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(DATAFOREST)

Mosaic forest management at landscape scale enhance fungal diversity and production reducing the risk of large wildfires in Mediterranean ecosystems

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RESUMEN

Los bosques mediterráneos de roble (*Quercus*) alternados con matorrales de *Cistus* suponen uno de los ecosistemas más extendidos en la región mediterránea. Ambas especies presentan una gran producción y diversidad fúngica, que varían tanto en función de la edad de la masa como de su estructura. En estos ecosistemas se dan especies de hongos de alto valor que suponen una fuente de ingresos muy importante en la economía rural. A pesar de la importancia tanto ecológica como económica que estos ecosistemas pueden llegar a tener, están gravemente amenazados por los incendios forestales debido a la inflamabilidad de *Cistus ladanifer* y a la gran acumulación de matorral, como consecuencia de la despoblación rural. Este incremento del combustible disponible, unido a unas condiciones climáticas cada vez más extremas, favorece la existencia de incendios forestales de gran intensidad que afectan cada vez a más superficie. Debido al alto riesgo de incendios y al gran potencial micológico de ambas especies, una adecuada gestión de este paisaje es fundamental. Por todo ello, el objetivo de este estudio fue evaluar el potencial micológico de estos ecosistemas estudiando la producción, la diversidad y la composición de la comunidad fúngica con el fin de poder determinar las prácticas de gestión más adecuadas para fomentar la producción y diversidad fúngica, reduciendo simultáneamente el riesgo de incendios. Se recogieron esporocarpos durante cuatro años consecutivos (2012 – 2015) en parcelas de *Cistus* joven (1 m de altura), *Cistus* envejecido (2 m de altura) y en parcelas de *Quercus*. El análisis mostró que tanto la edad de la masa como la vegetación dominante en la parcela influye en la producción, diversidad y riqueza de esporocarpos, siendo las parcelas de *Cistus* joven las que mostraron una mayor producción. La diversidad fue significativamente superior en *Cistus*. Asimismo, se observaron diferencias en términos de la composición fúngica, que evolucionó desde una comunidad amplia y diversa en los rodales de *Cistus* en su fase inicial hasta una comunidad más reducida y menos diversa en los rodales de *Quercus*. Los rodales de *Cistus* de mayor edad mostraron una composición fúngica intermedia demostrando una transición entre ambas especies. En base a estos resultados, se sugiere que un manejo que propicie el rejuvenecimiento de la masa, pero que también mantenga ciertas áreas de vegetación senescente, daría lugar a una mayor producción y riqueza de esporocarpos, incluyendo especies de alto valor gastronómico, a la vez que se reduce la cantidad de combustible y con ello, el riesgo de ocurrencia de grandes incendios. Uno de los métodos a través de los que se puede conseguir es a partir de la aplicación de un modelo de mosaico a escala paisaje que permita que los diferentes estados de sucesión estén interconectados entre sí y con ello, una mayor diversidad de coberturas y de las diferentes comunidades fúngicas que ello conlleva.

Palabras clave: Cobertura vegetal, *Cistus ladanifer*, *Quercus*, paisaje, esporocarpos, sucesión vegetal.

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ABSTRACT

Mediterranean oak (*Quercus*) forests alternating with *Cistus* scrub are one of the most widespread ecosystems in the Mediterranean region. Both species have a high fungal production and diversity, both depending on the age of the stand and its structure. In these ecosystems there are species of fungi of high value that represent a very important source of income in the rural economy. Despite the ecological and economic importance of these ecosystems, they are severely threatened by forest fires due to the flammability of *Cistus ladanifer* and the large accumulation of shrubs as a result of rural depopulation. This increase in available fuel, together with increasingly extreme climatic conditions, favors the existence of high intensity forest fires that affect a larger area. Due to the high risk of fire and the great mycological potential of both species, a proper management of this landscape is essential. Therefore, the objective of this study was to evaluate the mycological potential of these ecosystems by studying the production, diversity and composition of the fungal community in order to determine the most appropriate management practices to promote fungal production and diversity, simultaneously reducing the risk of fire. Sporocarps were collected during four consecutive years (2012 - 2015) in plots of young *Cistus* (1 m tall), old *Cistus* (2 m tall) and *Quercus* plots. The analysis showed that both stand age and dominant vegetation in the plot influenced sporocarp production, diversity and richness, with young *Cistus* plots showing higher production. Diversity was significantly higher in *Cistus.* Differences were also observed in terms of fungal composition, which evolved from a large and diverse community in young *Cistus* stands to a smaller and less diverse community in *Quercus* stands. In older *Cistus* stands, the fungal composition was intermediate, demonstrating a transition between the two species. Based on these results, it is suggested that a management that favors the rejuvenation of the stand, but also maintains certain areas of senescent vegetation, would result in a greater production and richness of sporocarps, including species of high gastronomic value, while reducing the amount of fuel and thus, the risk of occurrence of large fires. One of the methods through which this can be achieved is through the application of a landscape-scale mosaic model that allows the different stages of succession to be interconnected with each other and thus a greater diversity of cover and the different fungal communities that this involves.

Keywords: Canopy cover, *Cistus ladanifer*, *Quercus*, landscape, sporocarps, forest succession.

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1. INTRODUCTION

1.1. Mycology in *Cistus* and *Quercus* ecosystems

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 & Ragazzi, 2008; Richard et al., 2004; 2005; Saitta et al., 2018). Macrofungal communities are essential and provide multiple services in forest ecosystems (Collado et al., 2021) as ectomycorrhizal and saprophytic fungi play a fundamental role in nutrient cycling (Cairney & Meharg, 2002). 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). 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 (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 demanded and marketable edible species (Comandini et al., 2006).

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). More open or closed canopy is also related to the age of the stand as well as to the silvicultural treatments that have been given (Bonet et al., 2004; Senn-Irlet & Bieri, 1999). Older shrublands generally have a more erratic and open canopy as a result of branch senescence, as observed by Cruz-Alonso et al. (2020), this openness promotes extreme temperatures and radiation (De Frenne et al., 2019; Kermavnar et al., 2020). A closer canopy buffers the extremes (De Frenne et al., 2019; Thom et al., 2020) creating better conditions for fungi. Senn-Irlet & Bieri, (1999) comparing young and old *Picea abies* stands found out 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).

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). In

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the absence of fire, these ecosystems dominated by *Cistus* shrublands are progressively occupied by other species of the genus *Quercus* (Hernández-Rodríguez et al., 2013) to a more advanced stage of succession. Thus, mycorrhizal species can infect tree roots from the shrub (Martín-Pinto et al., 2022). It is expected that throughout the succession the species will change until they stabilize in more advanced stages of development, changes in the forest stand and its vitality over time causes changes in the fungal community (Ágreda et al., 2014; Fernández-Toirán et al., 2006).

1.2. Wildfires

Wildfires are common ecological perturbations in forests, shrublands and grasslands around the world (Krawchuk et al., 2009). In particular, fire in the Mediterranean region has played an important role in shaping the landscape and determining ecosystems and species distribution, considered to be one of the most fire-prone regions worldwide (Naveh, 1975, 1989; Xofis et al., 2020). This susceptibility to fire has been one of the major forces of selection on Mediterranean vegetation, with many species adapted to recurrent fires to ensure their permanence (Naveh, 1975). The main causes of fire recurrence in the Mediterranean area are the high flammability of vegetation and long, hot and dry summers (Keeley et al., 2011; Rundel et al., 2018). Specifically in the study ecosystem, the flammability of *Cistus ladanifer* due to its aromatic compounds, and the invasion of *Cistus* in abandoned fields resulting from the depopulation of rural areas (Hernández-Rodríguez et al., 2015), are included among the main factors.

It is a ubiquitous element of the Mediterranean ecosystem to which it is highly resilient (Calvo et al., 2008). The problem is that due to the combination of climate change, land use and cover change and forest management policies, the size and severity of fires is expected to continue to increase in the future (González-De Vega et al., 2016). In part of the Mediterranean, the frequency of fires has doubled in relation to the 20th century, increasing the area burned by an order of magnitude (Pausas & Fernández-Muñoz, 2012). This was evidenced during the summer of 2022, with more than 450,000 ha affected by forest fires in Spain, which was the largest area burned in three decades. In the province of Zamora, where this study was conducted, more than 70,000 ha were affected by two mega-fires. Information provided by the Copernicus satellite showed that the Losacio mega-fire affected 31,473 ha, the largest fire recorded in Spain in the 21st century. The other mega-wildfire affected more than 30,000 ha, including a large area of the Sierra de la Culebra Natural Park, which is part of the Meseta Ibérica biosphere reserve, declared in 2015 by UNESCO. Forty-eight percent of this area burned during the two wildfires. The increase in these extreme events may exceed the resilience of vegetation (Williams et al., 2011) and thus alter its ability to recover (Viana-Soto et al., 2017). The impact of increased fire frequency on Mediterranean ecosystems is an aspect that requires further research given the increasing fire danger caused by climate change and land use abandonment (Hinojosa et al., 2021).

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1.3. Fire prevention forest management and mycological harvesting

Forest management is necessary to prevent such situations and their resulting costs, preventing the massive destruction of valuable ecosystems. The study ecosystem, dominated by *Quercus* and *Cistus*, is subject to a high frequency of fires that affect the plant and fungal communities it supports (Hernández-Rodríguez et al., 2013). Some studies are focused on assessing the effects of silvicultural practices on fungal yields. Among them, Blaser et al. (2013) compared managed and unmanaged forests in central Europe, finding a higher richness of wood saprotrophs in managed forests. Similarly, in the case of mycorrhizal fungi, Egli et al. (2010) found a higher proportion of mycorrhizal fungi in forests that had been managed for more than ten years than in those that had been managed for less than ten years. Therefore, the application of appropriate forest management that favors fuel reduction can also favor fungal richness and production, including the fructification of some highly valued fungal taxa (Hernández-Rodríguez et al., 2015; Mediavilla et al., 2019). Beneath future climate change scenarios and related changes in fire event occurrence, adaptive and sustainable forest management strategies are needed to prevent fire recurrence and reset historical fire intervals of ecosystems (Francos et al., 2020), while also implementing effective mycoselviculture to promote edible mushroom production in forests (Tomao et al., 2017). 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 to reduce the wildfire risk and to foster mycological resources.

The starting hypothesis of this study is that favoring a landscape that enforces the rejuvenation of the stand breaking the fuel continuity together with areas that are left in a state of senescence, fungi diversity will increase as the presence of vegetation in different stages of development which are associated with different fungal species of important ecological and commercial value is promoted.

2. OBJECTIVES

The aim of this work is to analyze the effect of stand age on the fungal community, both in terms of production and diversity in ecosystems dominated by *Quercus* and *Cistus*, as well as the effect it has specifically on mycorrhizal and saprophytic fungi.

For this purpose, the specific objectives of this work are stated as follows:

1) To analyze the production of sporocarps in fresh weight.
2) To analyze fungal species richness.
3) To analyze fungal species diversity.

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4) To analyze the effect of host species (*Cistus* or *Quercus*) and the stand age (young *Cistus*, old *Cistus* and *Quercus*) on fungal communities.

3. MATERIAL AND METHODS

3.1. Study site

The study area is located in the municipality of Rabanales, in the rural area of Aliste, Zamora province, in the central-western part of Spain, 750–780 m above sea level. The area is composed of high forest stands of *Quercus pyrenaica* with a canopy cover between 85 and 100% that has had some type of silvicultural treatment in the last 15 years. On the other hand, *Cistus ladanifer* stands are dense and practically monospecific, with a vegetation cover between 90 and 100%. The age of these stands can be determined based on the height of the plants themselves: the oldest *Cistus* stands are approximately 2 meters high and the youngest *Cistus* stands are 1 meter high.
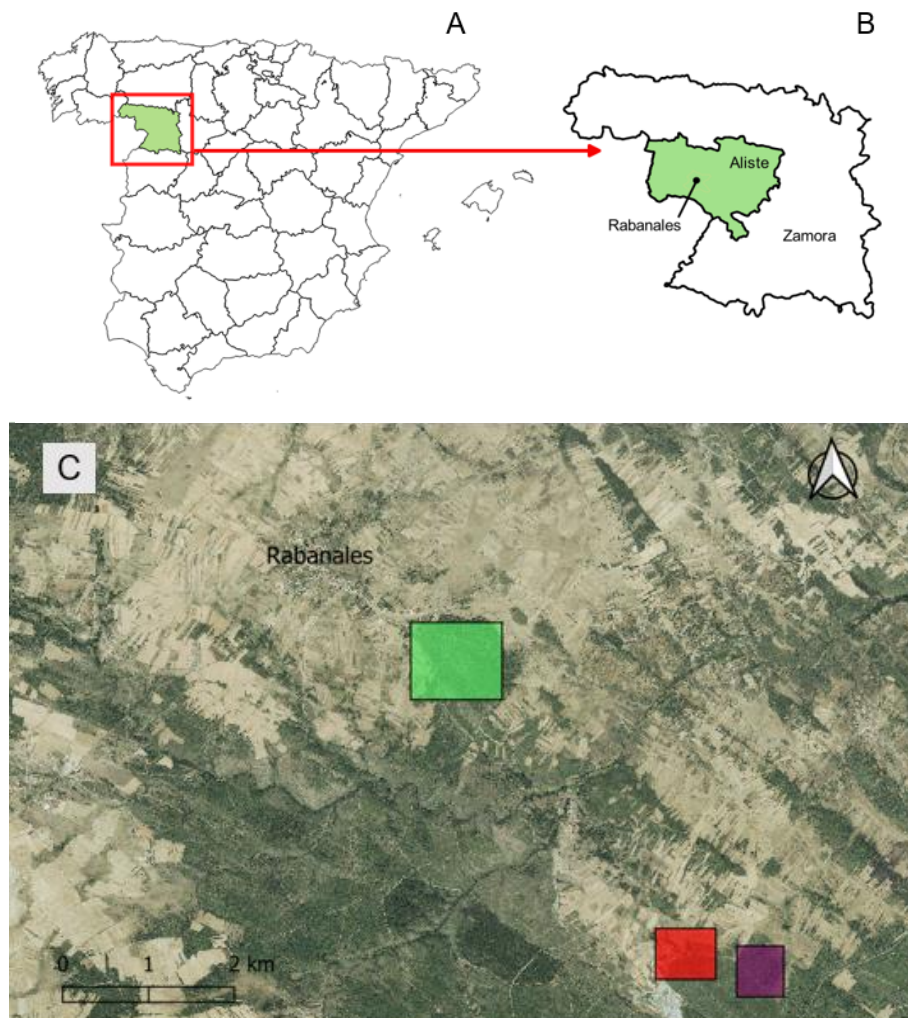

Figure 1. *Location of the study area in the national (A), provincial (B) and within the municipality of Rabanales (C). The sampling plots within the municipality of Rabanales (C), in green the Quercus plots, in red the old Cistus plots and in purple the young Cistus plots. Image source C: PNOA maximum actuality.*

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Regarding the climatology of the study area, climatic data have been extracted from the Spanish Meteorological Agency (AEMET) from the station located in Villardeciervos (Zamora), number 2775X. This municipality that lies 22.09 km away from the study area, at an altitude of 850 m. It is the closest complete station to the study area, as well as being located at the same altitude and with the same orientation with respect to the main mountain peaks. Average annual precipitation was 651.3 mm during the years in which the study was conducted. In 2012, annual rainfall was 463.6 mm, while the other three years presented a higher level of rainfall, 713.9 mm, 897.1 mm and 530.7 mm, respectively. Mean annual temperature was 11.4 ºC, ranging from 11ºC in 2012 to 11.8ºC in 2015. Frost and snowfall are common during the winter months. There is a dry season in summer, with the highest concentration of precipitation between October and April in all sampling areas.

Table 1. *Monthly mean maximum (T), monthly mean (tm), monthly mean minimum (t) temperatures, all expressed in ºC and monthly mean precipitation (P), in mm, in the study area during the sampling years (2012-2015). Data obtained from the AEMET station located in Villardeciervos.*

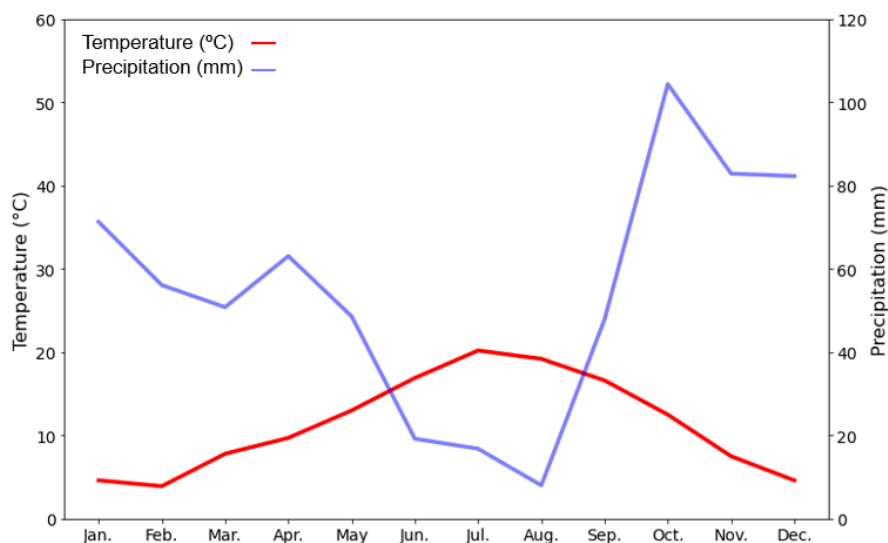|	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
T [ºC]	10,3	10,8	15,3	16,5	21,3	25,9	30,3	29,2	25,5	18,7	12,9	9,7
Tm[ºC]	4,6	3,9	7,8	9,7	13,0	16,9	20,2	19,2	16,6	12,5	7,5	4,6
T [ºC]	-1,3	-3,0	0,3	3,0	4,7	7,8	10,1	9,3	7,8	6,2	2,0	-0,6
P [mm]	71,3	56,1	50,8	63,1	48,6	19,2	16,8	8,0	47,9	104,4	82,9	82,3

Figure 2. *Ombrothermal diagram for the study area during the sampling years (2012-2015). (Own elaboration based on AEMET data).*

According to Köppen's Climate Classification (ITACyL, 2023), the climate classification of the area is Csb (Oceanic dry summer). Where:

- Group 'C': Temperate climate.
- Sub-group 's': Dry summer.
- Sub-division 'b': Warm summer.

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In terms of geology, Paleozoic metamorphic rocks, mainly Ordovician and Silurian shales (García Rodríguez et al., 1964) are present in this landscape. The soil in this area has been classified as Inceptisol suborder Xerept (Soil Survey Staff, 2010), characterized by its stoniness, acidity (pH 5.0 - 5.5) and the absence of calcium and phosphorus. Nitrogen and potassium availability is fluctuating, and the level of humidification is broadly good (García Rodríguez et al., 1964).

3.2. Description of vegetation in sampling areas

As mentioned above, the study area is composed of forests dominated by *Quercus pyrenaica* and *Cistus ladanifer*, being the main vegetation species of this study. These spaces have been widely used previously as an experimental area to test the effects of different fuel reduction treatments on fungal communities (Hernández-Rodríguez et al., 2013, 2015, 2017; Mediavilla et al., 2019).

Quercus plots are located within the Public Utility Mount No. 32 called "La Majadona", on the east side of the urban center of Rabanales. The exact location of the plots, in UTM coordinates is: UTM zone 29, X coordinate 728125 X and Y coordinate 4623486 (Fig.3). They have a southwest orientation and are located at an altitude of approximately 850 meters above sea level. The oak forest in this space was in latizal age, combined with a *Cistus ladanifer* undergrowth. In these stands, silvicultural treatments have been performed on the mass, such as intensive or moderate intensity thinning and total or partial clearing of the *Cistus* understory.
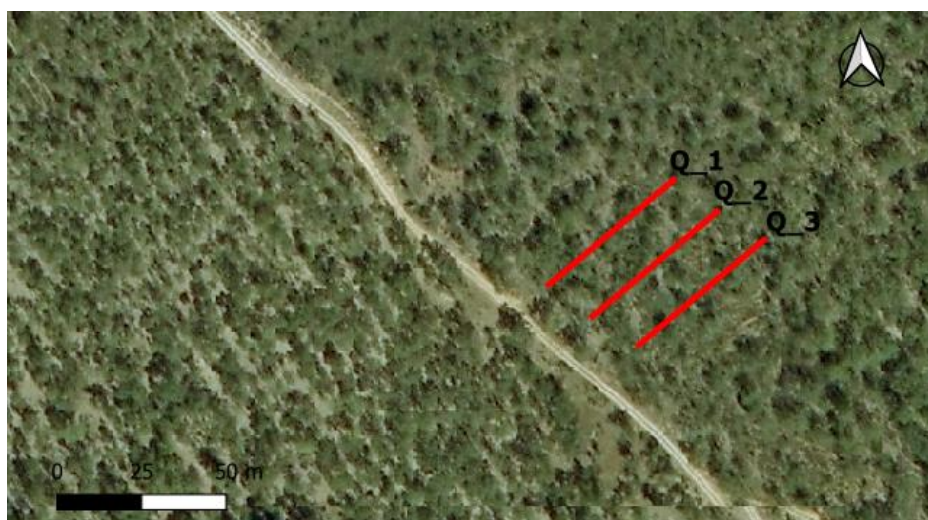

Figure 3. *Quercus sampling plots (named Q_1, Q_2 and Q_3). Image source: PNOA.*

In 2003, the *Cistus* plots were randomly selected in order to study the effect of fire on fungal succession, since the origin of all these plots was a fire, after which the characteristics of the stands in younger and more advanced stages of succession were similar (Hernández-Rodríguez et al., 2013). The average life span of this species is between 15 and 20 years (Oria-de-Rueda et al., 2008) and plots of advanced successional stage begin to be considered mature when they are very dense and the

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shrub is approximately 2 meters high (Hernández-Rodríguez et al., 2013). As mentioned above, the height of the scrub in the early-stage *Cistus* plots will be 1 meter in height and at a similar density. Over the years, these plots have been subjected to silvicultural treatments such as total or moderated clearing. The location of young *Cistus* plots is: UTM zone 29, X coordinate 731604 and Y coordinate 4619852 (Fig 4). Its orientation is northeast, and they are placed at an altitude of approximately 830 meters above the sea. Lastly, old *Cistus* plots are located in: UTM zone 29, X coordinate 730980 and Y coordinate 4619963 (Fig 5), with a northeast orientation and at an altitude above the sea of 840 metres.
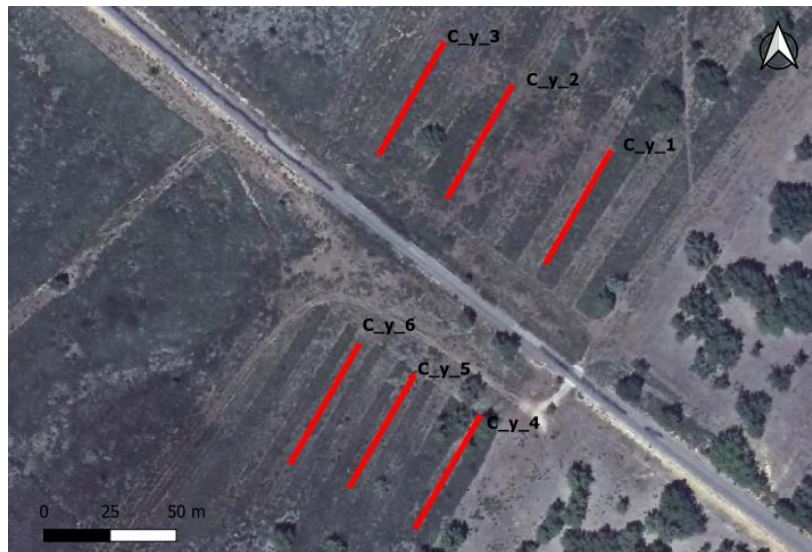

Figure 4. *Young Cistus sampling plots (named C_y_1, C_y_2, C_y_3, C_y_4, C_y_5 and C_y_6. Image source: PNOA.*

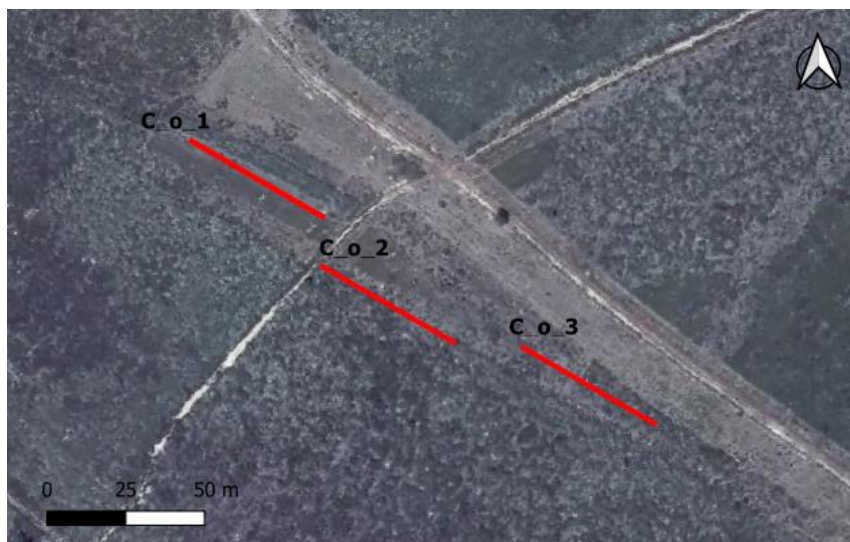**Figure 5.** *Old Cistus sampling plots (named C_o_1, C_o_2 and C_o_3. Image source: PNOA.*

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3.3. Sampling design, identification and classification

2 m x 50 m plots were stablished for sampling, in accordance with previous studies (Dahlberg & Stenlid, 1994; Smith et al., 2002). These plots were randomly located, using aleatory direction and distance from a reference point from representative areas in each stand type: young *Cistus*, old *Cistus* and *Quercus*. Considering the average period of fruiting bodies changes between species from 4 to 20 days (Vogt et al., 1992), finding a sampling frequency that would suit all species and not mislead the production values can be a challenge. Weekly sampling frequency has been used by several authors in prior research (Ohenoja & Koistinen, 1984). Sporocarps were collected weekly during the fall mushroom season from late October to late December during four consecutive years, from 2012 to 2015.

After the sporocarps were picked up, they were transferred to the laboratory where they were stored at 4ºC until they were properly processed and identified within the following 24 hours. Sporocarps fresh weight (kg·ha^{-1}) was also noted. Sporocarps were identified down to species level when it was possible for further statistical analysis as in other reference studies (Agerer, 2006; Tedersoo et al., 2010; Trudell et al., 2004). Sporocarps that could only be identified down to genus level were grouped into genus taxa. After sporocarps were identified, they were dried in vented hot air ovens at 35°C, once dried they were stored and used to complete the identification where necessary through microscopic key characters (Hernández-Rodríguez et al., 2015).

Fungal taxa names and authors were obtained from the Index Fungorum database (www.indexfungorum.org). Taxa were also classified according to their trophic group (saprotrophic or ectomycorrhizal) based on Põlme et al. (2020). Species traditionally consumed in the study region and those classified as edible in most of the consulted literature were listed as edible (Gassibe et al., 2015; Hernández-Rodríguez et al., 2015; Martínez de Aragón et al., 2007). Edible mushrooms with low culinary interest, given their low relevance for harvesting and possible commercialization, were classified as inedible.

3.4. Data analysis

Prior to data analysis, after the sporocarps identification process, they were classified into different categories: according to their guild in ectomycorrhizal (ECM) and saprophytic (S) and, according to their edibility in edible (E) or inedible (IE). Sporocarp production values (as mean annual fresh weight), diversity and richness were calculated for the whole fungal community and for the ectomycorrhizal and saprophytic communities (ECM/S) of each stand type.

In order to analyze the diversity in the fungal community, the Shannon Diversity Index (H') (Shannon & Weaver, 1949) was used, based on the fresh weight of the sporocarps and the total number of sporocarps. This variable was calculated from the formula below in which the coefficient pi indicates the proportion of total biomass of each fungal species:

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$$H' = -\sum pi(\ln pi)$$

Species richness, meanwhile, is defined as the total number of taxa found in each sampling year (Straatsma & Krisai-Greilhuber, 2003) in the different stand types (young *Cistus*, old *Cistus* and *Quercus*).

The effect of each stand type on production, diversity and richness values was studied using linear mixed-effects models (LME, p ≤ 0.05), which were performed using the Nlme package (Pinheiro et al., 2007) and applying Tukey's HSD test. These statistical analyses were performed in the R software environment (version 3.5.3; R Core Team, 2019). The relationship between fungal composition and the forest type was visualized using non-metric multidimensional scaling (NMDS) based on a Hellinger-transformed fungal matrix. The effects of forest types were analyzed using a permutational multivariate ANOVA (PerMANOVA) based on 999 permutations using the *adonis* function in the vegan package. The correlation between NMDS axes scores and explanatory variables was assessed using the *envfit* function in R.

4. RESULTS

4.1. General data

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. Although, most of the sporocarps were identified down to species level, it was not possible for some of them.

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. Old *Cistus* plots accounted for only 14.35% of ectomycorrhizal taxa production and *Quercus* plots for 23.53%. In the case of saprotrophic taxa, fresh weight production was also significantly higher in young *Cistus* compared with 5.52% in *Quercus* plots and 20.34% in old *Cistus* plots.

The species collected include 45 edible species, some with high gastronomic value, including: *Boletus edulis*, *Cantharellus cibarius*, *Macrolepiota procera* and *Lepista nuda*, among them. Some of these species occur in all three stand types (young *Cistus*, old *Cistus* and *Quercus*).

The taxa found in each plot are shown in Annex 1.
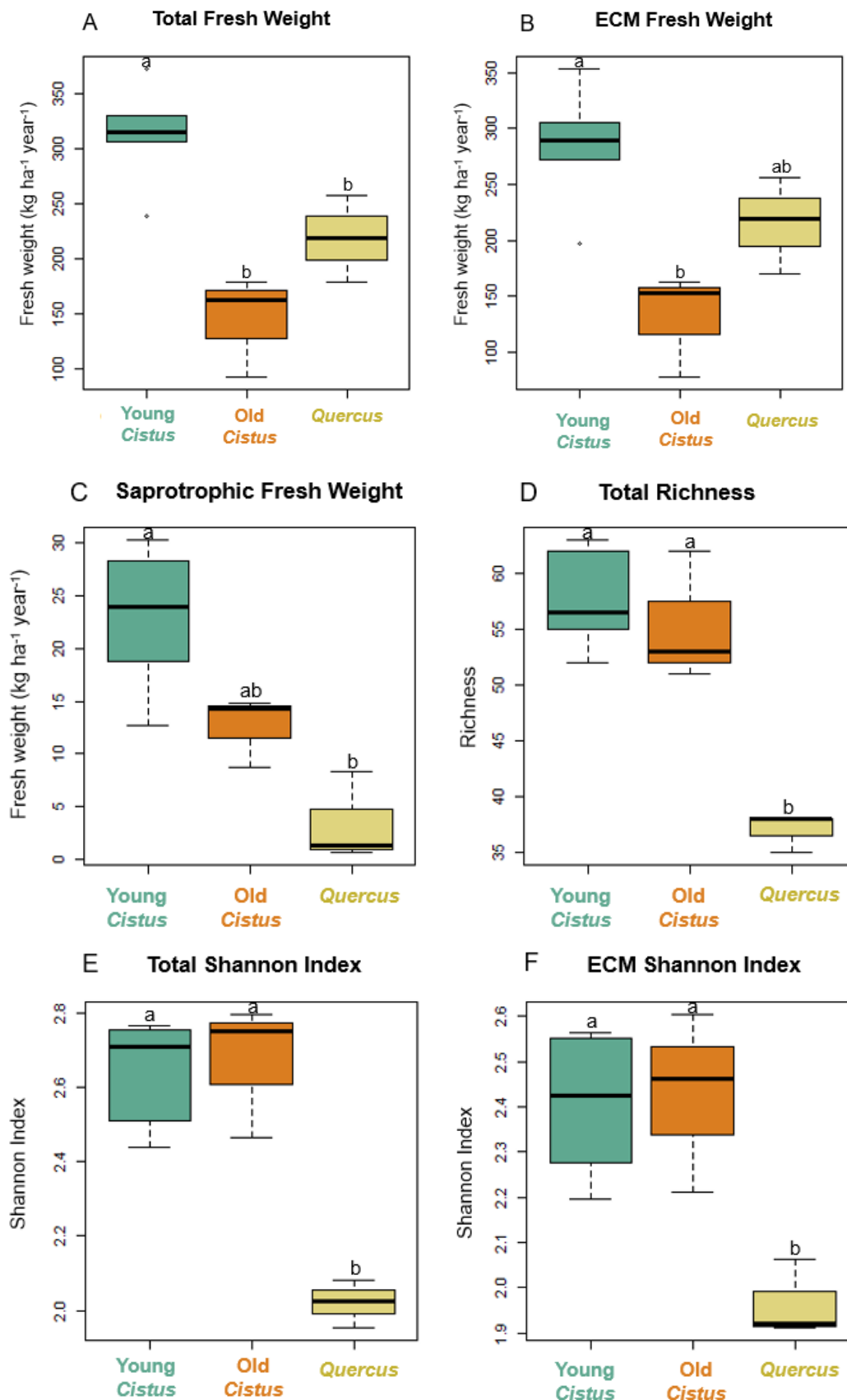
4.2. Effects on fungal production and richness

The total fresh weight of sporocarps collected was 990.17 kg·ha^{-1}, with an average of 247.54 kg·ha^{-1}·year^{-1}. A Tukey test for total sporocarp fresh weight showed that *Quercus*

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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. 6A). 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. 6B). Saprotrophic fresh weight production in old rockrose plots did not differ significantly from that of young rockrose or oak plots (p = 0.15) (Fig. 6C).

Total fungal richness was significantly higher in stands of young or old rockroses than in oak plots (p < 0.01; Fig. 6D). 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. 6E, F). However, in the case of saprophytic fungal diversity (Fig. 6G), the Shannon Index values for young and old *Cistus* and *Quercus* did not differ significantly (p = 0.06).

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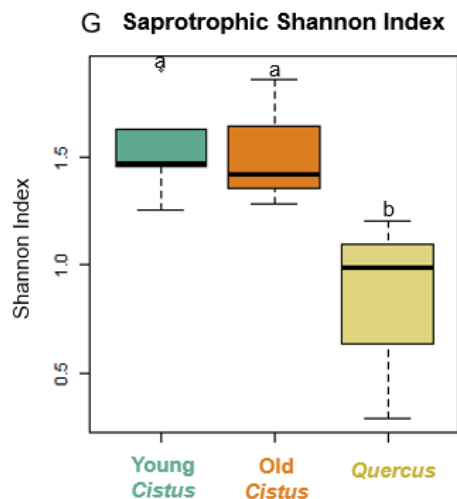
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Figure 6. *Sporocarp production, richness, and diversity in young Cistus, old Cistus, and Quercus stands. Annual fresh weight production of: (A) total sporocarps; (B) ectomycorrhizal (ECM) fungal sporocarps; and (C) saprotrophic sporocarps. (D) Total 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).*

4.3. Influence of the host on the composition of fungal taxa

NMDS (Fig.7) to observe the influence of the host on fungal community composition showed a stress of 0.087 and significant differences between both host species (p = 0.01). no overlap was observed between *Cistus* and *Quercus* fungal communities (Fig. 7). Richness of *Cistus* fungal community was greater than that of the *Quercus* fungal community.

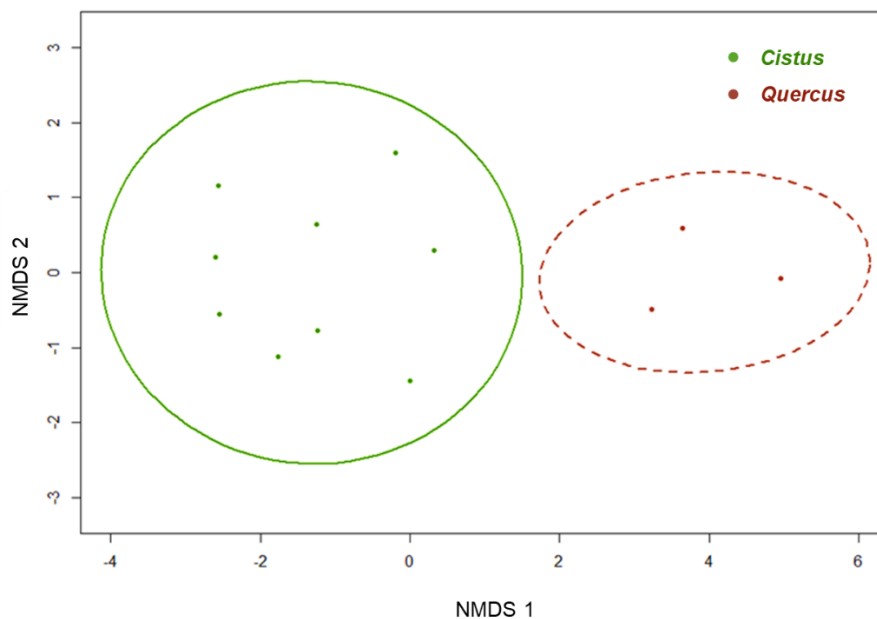**Figure 7.** *Non-metric multidimensional scaling (NMDS) of sporocarp production depending on host type.*

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NMDS analysis also showed that the species composition of the fungal communities in young and old *Cistus* plots were similar (Fig. 8), 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 (Fig. 8) revealed differences in the fungal communities present in *Cistus* of different stand ages (p = 0.001). Stands with the highest species diversity were young *Cistus* plots.
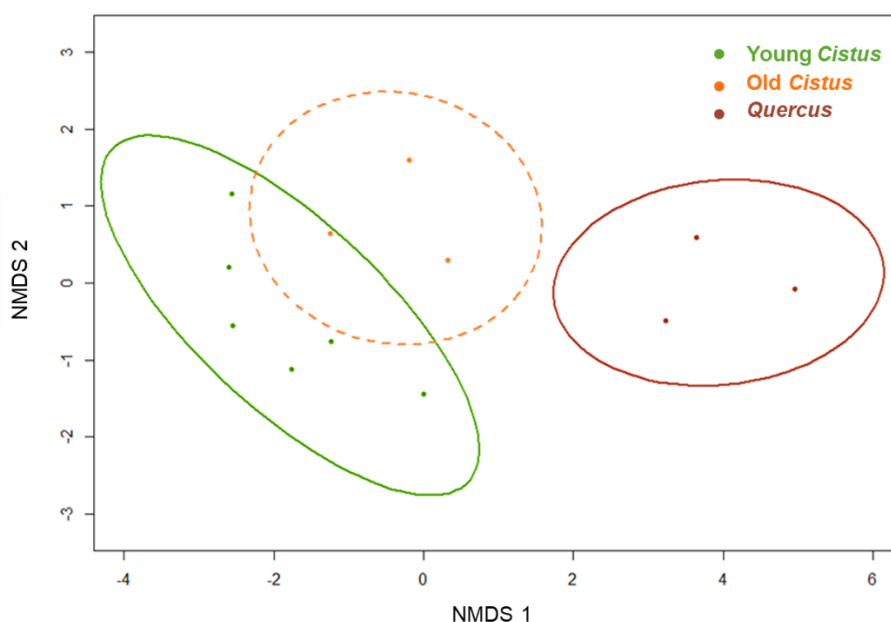

Figure 8. *Non-metric multidimensional scaling (NMDS) of sporocarp production depending on stand type.*

5. DISCUSSION

5.1. Sporocarp production and richness

Sporocarp production was higher in *Cistus* stands than in *Quercus* stands. This increased production could be the result of the microclimate created by the openness of the canopy, which favors temperature and humidity conditions that are more suitable for fungal fruiting in enclosed canopies. 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 canopy cover, negatively affects fungal community development (Tomao et al., 2020). The amount of canopy influences temperature, temperature variations, and water availability (Chazdon & 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

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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. Therefore, the higher the photosynthetic rate, and with it, the higher the carbon allocation, the more carbohydrates will be available for 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 & Albee, 1996; Ohenoja, 1988). In defoliation experiments, the number of sporocarps of ectomycorrhizal fungi produced in the vicinity of defoliated trees was 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 *Cistus* 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

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lower quality litter (Lin et al., 2019; Vivanco & 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.

5.2. Taxa composition

Cistus plots showed a larger fungal community assemblage than *Quercus* stands, which highlights the influence of this dominant vegetation species (Redondo et al., 2020). Given that *Cistus* and *Quercus* share a wide range of symbionts between them, environmental filtration tied to 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. The fungal community is restructured as the succession progresses towards more stable and smaller communities, with the disappearance of those species that are not adapted to the new conditions and the appearance, to a progressively reduced extent, of species that are adapted to the new conditions. 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) that likely favors the fructification of different saprotrophic species in these stands. Hence, a higher density in the *Cistus* shrub would favor fungal fructification in addition to a greater amount of organic matter, caused by a higher growth rate, that increases the availability of nutrients for saprotrophic species.

The NMDS analyses showed that the fungal community present in the old *Cistus* plots was closer to that found in the *Quercus* plots, which may be because *C. ladanifer* acts

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as a bridge species (Martín-Pinto et al., 2006; Milne, 2002) 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 & 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 & Mason, 1985). The host must have the capacity to provide the fungus with the nutrients it needs, and the fungus must be adapted to the conditions of that ecosystem and thus to the amount of nutrients it will be able to receive under those conditions. 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).

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., 2006), 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. Moreover, *Quercus* seedlings are likely to establish in areas shaded by an understory (Ritsche et al., 2021). All this favors the advance of succession toward the establishment of *Quercus* (Alday et al., 2016). 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, showed a transitional fungal community. Maintaining patches of vegetation in different stages of succession through a mosaic landscape may favor a larger fungal community. In this way, vegetative and fungal diversity would increase considerably since it would favor the diversification of ecosystems associated with different microclimatological conditions, structure and

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growth rates of the vegetation, and with it, different fungal communities, including fungi of interest.

5.3. Implications of this study in forest management

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., 2015). Zamora-Martínez & Nieto de Pascual-Pola (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 & 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., 2015). Creating differences in cover in the same forest will increase the diversity of both hosts and host-associated fungi, increasing stand diversity (Krah et al., 2018). 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). Gastronomic and marketable species are present in the three stand types, therefore the maintenance of senescent zones is not only ecologically valuable, but also economic. Applying a mosaic 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). In addition, 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 & Trappe, 1978; Hernández-Rodríguez et al., 2013). Each type of stand type recorded in this ecosystem benefits certain species or others, so establishing patches in the landscape that maintain different zones with different characteristics would have a positive impact on the richness and diversity of the ecosystem. Forest management practices to create a mosaic landscape model would enhance fungal richness and communities as well as forest succession, and also help to reduce fuel biomass (Sanz-Benito et al., 2022).

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6. CONCLUSION

According to the results obtained in this study, in a landscape composed of young and old *Cistus* scrub and *Quercus* forest stands, the highest production and richness of sporocarps is concentrated in the young *Cistus* stands. This suggests that both fungal productivity and richness is influenced by stand age, increasing in stands with a higher photosynthetic rate and lack of competition that allows a greater number of fungi to stablish until the community stabilizes as succession progresses, with some transfer between early and late stages. The role of forest management in these ecosystems, in order to increase productivity and fungal richness, is to facilitate the rejuvenation of the stand while maintaining certain areas in senescence, and with it, the fungi associated to them. These measures can favor greater fungal diversity, including edible and marketable species that can have an important impact on rural economies. Promoting a landscape with a mosaic pattern could achieve connectivity between the different stages of succession, favoring biodiversity and fire prevention through the reduction of available fuel, which would also increase the socioeconomic benefits of rural economies.

7. AKNOWLEDGES

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ANNEX 1

Table 2. *Total taxa recorded in each plot type according to their trophic group: ECM, ectomycorrhizal; S, saprophytic; M, mycoparasitic; U, unknown and according to their edibility (E, edible; IE, inedible). Plot type: C_young, Cistus young plots; C_old, Cistus old plots; Q, Quercus plots.*

Taxa	Guild	Edibility	Type plot		
			C_young	C_old	Q
Agaricus cupreobrunneus (Jul. Schäff. & Steer ex F.H. Møller) Pilát	S	E		x	
Agaricus silvicola (Vittad.) Peck	S	E		x	
Agaricus sylvaticus Schaeff.	S	E		x	
Agrocybe sp.	S	IE		x	
Amanita cistetorum (Contu & Pacioni)	ECM	IE	x		
Amanita citrina (Schaeff.) Pers.	ECM	IE	x	x	x
Amanita excelsa (Fr.) Bertill.	ECM	E	x		x
Amanita fulva Fr.	ECM	E		x	
Amanita mairei Foley	ECM	E	x		
Amanita muscaria (L.) Lam.	ECM	IE	x	x	x
Amanita muscaria var. *inzengae* (Neville & Poumarat)	ECM	IE	x		
Amanita pantherina (DC.) Krombh.	ECM	IE	x	x	x
Amanita rubescens Pers.	ECM	E	x	x	x
Amanita sp.	ECM	IE		x	
Apioperdon pyriforme (Schaeff.) Vizzini	S	E	x		
Boletus aereus Bull.	ECM	E			x
Boletus edulis Bull.	ECM	E	x	x	x
Boletus reticulatus Schaeff.	ECM	E			x
Boletus sp. L., Fr.	ECM	IE			x
Boletus spretus Bertéa	ECM	E			x
Calonarius elegantissimus (Rob. Henry) Niskanen & Liimat.	ECM	IE	x	x	x
Candolleomyces candolleanus (Fr.) D. Wächt. & A. Melzer.	S	IE	x	x	
Cantharellus cibarius (Fr.)	ECM	E	x	x	
Cantharellus pallens Pilát	ECM	E	x		
Cantharellus pruinosus Peck	ECM	E	x		
Chalciporus piperatus (Bull.) Bataille	M	IE	x	x	
Clitocybe brumalis (Fr.) Quél.	S	IE	x		
Clitocybe cistophila Bon & Contu	S	IE	x	x	
Clitocybe diatreta (Fr.) P. Kumm.	S	IE	x		
Clitocybe leucodiatreta Bon	S	IE	x	x	x
Clitocybe metachroa (Fr.) P. Kumm.	S	IE	x	x	
Clitocybe rivulosa (Pers.) P. Kumm.	S	IE	x	x	
Clitocybe odora (Bull.) P. Kumm.	S	IE		x	
Clitocybe sp. (Fr.) Staude	S	IE	x	x	
Clitocybe vibecina (Fr.) Quél.	S	IE	x	x	
Collybia sp. (Fr.) Staude	M	IE	x		
Cortinarius assiduus Mahiques, A. Ortega & Bidaud, Bull.	ECM	IE	x	x	
Cortinarius balteatocumatilis Rob. Henry ex P.D. Orton	ECM	IE	x		
Cortinarius brunneus (Pers.) Fr.	ECM	IE	x		
Cortinarius cinnamomeoluteus P.D. Orton	ECM	IE	x	x	x
Cortinarius cinnamomeobadius Rob. Henry, Bull.	ECM	IE	x	x	
Cortinarius cinnamomeus (L.) Gray	ECM	IE	x	x	x
Cortinarius croceus (Schaeff.)Gray	ECM	IE		x	
Cortinarius duracinus Fr.	ECM	IE	x		
Cortinarius flexipes (Pers.) Fr.	ECM	IE	x		
Cortinarius hepaticus Kytov., Niskanen & Liimat.	ECM	IE		x	
Cortinarius saturninus (Fr.) Fr.	ECM	IE	x		
Cortinarius scobinaceus Malençon & Bertault	ECM	IE	x	x	
Cortinarius sec. *caerulescens* (Scheff.) Fr.	ECM	IE	x	x	x
Cortinarius sec. *sanguinei*	ECM	IE	x		x
Cortinarius sec. *telamonia*	ECM	IE	x	x	
Cortinarius semisanguineus (Fr.) Gillet	ECM	IE	x		
Cortinarius sp. (Pers.) Gray	ECM	IE	x	x	x
Cortinarius trivialis J.E. Lange	ECM	IE			x
Cortinarius venetus (Fr.) Fr.	ECM	IE	x		
Cortinarius xerophilus Rob. Henry & Contu	ECM	IE	x	x	
Craterellus cornucopioides (L.) Pers.	ECM	E		x	
Cystoderma cinnabarina (Alb. & Schwein.) Harmaja	S	IE		x	
Cystoderma sp.	S	IE		x	
Cystoderma terrei (Berk. & Broome) Harmaja	S	IE	x		

Species					
Entoloma cistophilum Trimbach	S	IE	x		
Entoloma hebes (Romagn.) Trimbach	S	IE	x	x	
Entoloma hirtipes (Schumach.) M.M. Moser	S	IE	x	x	
Entoloma sericeum Quél.	S	IE	x	x	
Entoloma sp.	S	IE	x	x	
Fistulina hepatica (Schaeff.) With.	S	E			x
Flammulaster carpophilus (Fr.) Earle ex Vellinga	S	IE		x	
Galerina sp.	U	IE	x	x	
Galerina uncialis (Britzelm.) Kühner	S	IE	x		
Gymnopus dryophilus (Bull.) Murrill.	M	E	x	x	x
Gymnopus ocior (Pers.) Antonín & Noordel.	S	E	x		
Hebeloma cistophilum Maire	S	IE	x	x	x
Hebeloma hiemale Bres.	ECM	IE	x	x	
Hebeloma mesophaeum (Pers.) Quél.	ECM	IE	x		
Hebeloma sp.	ECM	IE	x	x	x
Hydnum repandum L.	ECM	E			x
Hygrocybe pratensis (Pers.) Murrill	S	E			x
Hygrophorus chrysodon (Batsch) Fr.	ECM	E	x	x	
Hygrophorus pseudodiscoideus (Maire) Malençon & Bertault	ECM	IE	x	x	x
Hygrophorus roseodiscoideus Bon & Chevassut	ECM	IE	x		
Hypholoma fasciculare (Huds.) P. Kumm.	ECM	IE	x	x	x
Inocybe geophylla P. Kumm.	ECM	IE	x		
Inocybe geophylla var. *lilacina* (Peck) Gillet	ECM	IE	x		
Inocybe grammata Quél.	ECM	IE		x	
Inocybe sp.	ECM	IE	x	x	x
Inosperma maculatum (Boud.) Matheny & Esteve-Rav.	ECM	IE	x		
Laccaria bicolor (Maire) P.D. Orton	ECM	E	x	x	x
Laccaria laccata (Scop.) Cooke	ECM	E	x	x	x
Laccaria sp.	ECM	IE			x
Lacrymaria lacrymabunda (Bull.) Pat.	S	IE	x		
Lactarius aurantiacus (Pers.) Gray	ECM	E	x		
Lactarius chrysorrheus Fr.	ECM	IE	x	x	x
Lactarius cistophilus Bon & Trimbach	ECM	IE	x	x	x
Lactarius hepaticus Plowr.	ECM	IE		x	x
Lactarius sanguifluus (Paulet) Fr.	ECM	E			x
Lactarius subumbonatus Lindgr.	ECM	IE			x
Lactarius tesquorum Malençon	ECM	IE	x	x	x
Leccinellum corsicum (Rolland) Bresinsky & Manfr. Binder.	ECM	E	x	x	
Leccinellum lepidum (H. Bouchet ex Essette) Bresinsky & Manfr. Binder.	ECM	IE	x		
Leccinum sp.	ECM	IE			x
Lentinellus micheneri (Berk. & M.A. Curtis) Pegler.	S	IE	x		
Lepista nuda (Bull.) Cooke	S	E	x		
Lycoperdon molle Pers.	S	E	x		
Lycoperdon perlatum Pers.	S	E	x	x	
Lyophyllum decastes (Fr.) Singer	ECM	E	x		x
Lyophyllum infumatum (Bres.) Kühner	ECM	E	x	x	
Lyophyllum loricatum (Fr.) Kühner	ECM	E			x
Lyophyllum semitale (Fr.) Kühner	ECM	E	x		x
Lyophyllum sp.	ECM	IE	x	x	x
Macrolepiota excoriata (Schaeff.) Wasser	S	E	x		
Macrolepiota mastoidea (Fr.) Singer	S	E	x		
Macrolepiota procera (Scop.) Singer	S	E	x		
Mycena aetites (Fr.) Quél.	S	IE	x	x	
Mycena arcangeliana Bres.	S	IE	x		
Mycena cinerella (P. Karst.) P. Karst.	S	IE	x		
Mycena clavicularis (Fr.) Gillet	S	IE	x		
Mycena epipterygia (Scop.) Gray	S	IE	x	x	x
Mycena leptocephala (Pers.) Gillet	S	IE	x		
Mycena maculata P. Karst.	S	IE			x
Mycena polygramma (Bull.) Gray	S	IE			x
Mycena pura (Pers.) P. Kumm.	S	IE	x	x	
Mycena sp.	S	IE	x	x	x
Neoboletus luridiformis (Rostk.) Gelardi, Simonini & Vizzini	ECM	IE		x	x
Omphalina sp.	S	IE	x	x	
Paxillus involutus (Batsch) Fr.	ECM	IE	x	x	x
Phlegmacium balteatum (Fr.) A. Blytt.	ECM	IE	x		
Phaeomarasmius erinaceus (Fr.) Scherff.	S	IE		x	
Phloeomana minutula (Sacc.) Redhead.	S	IE	x		
Pluteus sp.	S	IE	x		
Protostropharia semiglobata (Batsch) Redhead, Moncalvo & Vilgalys.	S	IE	x		
Psathyrella sp.	S	IE	x	x	

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

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