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RESEARCH

Mediterranean co-living: succession of soil mycorrhizal communities associated with *Halimium lasianthum* shrubs

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Abstract
Halimium lasianthum, a widespread shrub in the western Mediterranean, uniquely co-hosts ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi. Despite its ecological significance, *H. lasianthum* is understudied, and its mycorrhizal communities remain largely unknown. To understand the mycological ecology associated with *H. lasianthum*, we analyzed soil samples from intermediate and senescent understories in Ourense, northwest Iberian Peninsula. We assessed the richness, diversity, relative abundance and community composition of ECM and AM fungi. Environmental and soil variables were also examined to determine their influence on fungal distribution. Total fungal richness and abundance were higher in intermediate plots compared to senescent plots, with ECM fungi following the same trend. In comparison, AM fungal richness was higher in senescent plots ($p < 0.05$). ECM fungal community composition shifted with *H. lasianthum* age, whereas the Shannon diversity index and abundance of AM fungi remained stable. Soil pH was significantly correlated with the ECM community in intermediate plots, while the stability of the AM community was due to lower nutrient requirements and the production of resistant propagules. These findings could help to improve the management of *H. lasianthum* ecosystems to preserve the diversity of the mycorrhizal communities associated with this host species.

Keywords Cistaceae · Mycorrhizal fungi · Successional stages · Community reassembly · Illumina sequencing

Introduction

Halimium species, shrubs with small to large evergreen or semi-deciduous leaves, are quite specifics in the western Mediterranean biome (Civeyrel et al. 2011), and play an increasingly appreciated ecological role (Silva et al. 2022). They occur in areas of open vegetation as well as in degraded forest patches, forest boundaries, abandoned fields, grasslands, and in coastal sandy areas and dry dunes (Zunzunegui et al. 2009). Despite the wide distribution of *Halimium* spp. in the Mediterranean area, *Halimium* is one of the least studied genera in the Cistaceae family (Martín-Pinto et al. 2023). Consequently, the mycorrhizal biology of *Halimium* is barely known (Leonardi et al. 2020). However, the *Halimium* genus is known to form both ectomycorrhizae (ECM) and arbuscular mycorrhizae (AM) (Buscardo et al. 2012; Beddiar et al. 2015), acting as a dual-mycorrhizal plant (Leonardi et al. 2020). *Halimium* shrublands, like *Cistus ladanifer* shrublands, can host mushrooms of great commercial value, such as *Boletus edulis* and *Boletus aereus* (Oria de Rueda et al. 2008). *Halimium* has also been observed to share mycobionts with *Quercus* (Comandini et al. 2018), and studies in Portugal have shown that it shares symbionts with *Pinus* (Buscardo et al. 2012; Carvalho et al. 2018). Cistaceae can play an important role in secondary succession, enhancing the water retention, protecting the

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soil from erosion and desertification, and acting as a nurse species for tree species (Leonardi et al. 2020).

Mycorrhizal fungi are pervasive symbionts on vegetation roots: AM fungi are largely widespread and ECM fungi are a prevailing group in temperate ecosystems (Smith and Read 2008; Talbot et al. 2008). These organisms are important symbionts because they support plant growth, enhancing water, mineral, and nutrient uptake by the host (Dighton 2003). AM and ECM fungi have different strategies for obtaining nutrients and producing enzymes (Smith and Read 2008). Fungal communities' succession is complex and interact with multiple factors in addition to vegetation (Nielsen et al. 2010; Smith et al. 2014). In natural forest succession, the soil chemistry and nutrient availability of a stand changes over time, which affects the fungal community associated with the stand (Kyaschenko et al. 2017). Changes in the quality and quantity of vegetation inputs throughout the succession can also lead to variations in soil microbial biomass, activity, and community structure (Wardle et al. 2004; Smith et al. 2015; Shao et al. 2017). These changes may favor the appearance or disappearance of certain fungal species, depending on their ability to adapt to the new conditions throughout the forest succession and, therefore, Twieg et al. (2007) suggested categorizing fungal taxa into 'early-stage', 'multi-stage' (when they occur in multiple stages) and 'late-stage', depending on the age of the host. Jiang et al. (2021) considered C, N, water content, and pH to be the key environmental variables contributing to microbial community changes, with pH considered an essential predictor of soil microbial composition as a general rule (Duan et al. 2023).

The coexistence of multiple types of mycorrhizal partner within a single plant species is uncommon (Zanne et al. 2020). Given the importance of *Halimium* as a pioneer species in degraded areas and as a host for ECM and AM fungi (Martín-Pinto et al. 2023), it would be useful to have a better understanding of: (i) the fungi associated with *Halimium*; (ii) how the community evolves along the fungal succession; (iii) how ECM and AM fungi coexist as mycorrhizal partners and complement each other through the succession; and (iv) the influence of soil properties on the community composition (Albornoz et al. 2014). Furthermore, knowing whether ecologically and economically important fungi are present in *H. lasianthum* shrublands, as they are in other Mediterranean Cistaceae shrublands (Martín-Pinto et al. 2006; Oria-de-Rueda et al. 2008; Hernández-Rodríguez et al. 2015a) could contribute to rural development (Bonet et al. 2014) and help to establish management techniques for these shrublands, which are often unmanaged and damaged by fire (Martín-Pinto et al. 2006; Mediavilla et al. 2014). Therefore, the main objectives of this study were to analyze the richness, abundance, and Shannon diversity of ECM and AM fungi associated with *H. lasianthum* plots that were of intermediate age or senescent, and to determine how plant succession and environmental variables affect these communities. We hypothesized that, on the one hand, owing to the greater photosynthetic activity of intermediate-aged stands, the fungal diversity and richness would be greater than in senescent stands because more Carbon would be available to fungi and this community would be reduced as, on the other hand, the senescent stage approaches and plant activity is reduced, resulting in less diverse and more stable fungal communities. Furthermore, we anticipated a dominant ECM (ectomycorrhizal) community in the intermediate plots, owing to its late successional profile and high nutrient requirements. We expected this community to be subsequently replaced by a community dominated by AM (arbuscular mycorrhizal) fungi in the senescent. In addition, we expected that the composition of both intermediate and senescent plots would be influenced by soil parameters, particularly the ECM community.

Materials and methods

Study area and experimental design

A study site was established in the Galician region, which is located on the northwest side of the Iberian Peninsula, in the Edreiras mountains in Ourense province, Spain. The study area is characterized by Mediterranean conditions with a 10 °C mean annual temperature and an average rainfall of 1100 mm per year. The soil is composed of Alumni-umbric Regosols (FAO 1998) and the study area has a 10% slope. Further information about this study area can be found in Fernández et al. (2015), Fontúrbel et al. (2016) and Martín-Pinto et al. (2023). The study area is dominated by *Halimium lasianthum* (Lam.) Spach shrubs and is eventually colonized by secondary plant species such as *Pterospartum tridentatum*, *Erica cinerea*, *E. umbellata*, and *E. australis* were observed in the plots and surrounding areas. These species are typically pyrophytic and commonly found in areas frequently affected by wildfires in the studied area. However, the distribution of these secondary species was found to be just scarce scattered across the plots.

To reduce the influence of differences in geographical and climatic parameters on the fungal community (Castaño et al. 2018; Collado et al. 2019) all the plots were established in the same local area. *Halimium* stands of two different ages were selected to observe the effect of aging and succession on the associated soil mycorrhizal fungal community. Plots with a middle-aged *Halimium* understory (from now on referred to as intermediate age class plots of approximately 9 years) and plots with an old *Halimium* understory

(from now on referred to as senescent plots which had ages exceeding 16 years) (Table 1). All plots had a rectangular shape (50 × 16 m^2). To mitigate site effects, intermediate and old plots were sampled at each of the four sites, ensuring a minimum separation distance of 500 m to prevent pseudo-replication. Additionally, within each site, plots were positioned at least 200 m apart from one another.

Soil sampling and molecular work

Soil samples were collected during the spring of 2019. Superficial debris and stones were removed before extracting 15 soil core samples, 5 m apart along the centre-line of each plot using a cylindrical soil borer (2 cm radius, 20 cm deep, and 250 cm3), per plot, as described in Martín-Pinto et al. (2023), mixing it into only one pooled sample per plot in order to maintain heterogeneity, obtaining 24 pooled soil samples in total and processing them before 24 h. Samples were dried at room temperature and sieved through a 1 mm mesh sieve. A PowerSoil™ DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA) was used to extract DNA from 0.25 g of soil per sample. PCR reactions of each sample were carried out in triplicate to minimize PCR biases. PCR reactions were performed in 20 µL reaction volumes containing 11.22 µL of Modified Quantization (MQ) water, 1.60 µL of DNA template, 2.00 µL of 10 × buffer, 1.40 µL of MgCl2 (50 mM), 1.60 µL of dNTPs (10 mM), 0.50 µL of bovine serum albumin (2%), 0.80 µL of reverse and forward primers (10 µM), and 0.08 µL of Platinum Taq polymerase (Invitrogen, Carlsbad, CA, USA). The following PCR conditions were used: an initial denaturation step at 94 °C for 3 min; followed by 35 cycles of 94 °C for 45 s, 50 °C for 1 min, and 72 °C for 1.5 min; and finally, one cycle of 72 °C for 10 min. To amplify the ITS2 rDNA region (ca. 260 bp), we used the forward primer fITS7 and reverse primer ITS4, appended with Illumina adaptors as described by Ihrmark et al. (2012) and White et al. (1990). Sample-specific Multiplex Identification DNA-tags were used to label the ITS4 primer. A negative control comprising MQ water instead of DNA was included on each set of PCR replicates, which underwent PCR under the same experimental conditions and was shown to be amplicon-free on a gel. Sequencing was performed using an Illumina MiSeq platform (BaseClear BV, Leiden, the Netherlands).

pH was determined using 20 g per soil sample by water-based suspension at 1:2.5, dry matter (%) following UNE-ISO 11,465 rule, and plant available phosphorus (P) content (%) using the Olsen methodology. The Dumas methodology was used to determine the total carbon (C) content (%) and the total nitrogen (N) content (%).

Molecular and bioinformatic analysis

Poor-quality ends of sequences were removed in using a quality criteria value of q = 15 with Cutadapt. Sequences were joined using USEARCH v.10.0.240 (Edgar 2010) and cutadapt, with a minimum sequence length of 200 bp. Primers (ITS4 reverse and fITS7 forward) were removed and sequences with expected errors of > 1 were removed. A combined single sample was formed, its read count numbers were recorded creating an operational taxonomic unit (OTU), considering the number of detections per sample. Taxonomic assignment was carried out using the UNITE database (version v.8.0 released on November 18th, 2018) through the assignment of species hypothesis (SH) groups, which were defined based on dynamic sequence similarity thresholds (Kõljalg et al. 2013). OTUs with < 70% similarity or with < 200 bp pairwise alignment length to a fungal sequence were excluded. All OTUs detected were evaluated due to it ecological role valued in this study.

Mycorrhizal guild attribution was carried out by the PlutoF web workbench (https://plutof.ut.ee) (Abarenkov et al. 2010). A 90% similarity threshold was used for the assignment of functional groups following Põlme et al. (2020). Additional categories of ECM fungi following Geml (2019) and by Agerer (2006), Tedersoo and Smith (2013), and the DEEMY database (http://deemy.de).

Table 1 Average values of edaphic variables and shrub parameters across the different plots of the study area

Age	site	pH	*P* %	*N* %	C %	Soil dry matter %	Cover %	Height(cm)
Intermediate	1	4.46	8.99	0.70	11.50	94.76	17.07	26.73
	2	4.42	13.70	0.65	10.46	94.89	8.93	28.40
	3	4.34	13.80	0.68	11.83	93.03	12.93	27.33
	4	4.49	11.84	0.70	11.41	94.39	11.87	22.87
mean		**4.43**	**12.08**	**0.68**	**11.30**	**94.27**	**12.70**	**26.33**
Senescent	1	4.47	8.59	0.60	9.47	96.04	8.10	27.33
	2	4.45	11.24	0.61	9.63	95.88	4.87	25.63
	3	4.45	10.85	0.69	11.53	95.56	16.43	32.90
	4	4.45	9.23	0.59	9.13	96.40	9.43	26.43
mean		**4.46**	**9.98**	**0.62**	**9.94**	**95.97**	**9.71**	**28.08**

Statistical analysis

The data used for statistical analyses were log-transformed when needed to achieve the parametric criteria of normality and homoscedasticity. Fungal data were normalized by rarefying the abundance data to the smallest number of sequences per plot. In addition, soil variable data were scaled using base R. To estimate the relative abundance of each OTU, the number of sequences associated with each OTU was first counted. This count was then divided by the total number of sequences across all OTUs within the sample, providing the data necessary to analyze the abundance for each functional fungal group. Shannon's H' diversity index, H' = –Σpi (lnpi), was estimated for each treatment, where pi indicates the relative abundance of fungal species (Kent and coker 1993; Taylor et al. 2016). All diversity measures were analyzed using the Biodiversity R package in R version 4.0.3 (R Core Team 2020). Differences across treatments were assessed using linear mixed effects (LME, $p \leq 0.05$) models using the package Nlme (Pinheiro et al. 2016) by taking into consideration the variables were the fixed factors meanwhile the plots were the random ones. The LME models were used to prevent false-positive associations due to the relatedness structure in the sampling. Post-hoc test to explore significant differences between site and age were analyzed by Tukey's HSD test. The influence of edaphic variables (pH, P, N, C, and dry matter) on mycorrhizal community composition was evaluated by performing Non-Metric Multidimensional Scaling (NMDS) based on a Hellinger-transformed OTU and environmental scaled data matrix. The influence of *Halimium* understory age was analyzed by performing a permutational multivariate ANOVA (PERMANOVA) based on 999 permutations using the *adonis* function in the 'vegan' package (Oksanen et al. 2015). The *betadisper* function was used to analyze the beta-dispersion of AM and ECM fungal community compositions. Finally, the *envfit* function in R was used to assess correlations between explanatory variables and NMDS axes scores. OTU abundance was visualized using Krona tools (Ondov et al. 2011) Finally, a Multilevel Pattern Analysis has been carried using the function multipatt (De Cáceres 2013) in order to determine the occurrence of indicator species associated to the different groups regarding the age.

Results

Richness, diversity, and abundance of mycorrhizal fungi

The four dominant ECM taxa were the following, from highest to smallest: Agaricales (36%), Boletales (27%), Thelephorales (14%) and Russulaceae (10%) (Fig. 1). Inside the Agaricales taxa, *Amanita* genus is the more represented while in the case of Boletales was *Rhizopogon*, regarding Theleophorales, the principal genus found is *Tomentella* and finally for Russulaceae the main genus in terms of abundance was *Russula*.

The ANOVA of the total fungal community (Table 2) revealed significant differences in terms of richness ($p = 0.023$) and abundance values ($p = 0.000$) between intermediate plots and senescent plots, with intermediate plots having significantly higher values (Fig. 2A), following our first and second hypothesis. Likewise, the richness ($p = 0.003$) and abundance values ($p = 0.001$) of the ECM fungal community in intermediate plots were significantly different to those in senescent plots, with intermediate plots having significantly higher values (Fig. 2C). By contrast, the diversity ($p = 0.025$) and richness values ($p = 0.035$) of the AM fungal community in senescent plots were significantly different to those in intermediate plots, with senescent plots having significantly higher values (Fig. 2B).

Fungal communities in the two *Halimium* age classes

Considering AM community composition, the NMDS analysis generated a stress value (0.172), indicating a good representation of the community; however, no significant differences were found ($p = 0.173$) between intermediate and senescent *Halimium* plots (Fig. 3A). Furthermore, beta dispersion was not significant (0.945). The only environmental variable that influenced the AM fungal distribution was dry matter ($p = 0.023$) (Table 3). Moreover, the two ellipses showed a large overlap, indicating that most AM fungal species were detected in both intermediate and senescent *Halimium* plots.

Regarding ECM community composition (Fig. 3B), the NMDS analysis also generated a stress value (0.191) and revealed significant differences ($p = 0.004$) related to *Halimium* age. The distribution of the ECM fungal community detected in senescent *Halimium* plots appeared to be much less dispersed than in intermediate plots. However, beta dispersion analysis was not significant ($p = 0.265$), indicating that any observed differences are not due to differing levels of within-group dispersion. The only environmental variables that marginally influenced ($p < 0.1$) the distribution of the ECM fungal community was soil pH (Table 3) in senescent plots and soil N content in intermediate plots.

The Multilevel Pattern Analysis for indicator species was carried out over the ECM community as it was the only one which showed a significant difference in terms of community composition (Table 4). From a total number of 78 species, just five resulted as indicator species being two related to the senescent plots and three for intermediate ones. The senescent associated species were *Rhizopogon evadens* and *Rhizopogon luteolus* while those related to intermediate

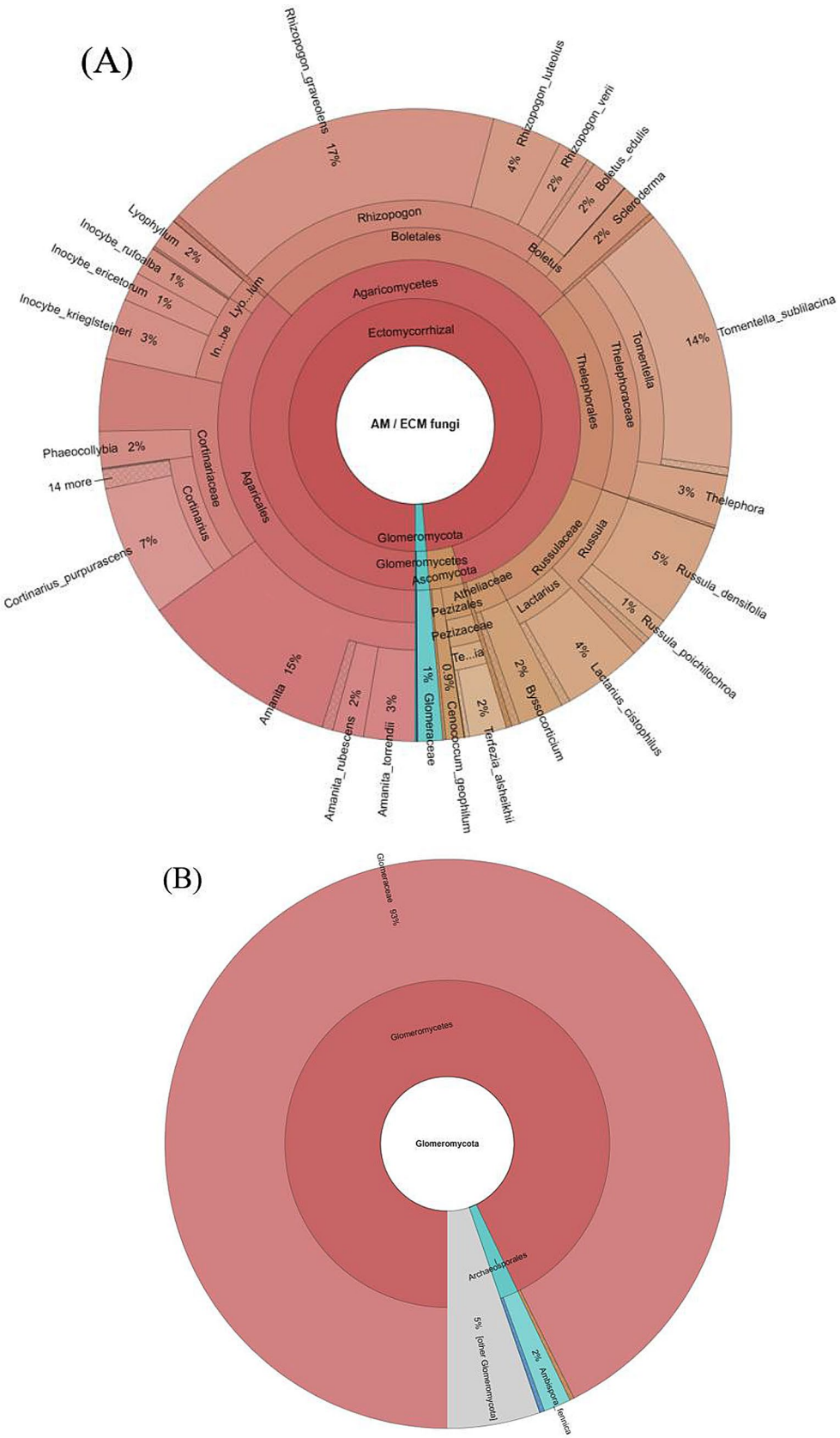

Fig. 1 Krona charts showing the relative abundance of (**A**) the ECM and AM total fungal taxa in each division, class, order and family and (**B**) the AM/ ECM fungal guilds in the division of Glomeromycota based on sequence abundance

Table 2 Shannon diversity index (H), proportional species richness, and abundance estimation for the total fungal community, arbuscular mycorrhizal (AM) fungal community, and the ectomycorrhizal (ECM) fungal community estimated by an ANOVA test

	Total fungal OTUs			AM fungal OTUs			ECM fungal OTUs		
	H	*R*	Abundance	H	*R*	Abundance	H	*R*	Abundance
F-value	0.06	5.93	14.44	5.74	5.02	0.19	0.00	10.63	13.3
P-value	0.80	**0.02**	**<0.01**	**0.02**	**0.03**	0.66	0.94	**<0.01**	**<0.01**

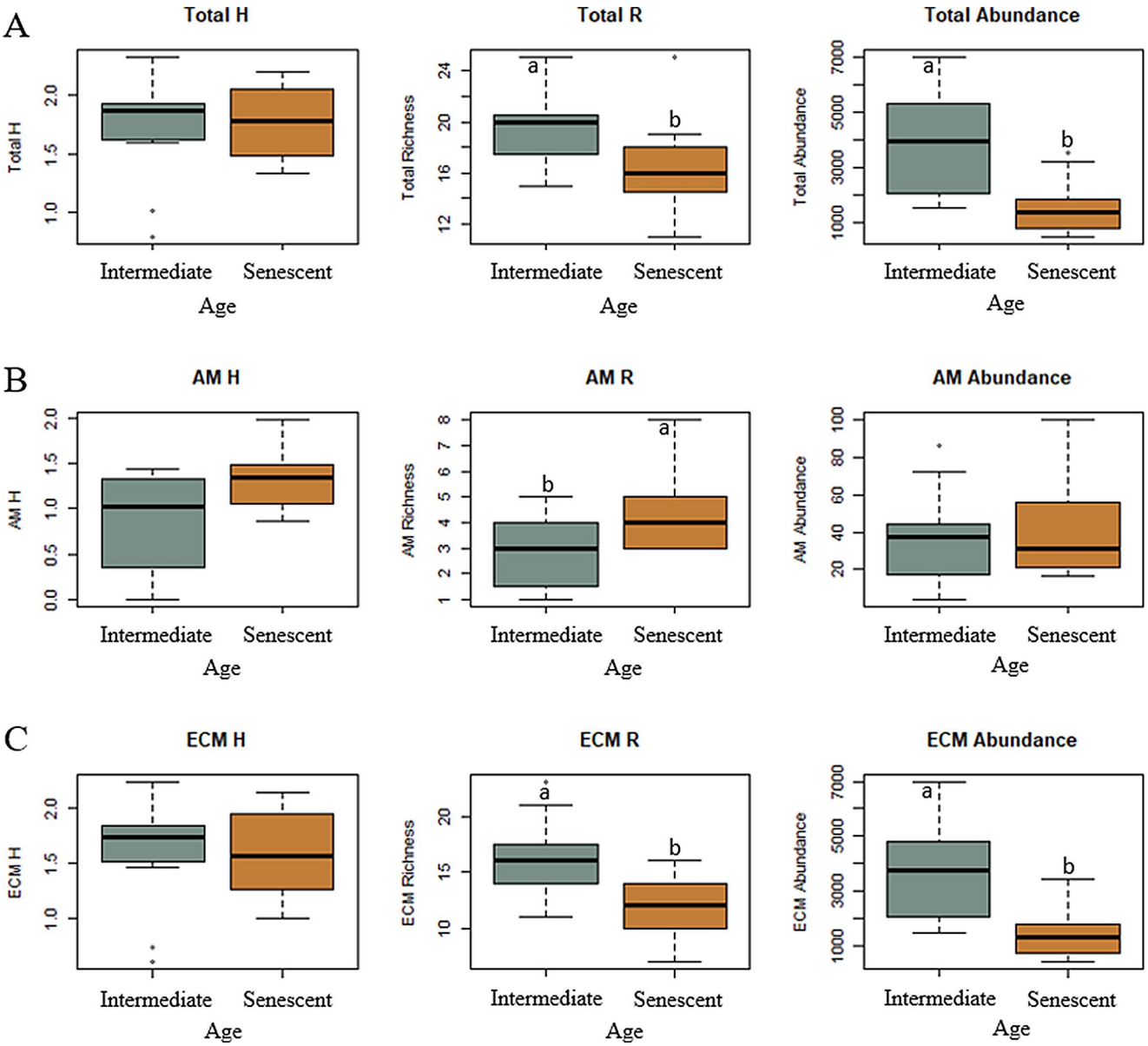

Fig. 2 Shannon diversity index (H) (left), proportional species richness (R) (middle), and abundance estimation (right) for the total fungal community (**A**); for the arbuscular mycorrhizal (AM) fungal community (**B**), and for the ectomycorrhizal (ECM) fungal community (**C**) estimated using Linear Mixed Effects (LME). The means and the interval distribution of the data as shown. Different lowercase letters indicate significant differences based on LME models ($p < 0.05$)

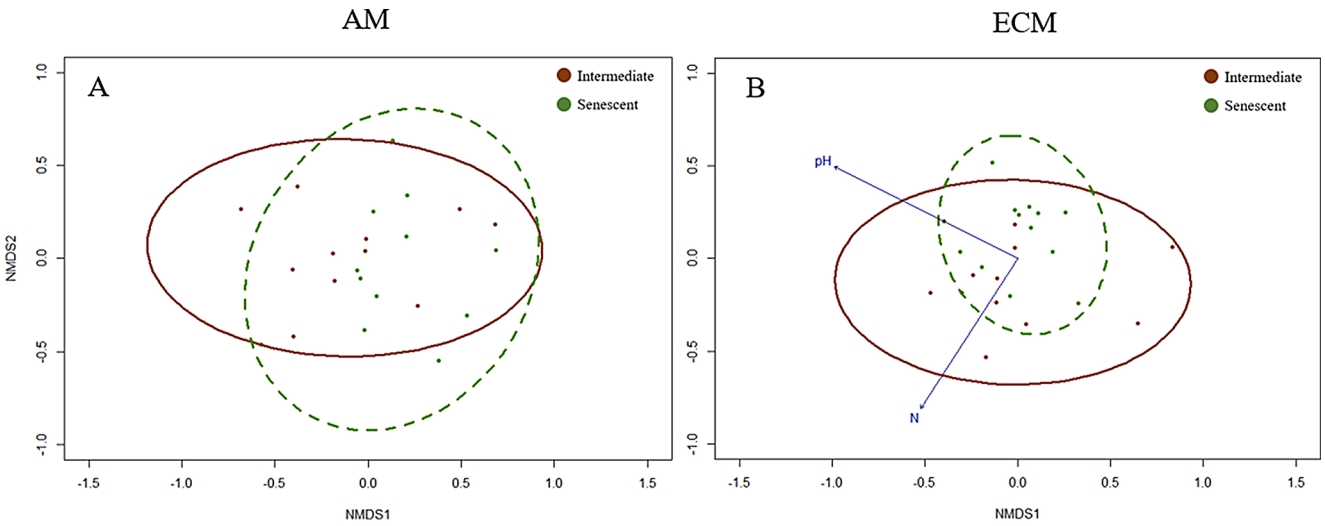

Fig. 3 Non-metric multidimensional scaling (NMDS) of the total arbuscular mycorrhizal (AM) fungal community (**A**) and ectomycorrhizal (ECM) fungal community (**B**) detected in senescent plots (old, green ellipse) and intermediate plots (young, red ellipse) of *Halimium*. Ellipses represent the distribution of the fungal community associated with each plant age. Explanatory edaphic variables are shown in blue: N, total nitrogen; pH, soil pH

Table 3 Significance of edaphic explanatory variables for soil fungal community composition in the study area. Values in bold indicate significant differences ($p < 0.05$)

	AM fungal OTUs		ECM fungal OTUs	
	r2	*P* value	r2	*P* value
pH	0.303	0.73	0.245	**0.05** ·
P	0.067	0.48	0.005	0.94
N	0.147	0.21	0.199	0.09
C	0.175	0.15	0.121	0.26
Soil dry matter	0.281	**0.02***	0.153	0.19

Table 4 Multilevel pattern analysis values for the significant ECM indicator species regarding the age of the plot. Values in bold indicate significant differences ($p < 0.05$)

Indicator species		
Species	Stat.	*p*-value
Senescent		
Rhizopogon evadens	0.618	**0.003**
Rhizopogon luteolus	0.450	**0.010**
Intermediate		
Tomentella sublilacina	0.424	**0.024**
Cenococcum geophilum	0.373	**0.046**
Russula poichilochroa	0.351	**0.019**

plots were *Tomentella sublilacina*, *Cenococcum geophilum* and *Russula poichilochroa*.

Discussion

Effect of stand age on soil mycorrhizal community

The richness and abundance of ECM and AM fungi were higher in middle-aged stands (i.e., intermediate plots) compared to senescent stands. Middle-aged stands can support high fungal diversity because they represent an intermediate stage with optimal soil development, pH, and nutrient concentrations, favoring a diverse fungal community over late successional stages (Dong et al. 2016). Stand age could be a key driver for fungal communities (Wang et al. 2012; Unuk et al. 2019). In previous studies, fungal diversity has been found to decrease with vegetation succession (Hui et al. 2018). The reduction could be caused by differences in the ability of the microorganisms to adapt to both physical and chemical changes in the soil (Liu et al. 2020), which are strongly associated with vegetative growth, root growth, and root exudates (Kuzyakov and Razavi 2019). Carbohydrate supply may also be an important determinant in the selection of mycorrhizal symbionts because late-stage fungi require greater amounts of sugars and probably more complex mixtures of vitamins than those present in the soil, which they obtain from their host (Dighton and Mason 1985). Lower production in senescent stands owing to a reduction of photosynthetic activity results in decreased growth (Hernández-Rodríguez et al. 2015b) and, hence, a decrease in the nutrient supply to the fungal community. It has been suggested that root exudate components are different in stands of different ages, which directly affects the proportional richness and structure of the rhizosphere microorganism community (Lladó et al. 2018). Given that soil enzymatic activity increases in parallel with increasing plant needs during plant growth (Chen et al. 2010), this suggests that the rhizosphere may change depending on the growth stage of the plant. Both the richness and composition of these communities can vary depending on the availability of nutrients in the soil (Dong et al. 2021). However,

no big differences have been seen in the soil parameters of both sites (Table 1).

In line with the general trend shown by the total fungal community, ECM fungi showed significantly higher levels of richness and abundance in intermediate stands than in senescent stands. The colonization patterns of ECM fungi are strongly linked to the physiology of their hosts and, hence, the ECM fungal community changes substantially with stand age (Twieg et al. 2007). Multiple studies have previously reported that mycorrhizal fungal communities, such as ECM fungi, of young and mature trees differed (Unuk et al. 2019). Available resources, such as carbohydrates, for ECM fungi decrease at more advanced stages of development because growth patterns change, becoming slower (Tomao et al. 2020). According to Zhang et al. (2018), the reason for this is that the ability of vegetation to acquire resources and the C: N:P ratio in plant tissues varies with age. Although some ectomycorrhizal (ECM) fungi act as saprophytes (Koide et al. 2008; Lindahl and Tunlid 2015; Teste et al. 2020), the majority rely entirely on the resources obtained from their host plants. When resource availability diminishes due to stand senescence, the fungal community is likewise adversely affected, leading to a reduction in fungal diversity and abundance. The latest findings align with our first two hypotheses. By contrast, AM fungi did not seem to follow this general trend, as the AM community composition remained stable throughout the succession, showing greater diversity and richness in older stands. Bennett et al. (2013) observed that older successional stages have fewer AM fungi–plant interactions than younger stages, which may influence their non-significant higher abundance, but have a greater richness and diversity due to more specialist interactions. In addition, the greater richness of ECM fungi in intermediate plots could inhibit the decomposition of organic matter, reducing the nutrient availability for AM fungi, whereas in senescent plots, which have lower ECM fungal richness and abundance, AM fungi are promoted (Neuenkamp et al. 2018). Furthermore, given that root colonization by AM fungi is reduced by shade, the denser canopy in intermediate plots could have had a negative influence on root colonization by AM fungi (Chagnon et al. 2013), being a possible remedy the reduction of density through clearing technics.

Like ECM fungi, AM fungi also receive C from the host plant as a reward for providing the host with water and minerals (Chen et al. 2018; Gui et al. 2017; Bi et al. 2020). However, unlike ECM fungi, Barto and Rillig (2010) questioned whether C limitation could affect AM fungal colonization. Our observations indicated that the composition of the AM fungal community remains stable support this hypothesis. Martínez-García et al. (2011) reported that they did not find a clear link between the AM fungal community and the plant status and that AM fungal propagules of active symbionts could stay in the soil and be supported by herbaceous species growing below the shrubs. Douds (1994) observed that AM fungal spores can develop modest hyphal growth even lacking the host in the soil. Therefore, in senescent vegetation, with fewer resources, this may help the AM fungal community to show resilience to changes or disturbances in nutrient acquisition and, hence, maintain the composition of the community (Amalia et al. 2021). It has to be stated that the use of ITS primers for barcoding studies on AM fungi, instead of the 18 S region, could distort the interpretation of community patterns, underestimating the existing diversity (Berruti et al. 2017).

Influence of edaphic variables on the fungal community

There is a strong relationship between soil fungal diversity and edaphic variables (Zhang et al. 2017). In this study, the edaphic variables that most affected ECM fungal community composition were pH in senescent plots and N in intermediate plots, whereas AM fungi were affected by the quantity of dry matter. It is interesting that the only environmental variable that significantly influenced the AM fungal community composition was dry matter content given that a correlation has been shown between leaf concentration and AM fungal colonization (Olsson et al. 2007). Furthermore, AM fungi tend to accelerate litter decomposition rates and promote N uptake (Gui et al. 2017; Bi et al. 2020), which increases the soil C content (Daynes et al. 2013), coinciding with their higher richness levels in senescent plots where litter production is higher.

The association between soil pH and ECM fungi in senescent stands, contrary to what we proposed in our third hypothesis, may be due to pH stabilization throughout the succession. The composition of the ECM fungal community may change in response to soil pH variations as well as between early and more advanced successional stages (Fujiyoshi et al. 2011). Older plots tend to have a higher pH content and a lower richness and abundance of ECM fungi, which tend to dominate in low pH soils (Olsson et al. 2007). Moreover, soils with a high acidity tend to have an AM fungal community (Chagnon et al. 2013). An interesting management could be the implementation of mosaic design, maintaining diversity in stand age as its associated community through rejuvenation of aged areas recovering initial states of succession (Magarzo et al. 2023).

ECM fungi play an essential role in supplying N to plants (Pellitier and Zak 2018). These fungi are capable of greatly increasing the volume of soil available to the fine roots of their host plants, increasing the uptake of inorganic N by plants (Smith and Read 2008). In addition, they are able

to assimilate amino acids and amino sugars from the soil solution (Lilleskov et al. 2002), degrade proteins (Read and Perez-Moreno 2003) and transfer N content to plants (Näsholm et al. 2009). Therefore, at early successional stages, given that there is a greater abundance of ECM fungi than at later successional stages, a greater amount of N could be provided to the host plants. In senescent stands, most of the mobile mineral nutrients, namely N, P and potassium, are reabsorbed from the leaves to increase plant growth and form new leaves (Franklin and Ågren 2002; Niinemets et al. 2012), reducing their availability to fungi. However, the presence of AM fungi in associations it is essential to cover the plant necessities in P-deficient soils (Alguacil et al. 2008).

Despite *Rhizopogon* species were found to be linked mainly with *Pinus* stands (Molina and Trappe 1994), our species indicator analysis, showed this genus associated to senescent plots, which it has been previously linked to *Halimium* species (Leonardi et al. 2020). It has been observed associated to diverse energy sources (Beiler et al. 2010) facilitating its resistance in senescent plots. Furthermore, *R. evadens* it is associated to mature forests and its resistance also could be associated to it capacity of monopolize root tips (Kennedy et al. 2009). On the other hand, the species strongly linked by the analysis belonged to three different genera. Firstly, *Tomentella sublilacina* has a strong capacity of restoration after disturbance due to animal and aerial dispersion capacity being is quite dominant in matured forest ecosystems (Lilleskov and Bruns 2005). However, it has been associated also to bud-bursting trees (Unuk Nahberger et al. 2021), indicating also a wide range of hosts which could capacitate it more to be attached to younger plots in our study. Regarding *Cenococcum geophilum*, it is associated to cistaceous stands (Obase et al. 2017; Leonardi et al. 2020), and its relevance in an intermediate successional stage could be related to a possible role in primary nutrition due to its resistance to disturbance (Parladé et al. 2014). No information relating *Russula poichilochroa* to the intermediate stage could be found through bibliography.

Conclusions

The aim of this study was to understand the contribution of the soil mycorrhizal community associated with *H. lasianthum* during the final steps of its life cycle to help in the future design of management plans related to this type of shrub ecosystem through the development of age-related mosaic planification. As expected, the ECM and AM fungal community was richer and more abundant in the *H. lasianthum* intermediate plots, which are likely to have higher photosynthetic activity than the *H. lasianthum* senescent plots. Our observations also support those of previous studies that ECM fungal communities dominate in low pH and N-rich soils. AM fungal richness was greater in senescent plots; however, contrary to our expectations, our community analysis revealed that the Shannon diversity index and abundance did not vary significantly with stand age, giving the impression that the AM fungal community remained stable as the stand aged. Further research at a taxonomic level should be carried out to improve the characterization of the fungi associated with this widespread plant.

Despite the relevant results and conclusions found, we have to consider that our findings may be influenced by the presence of host plants situated close to the *Halimium* plants in the plots. The proximity of these hosts can enhance fungal diversity through spore dispersal mechanisms, facilitating the easier migration of fungal spores. Since fungi often depend on specific host plants for their growth and reproduction, the availability of nearby hosts can create a favorable environment for fungal colonization and development. As a result, the presence of these hosts can significantly affect the composition and abundance of the fungal community within the plots.

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Author contributions P. M-P. and C.F. worked on the conceptualization and on the supervision. P. M-P., C.F., R S-M. and I. S-B. worked on the Methodology and Investigation. R. S-M. did formal analysis. I. S-B. did the data curation and wrote the original draft. P. M-P., O. M., T. D., I. S-B. worked on writing- Reviewing and Editing. J.A. O-R. did the validation and P. M-P. got the funding acquisition.

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Data availability Sequence data that support the findings of this study have been deposited in GenBank: provisional submision number SUB11719157.

Declarations

Competing interests The authors declare no competing interests.

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