal community composition showed a weak stress of 0.087 and significant differences between both host species ($p = 0.01$). The β-dispersion showed a non-significative value (0.301) indicating a proper clustering of both groups. No overlap was observed between *Cistus* and *Quercus* fungal communities (Fig. 2A).

NMDS analysis depending on the plot type also showed a good stress (0.0878) and a non-significative β-dispersion (0.369), indicating again well-fitted clustering. Species composition of the fungal communities in young and old *Cistus* plots were similar (Fig. 2B), although the fungal community in old *Cistus* plots was closer to the composition present in the *Quercus* plots but did not overlap. This NMDS analysis of both host species and stand age revealed differences in the fungal communities present in *Cistus* of different stand ages ($p = 0.001$). Taxa found in each plot are shown in the Table 1.

4. Discussion

4.1. *Sporocarp production and richness*

Sporocarp production was higher in *Cistus* stands than in *Quercus* stands. Santos-Silva et al. (2011) observed that sporocarp production, particularly that of mycorrhizal species, is related to the proximity of tree canopies. Exposure to sunlight, which is related to the amount of

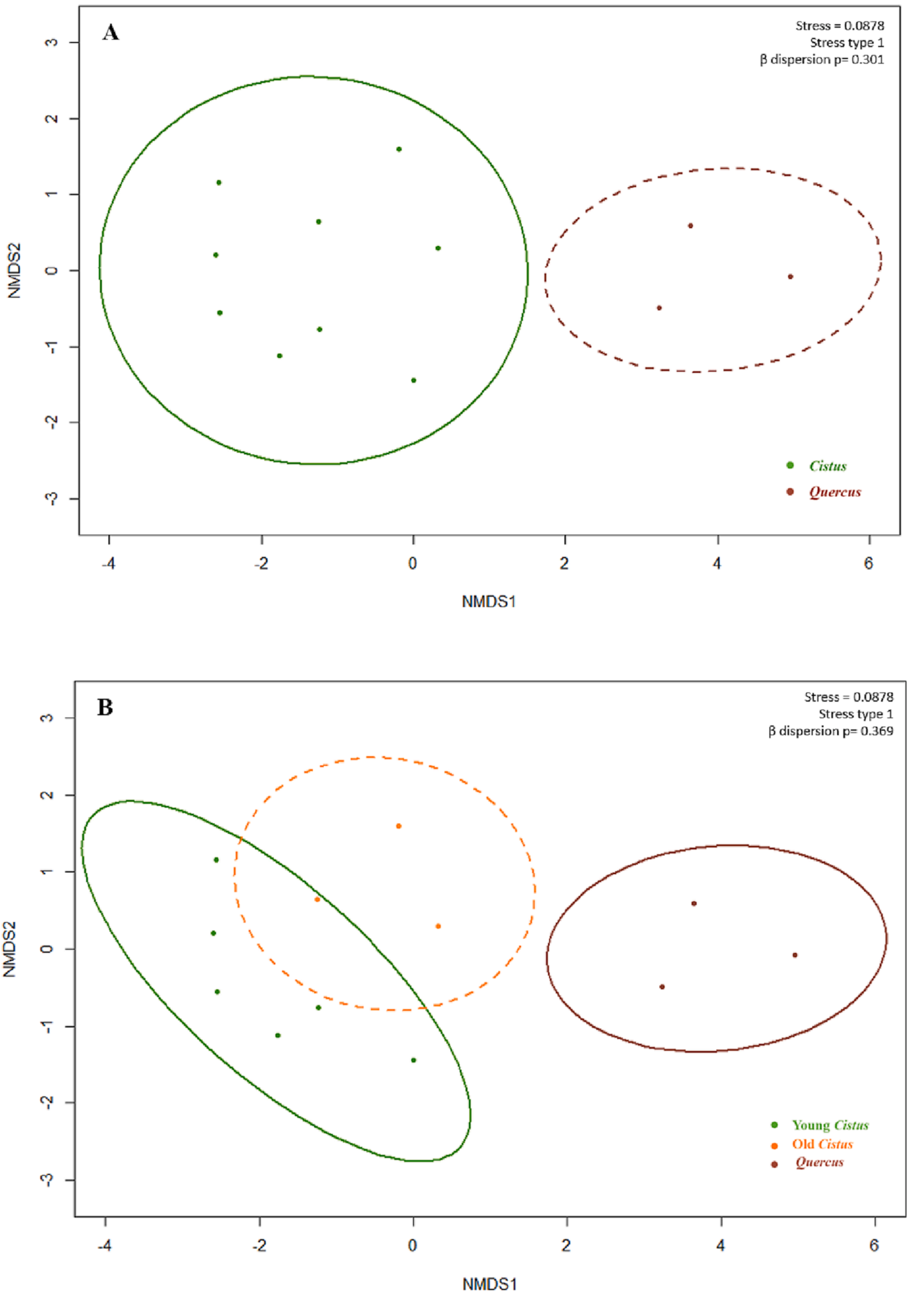

Fig. 2. Non-metric multidimensional scaling (NMDS) of sporocarp production depending on host type (A) and depending on plot type (B).

canopy cover, negatively affects fungal community development (Tomao et al., 2020). The amount of canopy influences temperature, temperature variations, and water availability (Chazdos & Fetcher, 1984). Soil temperature is an important limiting factor for fungal growth (Timling et al., 2012), and high rainfall is associated with a high level of biodiversity (Tedersoo et al., 2014). In young *Cistus* stands, the shrub layer is denser than in *Quercus* stands, and cover is closer to the ground, which allows less light at ground level, which makes the humidity and temperature conditions more suitable for fungal fructification (Egli et al., 2010). By contrast, more open canopies lead to alterations in the microclimate, such as increases in the surface temperature (Bässler et al., 2010), which significantly affect fungal fruiting (Krah et al., 2022).

The higher level of ectomycorrhizal fresh weight production in young *Cistus* stands than in the other stand types can be explained by the possible higher photosynthetic rate of these stands. This leads to an even greater growth of shrubs in young stands, with higher nutrient requirements, affecting in particular the ectomycorrhizal species with which they have a symbiotic relationship (Ortega-Martínez et al., 2011, Tahvanainen et al., 2016, Tomao et al., 2017). Trees require more nutrients when their growth rates are higher, so fungi could take advantage of this situation to obtain nutrients that they cannot obtain on their own (Ortega-Martínez et al., 2011). This dependence on photosynthesis is increased during the fruiting period (Nara et al., 2003). According to Waring (1987), the allocation of carbon follows a hierarchy, which means that when carbon has already been invested in the growth of photosynthetic organs, the remaining photosynthates are directed to stores in roots that are available to mycorrhizal fungi. A reduction or interruption in the flow of carbohydrates affects fungal fruiting, such as the removal of photosynthetic parts of the tree (Kropp and Albee, 1996; Ohenoja, 1988). In defoliation experiments, the number of sporocarps of ectomycorrhizal fungi produced in the vicinity of defoliated trees was

Table 1
Total taxa recorded in each plot type according to their trophic group: ECM, ectomycorrhizal; S, saprophytic; M, mycoparasitic; U, unknown. Plot type: C_y, *Cistus* young plots; C_o, *Cistus* old plots; Q, *Quercus* plots.

Taxa	Guild	Type plot		
		C_young	C_old	Q
Agaricus cupreobrunneus (Jul. Schäff. & Steer ex F.H. Møller) Pilát	S		x	
Agaricus silvicola (Vittad.) Peck	S		x	
Agaricus sylvaticus Schaeff.	S		x	
Agrocybe sp.	S		x	
Amanita cistetorum (Contu & Pacioni)	ECM	x		
Amanita citrina (Schaeff.) Pers.	ECM	x	x	x
Amanita excelsa (Fr.) Bertill.	ECM	x		x
Amanita fulva Fr.	ECM		x	
Amanita mairei Foley	ECM	x		
Amanita muscaria (L.) Lam.	ECM	x	x	x
Amanita muscaria var. *inzengae* (Neville & Poumarat)	ECM	x		
Amanita pantherina (DC.) Krombh.	ECM	x	x	x
Amanita rubescens Pers.	ECM	x	x	x
Amanita sp.	ECM		x	
Apioperdon pyriforme (Schaeff.) Vizzini	S	x		
Boletus aereus Bull.	ECM			x
Boletus edulis Bull.	ECM	x	x	x
Boletus reticulatus Schaeff.	ECM			x
Boletus sp. L., Fr.	ECM			x
Boletus spretus Bertéa	ECM			x
Calonarius elegantissimus (Rob. Henry) Niskanen & Liimat.	ECM	x	x	x
Candolleomyces candolleanus (Fr.) D. Wächt. & A. Melzer.	S	x	x	
Cantharellus cibarius (Fr.)	ECM	x	x	
Cantharellus pallens Pilát	ECM	x		
Cantharellus pruinosus Peck	ECM	x		
Chalciporus piperatus (Bull.) Bataille	M	x	x	
Clitocybe brumalis (Fr.) Quél.	S	x		
Clitocybe cistophila Bon & Contu	S	x	x	
Clitocybe diatreta (Fr.) P. Kumm.	S	x		
Clitocybe leucodiatreta Bon	S	x	x	x
Clitocybe metachroa (Fr.) P. Kumm.	S	x	x	
Clitocybe nivulosa (Pers.) P. Kumm.	S	x	x	
Clitocybe odora (Bull.) P. Kumm.	S		x	
Clitocybe sp. (Fr.) Staude	S	x	x	
Clitocybe vibecina (Fr.) Quél.	S	x	x	
Collybia sp. (Fr.) Staude	M	x		
Cortinarius assiduus Mahiques, A. Ortega & Bidaud, Bull.	ECM	x	x	
Cortinarius balteatocumatilis Rob. Henry ex P.D. Orton	ECM	x		
Cortinarius brunneus (Pers.) Fr.	ECM	x		
Cortinarius cinnamomeoluteus P.D. Orton	ECM	x	x	x
Cortinarius cinnamomeobadius Rob. Henry, Bull.	ECM	x	x	
Cortinarius cinnamomeus (L.) Gray	ECM	x	x	x
Cortinarius croceus (Schaeff.)Gray	ECM		x	
Cortinarius duracinus Fr.	ECM	x		
Cortinarius flexipes (Pers.) Fr.	ECM	x		
Cortinarius hepaticus Kytov., Niskanen & Liimat.	ECM		x	
Cortinarius saturninus (Fr.) Fr.	ECM	x		
Cortinarius scobinaceus Malençon & Bertault	ECM	x	x	
Cortinarius sec. *caerulescens* (Scheff.) Fr.	ECM	x	x	x
Cortinarius sec. *sanguinei*	ECM	x		x
Cortinarius sec. *telamonia*	ECM	x	x	
Cortinarius semisanguineus (Fr.) Gillet	ECM	x		
Cortinarius sp. (Pers.) Gray	ECM	x	x	x
Cortinarius trivialis J.E. Lange	ECM			x
Cortinarius venetus (Fr.) Fr.	ECM	x		
Cortinarius xerophilus Rob. Henry & Contu	ECM	x	x	
Craterellus cornucopioides (L. Pers.	ECM		x	
Cystoderma cinnabarina (Alb. & Schwein.) Harmaja	S		x	
Cystoderma sp.	S		x	
Cystoderma terrei (Berk. & Broome) Harmaja	S	x		
Entoloma cistophilum Trimbach	S	x		
Entoloma hebes (Romagn.) Trimbach	S	x	x	
Entoloma hirtipes (Schumach.) M.M. Moser	S	x	x	
Entoloma sericeum Quél.	S	x	x	
Entoloma sp.	S	x	x	
Fistulina hepatica (Schaeff.) With.	S			x
Flammulaster carpophilus (Fr.) Earle ex Vellinga	S		x	
Galerina sp.	U	x	x	
Galerina uncialis (Britzelm.) Kühner	S	x		
Gymnopus dryophilus (Bull.) Murrill.	M	x	x	x
Gymnopus ocior (Pers.) Antonín & Noordel.	S	x		
Hebeloma cistophilum Maire	S	x	x	x
Hebeloma hiemale Bres.	ECM	x	x	
Hebeloma mesophaeum (Pers.) Quél.	ECM	x		
Hebeloma sp.	ECM	x	x	x
Hydnum repandum L.	ECM			x
Hygrocybe pratensis (Pers.) Murrill	S			x
Hygrophorus chrysodon (Batsch) Fr.	ECM	x	x	
Hygrophorus pseudodiscoideus (Maire) Malençon & Bertault	ECM	x	x	x
Hygrophorus roseodiscoideus Bon & Chevassut	ECM	x		
Hypholoma fasciculare (Huds.) P. Kumm.	ECM	x	x	x
Inocybe geophylla P. Kumm.	ECM	x		
Inocybe geophylla var. *lilacina* (Peck) Gillet	ECM	x		
Inocybe grammata Quél.	ECM		x	
Inocybe sp.	ECM	x	x	x
Inosperma maculatum (Boud.) Matheny & Esteve-Rav.	ECM	x		
Laccaria bicolor (Maire) P.D. Orton	ECM	x	x	x
Laccaria laccata (Scop.) Cooke	ECM	x	x	x
Laccaria sp.	ECM			x
Lacrymaria lacrymabunda (Bull.) Pat.	S	x		
Lactarius aurantiacus (Pers.) Gray	ECM	x		
Lactarius chrysorrheus Fr.	ECM	x	x	x
Lactarius cistophilus Bon & Trimbach	ECM	x	x	x
Lactarius hepaticus Plowr.	ECM		x	x
Lactarius sanguifluus (Paulet) Fr.	ECM			x
Lactarius subumbonatus Lindgr.	ECM			x
Lactarius tesquorum Malençon	ECM	x	x	x
Leccinellum corsicum (Rolland) Bresinsky & Manfr. Binder.	ECM	x	x	
Leccinellum lepidum (H. Bouchet ex Essette) Bresinsky & Manfr. Binder.	ECM	x		
Leccinum sp.	ECM			x
Lentinellus micheneri (Berk. & M.A. Curtis) Pegler.	S	x		
Lepista nuda (Bull.) Cooke	S	x		
Lycoperdon molle Pers.	S	x		
Lycoperdon perlatum Pers.	S	x	x	
Lyophyllum decastes (Fr.) Singer	ECM	x		x
Lyophyllum infumatum (Bres.) Kühner	ECM	x	x	
Lyophyllum loricatum (Fr.) Kühner	ECM			x
Lyophyllum semitale (Fr.) Kühner	ECM	x		x
Lyophyllum sp.	ECM	x	x	x
Macrolepiota excoriata (Schaeff.) Wasser	S	x		
Macrolepiota mastoidea (Fr.) Singer	S	x		
Macrolepiota procera (Scop.) Singer	S	x		
Mycena aetites (Fr.) Quél.	S	x	x	
Mycena arcangeliana Bres.	S	x		
Mycena cinerella (P. Karst.) P. Karst.	S	x		
Mycena clavicularis (Fr.) Gillet	S	x		
Mycena epipterygia (Scop.) Gray	S	x	x	x
Mycena leptocephala (Pers.) Gillet	S	x		
Mycena maculata P. Karst.	S			x
Mycena polygramma (Bull.) Gray	S			x
Mycena pura (Pers.) P. Kumm.	S	x	x	
Mycena sp.	S	x	x	x
Neoboletus luridiformis (Rostk.) Gelardi, Simonini & Vizzini	ECM		x	x
Omphalina sp.	S	x	x	
Paxillus involutus (Batsch) Fr.	ECM	x	x	x
Phlegmacium balteatum (Fr.) A. Blytt.	ECM	x		
Phaeomarasmius erinaceus (Fr.) Scherff.	S		x	
Phloeomana minutula (Sacc.) Redhead.	S	x		
Pluteus sp.	S	x		
Protostropharia semiglobata (Batsch) Redhead, Moncalvo & Vilgalys.	S	x		
Psathyrella sp.	S	x	x	

(*continued on next page*)

Table 1 (*continued*)

Taxa	Guild	Type plot		
		C_young	C_old	Q
Ramaria sp.	ECM	x	x	
Rhodocollybia butyracea (Bull.) Lennox	S	x	x	x
Rhodocybe truncata (Schaeff.) Singer	S	x	x	
Ripartites sp.	S			x
Ripartites tricholoma (Alb. & Schwein.) P. Karst.	S	x	x	
Russula adusta (Pers.) Fr.	ECM			x
Russula aeruginea Lindblad ex Fr.	ECM		x	
Russula cistoadelpha M.M. Moser & Trimbach	ECM		x	
Russula cyanoxantha (Scheffer.) Fr.	ECM			x
Russula insignis Quél.	ECM			x
Russula rosea Pers.	ECM			x
Russula rubroalba (Singer) Romagn.	ECM	x		x
Russula sp.	ECM	x	x	x
Russula subfoetens W.G. Sm.	ECM			x
Russula tinctipes J. Blum ex Bon	ECM			x
Russula vesca Fr.	ECM		x	
Stereum hirsutum (Willd.) Pers.	S	x	x	
Thelephora terrestris Ehrh. Ex Fr.	U		x	
Tricholoma acerbum (Bull.) Quél.	ECM			x
Tricholoma albobrunneum (Pers.) P. Kumm.	ECM	x	x	
Tricholoma cinnamomeoluteus	ECM		x	
Tricholoma equestre (L.) P. Kumm.	ECM	x	x	
Tricholoma portentosum (Fr.) Quél.	ECM	x		x
Tricholoma saponaceum (Fr.) P. Kumm.	ECM	x	x	x
Tricholoma sp. (Fr.) Staude	ECM	x		
Tricholoma terreum (Schaeff.) P. Kumm.	ECM	x		
Tricholoma ustale (Fr.) P. Kumm.	ECM	x		
Tricholomella constricta (Fr.) Zerova ex Kalamees.	ECM	x		
Tubaria sp.	S	x	x	
Xerocomellus chrysenteron (Bull.) Šutara..	ECM			x
Xerocomus ferrugineus (Schaeff.) Alessio	ECM			x
Xerocomus sp.	ECM			x

only a third of that produced in the vicinity of control trees (Kuikka et al., 2003). The lower levels of sporocarp biomass produced in old *Cistus* and *Quercus* stands compared with young *Cistus* stands may also be related to the photosynthetic rate. At more advanced stages of development, growth patterns are modified and become slower, so the amount of carbohydrates in the roots available to the ectomycorrhizal fungi decreases (Tomao et al., 2020). Ortega-Martínez et al. (2011) studied the influence of stand age on sporocarp formation by two ectomycorrhizal species: the fresh weight production of both species was up to 50% higher in young *Pinus sylvestris* stands than in old stands, demonstrating that ectomycorrhizal fungi are able to obtain greater quantities of carbohydrates from the roots of young host plants. The biomass of ectomycorrhizal sporocarps is known to be highly correlated with the starch concentration in fine roots (Kuikka et al., 2003).

The fresh weight production of sporocarps of saprophytic fungi was also significantly higher in young rockrose stands than in old *Cistus* and *Quercus* stands. Egli et al. (2010) reported that the growth rate of young stands is higher than that of older stands, resulting in the formation of greater quantities of litter biomass, which favors the appearance of saprophytic fungi. The decrease in productivity in oak stands may be because there is less litter biomass available to saprophytic fungi. Oaks have marcescent leaves that do not fall to the ground until the new leaves come out, which decreases the amount of nutrients available to saprophytic fungi in the fall. Leaf litter is one of the main sources of nutrients in forest soils (Hobbie, 2015) because it is one of the principal providers of potassium, calcium, and magnesium (Bani et al., 2018). The quality of the leaf litter greatly influences its decomposition rate, with higher quality litter (i.e., litter with a high nitrogen content and low levels of lignin, phenols, and tannins) decomposing faster than lower quality litter (Lin et al., 2019; Vivanco and Austin 2008). In general, leaves of broadleaf species have higher concentrations of nutrients and lower concentrations of lignin and polyphenols compared with coniferous litter (Manzoni et al., 2010) and, hence, degrade more rapidly (Lladó et al., 2017). However, the nutrients of *Quercus* leaves may be degraded during the marcescence period and, therefore, when the leaves finally fall to the ground, they may have lost most of their nutrients.

In terms of richness, the number of fungal taxa associated with young and old *Cistus* stands was much higher than in *Quercus* stands. Hernández-Rodríguez et al. (2013) previously observed that the richness found in young and old plots of *Cistus* was similar to or higher than that found in mature stands of other forest species. The young *Cistus* stands observed in this study were pioneer vegetation that originated after a disturbance. New species of ectomycorrhizal fungi can colonize new areas after a disturbance occurs because competition is reduced (Buscardo et al., 2010). At the early stages of succession after a disturbance, the fungal community that develops will be formed by those propagules that have survived and by propagules that reach the site (Kipfer et al., 2011), thereby increasing the richness present in these stands. The ectomycorrhizal associations formed at this stage have low specificity (Richard et al. 2009). During the development of plant species, there is a succession of associated fungi (Gassibe et al., 2011). The maintenance of areas with an advanced stage of stand succession areas favors species that are only adapted to these stages (Hernández-Rodríguez et al., 2015). According to Salo et al. (2019), numerous fungal species appear immediately after a disturbance such as a fire and then disappear in the following years.

Management of these shrublands to improve fungal richness and diversity should also benefit the richness and diversity of other species associated with them, such as mycophagous fauna (Fogel and Trappe, 1978; Hernández-Rodríguez et al., 2013). Even though total sporocarp and ectomycorrhizal sporocarp production levels were lower in old *Cistus* stands than in young *Cistus* stands, richness levels were high. However, rejuvenating senescent shrub stands not only results in higher mushroom production but also reduces the risk of fire (Hernández-Rodríguez et al., 2013). For example, Zamora-Martínez and Nieto de Pascual (1995) observed productions of *Lactarius deliciosus* from open canopy conditions in a mature stand of 25.9 kg ha^{-1}. By modifying the structure of mature stands to simulate young stand conditions, new species can proliferate (Bonet et al., 2004). Medium-intensity harvesting has been shown to favor mushroom production (Tomao et al., 2017). For example, Salerni and Perini (2004) observed that by removing approximately 20% of the basal area of the stand, the production of *Boletus edulis* sporocarps was considerably increased. Likewise, higher sporocarp fructification levels were achieved in *C. ladanifer* scrublands with 80% canopy cover than with full canopy cover (Hernández-Rodríguez et al., 2013). A mosaic landscape management approach promotes ecosystem multifunctionality, habitat diversity, resilience and supports connectivity along the different stages of succession (Martínez-Sastre et al., 2017). Applying this structure could provide economic benefits for rural societies while conserving biodiversity, combined with efficient management for fire prevention, while also considering socioeconomic and environmental limitations (Sanz-Benito et al., 2022). Management aimed at greater fungal production and diversity should be carried out using techniques that have a minimal impact on the ecosystem and that have a positive effect on the production of economically valuable edible fungi (Bonet et al., 2012). Maintaining conditions such as vegetation cover or the availability of woody debris, for example, allows mycorrhizal and saprophytic species to be sustained in the presence of disturbances (Tomao et al., 2020).

4.2. *Taxa composition*

Cistus plots showed a differentiated fungal community assemblage than *Quercus* stands, which highlights the influence of this dominant vegetation species (Redondo et al., 2020). This could be explained as the influence of the host genotype on the fungal symbionts; however, given that *Cistus* and *Quercus* share a wide range of symbionts between them, environmental filtering linked to the site conditions (Comandini et al., 2006; Pérez-Izquierdo et al., 2017; Toju et al., 2013) may explain the more diverse fungal community found in the *Cistus* stands. Furthermore, the dense vegetation cover close to the soil in young *Cistus* stands protects the soil, promoting humidity conservation, which fosters sporocarp development by saprotrophic fungi (Mediavilla et al., 2021). There is also a huge amount of nutrient-rich organic matter coming from fallen *Cistus* leaves and flowers each year (Frazão et al., 2018; Gallego et al., 2020) that likely favors the fructification of different saprotrophic species in these stands. However, it is necessary to take into account that the number of *Cistus* plots was larger than the *Quercus* ones due to the sum of those with different age types. At landscape level, *Cistus* scrublands present a wider heterogeneity in terms of structure being necessary for us include this age-related differentiation. Nevertheless, this contingency amplified the community presented by *Cistus*, but still the clustering is quite strong as we can note through the stress and β-diversity.

The NMDS analyses showed that the fungal community present in the old *Cistus* plots was closer to that found in the *Quercus* plots, maybe because *C. ladanifer* could act as a bridge species (Milne, 2002; Martín-Pinto et al., 2006) in the succession to *Quercus* for those fungal species that can establish relationships with both hosts. The fungal composition varies depending on the needs of these fungi as fungal succession is mainly conditioned by their nutrient requirements (Savoie and Largeteau, 2011). In young *Cistus* stands there might be a greater number of fungal species than in old *Cistus* stands because of the greater nutrient availability and organic matter content or because the fungal species have higher nutritional needs. Zhang et al. (2018) showed that the amount of carbon, potassium, or phosphorus available has a strong influence on fungal composition, demonstrating the importance of nutrients in shaping fungal communities. As the age of the stand increases, the fungal community stabilizes, with those species that are able to adapt to the new conditions remaining and new species appearing as the conditions that they require develop. In the succession to mature stands, the supply of carbohydrates provided by the host is a decisive factor for mycorrhizal fungi (Dighton and Mason, 1985). For certain mycorrhizal species, for instance, it is easier to colonize a new host once it has become established on another host tree (Hagerman et al., 1999). Moreover, Cistus is characterized as a more generalist host, which implies a wider community than the observed in Quercus, being a more specific mycorrhizal host with a fewer species composition but more characterized (Comandini et al., 2006). It is a remarkable that the weak stress values and the β-dispersion, both indicators of clustering and dissimilarities, showed that the groups were quite well fitted with low variance inside of them, both at species level and at plot type level. These meant, despite the lower richness, that *Quercus* diversity display a relevant role in the overall diversity of the landscape as in the successional process.

In a forest succession, early colonizing plants facilitate the establishment of vegetation at more advanced stages of development by modifying the environment (Butterfield et al., 2010). Plants regulate fungal community diversity and structure through their supply of carbon given that richness and diversity are related to root nutrient contents (Johnson et al., 2005), particularly the concentrations of glucose and fructose, as well as the amount of starch available in fine roots (Pena et al., 2010). Variations in plant carbon production affect soil properties (Giesler, et al., 2007; Högberg et al., 2007), which affect the fungal community, which in turn can also lead to changes in soil composition (Pena et al., 2010). These changes in soil chemistry may influence fungal diversity throughout the succession (Zhang et al., 2018). As a result of the early colonizers, the environment changes, leading to secondary succession, which leads to changes in the microclimate, including an increase in soil infiltration (Lasanta et al., 2000) or mineral enrichment that increases the nutrient concentration of the soil (Maltez-Mouro et al., 2005). Shrublands become fertility islands (Pajunen et al., 2012), resulting in the modification of microenvironmental conditions (Gómez-Aparicio et al. 2005). Specifically, Ibáñez (2001) demonstrated that *Cytisus scoparius* and *Genista florida* improve soil fertility and moisture conditions. All this favors the advance of succession toward the establishment of *Quercus* (Alday et al., 2016). Furthermore, it has been seen that the Cistaceous species *Helianthemum bicknellii* can facilitate the ectomycorrhizal infection of *Quercus* (Dickie et al., 2004), added to which, *Quercus* seedlings are more likely to establish in areas shaded by an understory (Ritsche et al., 2021). All these factors point to a progressive restructuring of the fungal community associated with each successional stage, where intermediate scenarios, in this case, old *Cistus* stands, show a transitional fungal identity. Therefore, maintaining patches of different successional stages could help to drive fungal community development, maintaining ecological landscape connectivity and resilience (Martínez-Sastre et al., 2017; Ritsche et al., 2021) thanks to the retention effect performed by older stands (Koivula and Vanha-Majamaa, 2020) and the provision of niches in younger stands (Martínez-Sastre et al., 2017).

5. Conclusions

According to the results, in a landscape composed of young and old *Cistus* shrublands and *Quercus* forests, sporocarp production and richness is higher in young *Cistus* stands than in the other stands. Suggesting that productivity and richness are influenced by stand age, due to the higher photosynthetic rate and lack of competition that allows more fungi species to establish until the community stabilizes. These leads to a more characterized and proper fungal community in *Quercus* stand, with some transfer of taxa from early to late stages, generating a more diverse landscape system in terms of forest structure and fungal communities, having an important role regarding gamma diversity at landscape level. Forest management that facilitates the rejuvenation of stands, while maintaining mature areas, would increase fungal richness and production, including those edible species that can have a positive impact on local economies. Promoting a mosaic landscape would achieve successional connectivity, favoring biodiversity and fire prevention by reducing the amount of fuel, and would increase the socio-economic benefits of rural economies.

CRediT authorship contribution statement

Alba Magarzo: Writing – original draft. **Ignacio Sanz-Benito:** Supervision, Writing – review & editing. **Olaya Mediavilla:** Data curation, Investigation, Writing – review & editing. **María Hernández-Rodríguez:** Data curation, Formal analysis, Investigation, Methodology. **Juan Andrés Oria-de-Rueda:** Conceptualization, Supervision. **Tatek Dejene:** Formal analysis, Supervision, Writing – review & editing. **Pablo Martín-Pinto:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

No data was used for the research described in the article.

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