



Patterns and Drivers of Plant Arbuscular Mycorrhizal Traits Across a Peco-Climatic Gradient in Mediterranean Agroecosystems Under Desertification Risk

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Abstract

Desertification is a global concern, reducing vegetation cover and soil fertility. Arbuscular mycorrhizal symbiosis (AM), the most common plant-fungi association, can enhance plant fitness and stress tolerance. Despite its significance, comprehensive data on community-wide patterns and drivers of plant AM traits are limited in the Mediterranean, one of the regions most vulnerable to desertification. We examined four traits: colonization frequency, intensity, arbuscule abundance, and spore density in the rhizosphere of 20 plant species across ten agroecosystems in desertification-prone areas of Italy, Spain, and Portugal. We analysed whether these traits varied across Raunkiaer's plant life forms and were affected by vegetation cover, soil properties, precipitation, and temperature, both overall and regionally, to explore potential context-dependency. All plants showed a high frequency of AMF colonization, with an average intensity of 54%, indicating obligate AMF interactions, and arbuscule abundance was significantly correlated with spore density. These traits were significantly higher in microhabitats dominated by trees and shrubs compared to those dominated by herbaceous plants. Phanerophytes (perennials) presented lower trait values than therophytes (annuals), while the highest values were found in hemicryptophytes. Lampedusa, a region with hotter and drier climate conditions in Southern Europe, had significantly lower AMF trait levels, though Spanish site values resembled those in Sicily more than Portugal. Soil organic carbon, nitrogen, and the overall positive interaction between precipitation and temperature significantly influenced all AMF traits. However, the magnitude and direction of soil and climate related effects differed among regions, indicating strong context dependency. Our study contributes to better define indicators for monitoring desertification and evaluating restoration efforts while highlighting the need of site-specific evaluations and careful interpretation of broad generalisations.

Keywords Arbuscular Mycorrhizal Fungi (AMF) · Plant symbiosis · Desertification · Mediterranean ecosystems · Plant life- forms · Soil organic carbon

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Introduction

Land degradation threatens biodiversity and ecosystems, leading to vegetation loss, soil decline, and desertification [1, 2]. Arbuscular mycorrhizal fungi (AMF) symbiosis, the primary plant-fungi interaction worldwide, aids in combating desertification by reducing nutrient leaching, improving nutrient uptake, and boosting resistance to stressors such as warming and drought [3, 4]. Low AMF colonization intensities reduce host plant growth and stress tolerance, finally influencing vegetation dynamics [5–8]. AMF radical mycelium biomass can be up to four times higher than extraradical biomass, aiding therefore ecosystem services such as soil carbon storage [7, 9]. AMF root colonization and soil spore density have been used as key indicators of environmental change, reflecting respectively nutrient exchange efficiency and reproductive capacity [10, 11].

Abiotic factors, such as temperature, precipitation, and soil properties, influence plant-AMF relationships, but the findings vary widely. Increased temperatures can stimulate AM symbioses globally due to a change in energy allocation from storage (e.g. in vesicles) in cooler climates to hyphal expansion and spore production in warmer conditions [5]. However, such relationship is variable, with other studies reporting negative effects on hyphal development [12], positive effects on spore abundance with no impact on hyphal density [13] or variable responses shifting from positive to negative depending on warming intensity [5, 14]. Precipitation increases soil moisture and permeability, thus favouring plant growth, although its cascading influence on AMF root colonization is relatively limited on a global scale [15]. Conversely, the role of precipitation seems to be more relevant in drier regions such as the Mediterranean, for example constituting a primary factor impacting AMF colonization and spore abundance within the rhizosphere of a key tree species [16] and modulating the abundances of different AMF families [17].

Soil properties are also relevant factors in modulating plant-AMF colonization. Among these properties, soil organic carbon (SOC) may represent an important indicator, once carbon dynamics from the atmosphere to the soil are strongly mediated by plant-AMF relationships [9, 10]. Additionally, SOC levels influence the dynamics of other nutrients like nitrogen (N) and cation exchange capacity (CEC) [18]. N is a key element for plant growth, and together with phosphorus (P), is reported as the main nutrient AMF deliver to plants. However, the relationship of N and AMF root colonization are still not fully understood, with positive, neutral and negative effects observed in field and laboratory studies so far [5, 6, 15]. Given the main

nutrient exchange objective of plant-AMF relationship, in more fertile soils, such relationships are supposed to be less crucial once plants can access easily [10, 19, 20]. However, existing studies show that typically only a subset of soil variables account for AMF patterns, with effects that vary consistently or even contrast across different study areas, plant species, or spatial gradients [14, 21–23]. Additionally, the absence of standardized methods for selecting soil variables complicates the comparison and interpretation of soil properties' effects on AMF.

Several studies show that vegetation cover and plant life form are highly influential among biotic factors affecting AMF plant-root colonization. For example, vegetation cover can negatively affect AMF colonization by reducing plant carbon production through shading. In turn, cover can create favourable microenvironments by lowering temperature extremes and increasing SOC, thus with potential positive effects on AMF [24–26]. Plant life forms, such as those defined by the Raunkiaer, provide a consistent way to categorize plants based on their response to environmental stress [27]. Therefore, the magnitude of interaction with AMF is expected to vary across different plant life forms. However, how different cover types and plant life forms may predict AMF traits over broader scales remains largely unexplored [7, 28–30]. Recent molecular studies have advanced understanding of AMF distribution, diversity, and how biotic and abiotic variables modulate community composition [3, 5, 31–35]. However, few studies have evaluated simultaneously different AMF traits across a comprehensive set of plant species, cover types, and life forms in field conditions, particularly within the Mediterranean region e.g. [36, 37]. Additionally, it remains uncertain how such colonization patterns vary across larger spatial scales and pedoclimatic gradients, thereby limiting our understanding of the variability in the intimacy of plant-AMF relationships and consequent vegetation responses to climate change and desertification.

Our study aims to address these gaps by quantifying AMF traits (colonization frequency, intensity, arbuscule abundance, and spore density) of AMF in the rhizosphere of representative Mediterranean plant species. We tested their relationship with soil properties and climatic variables across a broad spatial gradient, from Sicily (Italy) to Extremadura (Spain) and Alentejo (Portugal), all areas highly vulnerable to desertification. Our objectives are to answer three main questions: (1) How significant is vegetation cover and plant life form in determining AMF traits? (2) What is the connection between soil physico-chemical properties and AMF traits? (3) Are the patterns and drivers of AMF traits consistent across different spatial scales?

Methods

Study Areas and Species Selection

Research was conducted at 10 sites across three Mediterranean Europe regions: four in southern Italy (Sicily), three in central Spain (Extremadura), and three in southern Portugal (Alentejo) (Fig. 1, Table S1). The sites represented extensively managed agroecosystems over a broad area with diverse climate, soil, and land cover, from mixed broad-leaf and coniferous forests to open pasturelands. All sites share high desertification sensitivity index [1]. For details, see [18, 38]. Lampedusa, located 150 km from Sicily has a distinct climate (Table S1) and vegetation (i.e. dominance of garrigue vegetation with endemic species and other species only found in the driest parts of Sicily), was treated separately. Plant species sampling aimed to include native species representative of each site (i.e. contributing to predominant cover) (Table S2, Table S3), as well as to comprehend different life forms according to Raunkiaer's classification obtained from <https://floraveg.eu>; [39]. This classification categorises such life forms considering the position and protection of the renewal buds and is widely

used to group plants in seasonal climates [27]. As a complementary sampling, we included one exotic species, the prickly pear (*Opuntia ficus-indica*), cultivated in one Sicilian site, in order to diversify the plant traits analyzed, given the known resistance to desertification of this cultivated species [40].

In total we analysed AMF colonization frequency, intensity and arbuscule abundance in 195 plant root samples and spore density in their rhizosphere soil. Plant specimens were assigned to 20 species across 11 families, including new quantitative records for AM symbiotic status for 12 wild species, not previously documented, and the first report for an endemic Sicilian species.

Root Colonization by Arbuscular Mycorrhizal Fungi (AMF)

In May 2018 and May 2022, we randomly collected healthy individual plants (i.e., predominantly green leaves, new shoots, and/or flowers) with similar heights (approximately 40–60 cm) across all vegetation cover types, manually extracting them with the topsoil (0–30 cm) in order to include their rhizosphere soil. Within a 5 m radius circular

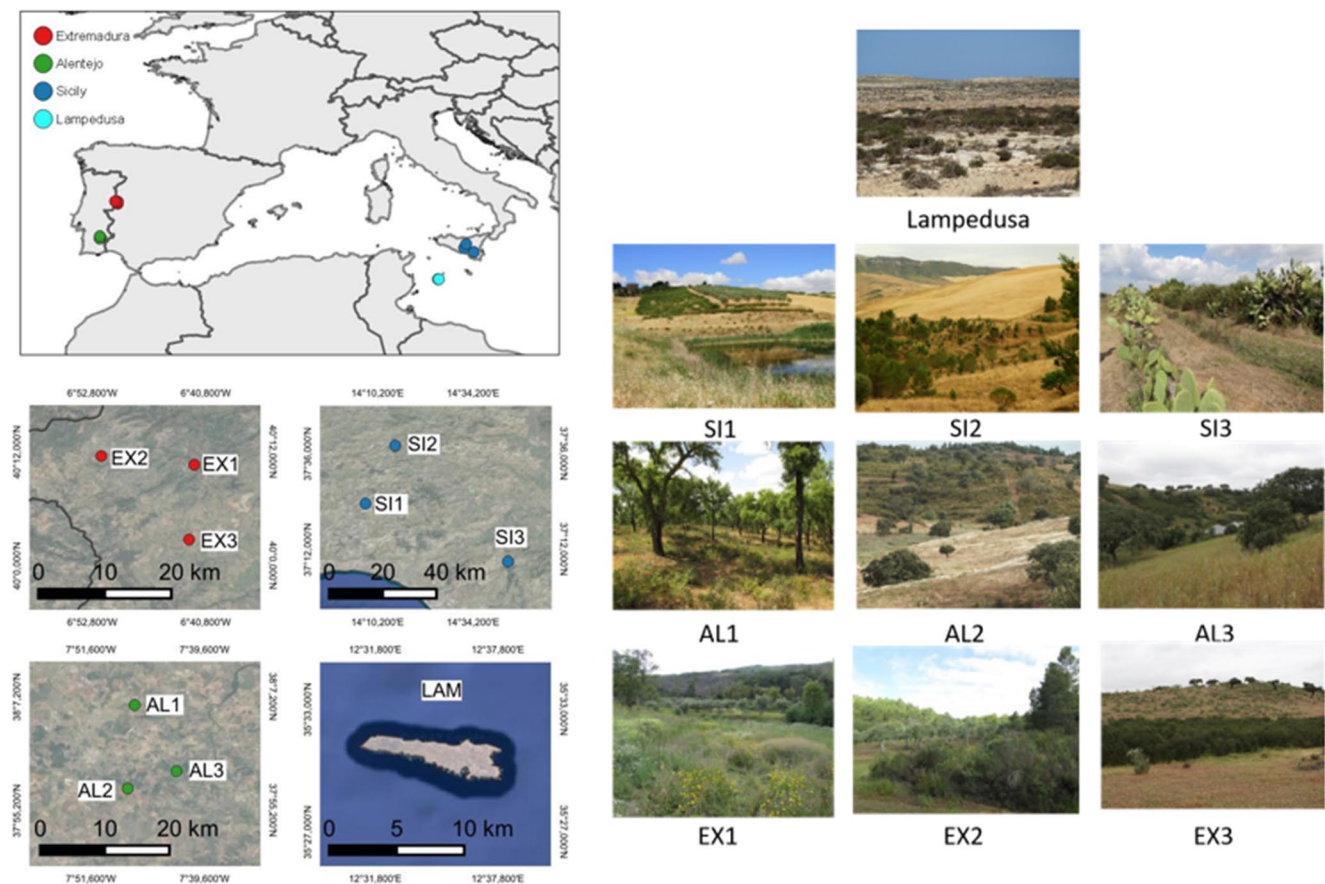


Fig. 1 Location and landscapes of the study sites across the four regions of Lampedusa (LAM) and Sicily (SI, Italy), Extremadura (EX, Spain) and Alentejo (A, Portugal)

plot around each sampled individual, dominant vegetation was classified into three main types (trees, shrublands, and herbaceous vegetation) with an additional prickly pear class for the Sicilian site (Figure S1). In the laboratory, roots were gently washed to remove any adherent soil and stored in distilled water at 4 °C until analysis. Subsamples of the finest roots were washed and stained following the procedure described by Phillips and Hayman [41], which involves three main steps: clearing with KOH (10%), acidification with HCl (2%), and staining with trypan blue (0.05%) in lactic acid. The stained roots were then immersed in lactic acid and stored in 20 ml tubes at 4 °C in the dark until further analysis. Quantitative assessment of AMF colonization on 1 cm finest root fragments ($N = 50$ when available and at least 25 per individual) was performed using a compound microscope at 50x magnification, following the procedure of Trouvelot et al. [42] and using the INOQ Calculator Advanced provided by Mercy [43]. This method determines the following parameters: frequency of root infection (F, hereafter frequency), estimated as percentage of root fragments containing any fungal structures (hyphae, vesicles, or arbuscules), indicating the overall colonization occurrence in the root system; colonization intensity of root cortex (M, hereafter intensity) providing the mean degree of colonization across all fragments, and arbuscule abundance in root cortex (A, hereafter arbuscule abundance), the proportion of colonized root cortex containing arbuscules, calculated as the percentage of arbusculated area relative to the total colonized area. All variables were expressed as percentages.

AMF Spore Density in Soil

Spores of arbuscular mycorrhizal fungi were isolated using the wet sieving and decanting method described by Gerde-mann and Nicolson [44], followed by density sucrose gradient centrifugation [45]. 100 g of air-dried root-rhizosphere soil was placed in a glass container with 1000 ml of tap water. The root-soil mixture was then vigorously mixed with a glass rod for 30 s. After a 10-second pause to allow heavier particles and organic matter to settle, the remaining soil-root-hyphae spore suspension was gently poured through a set of three sieves. The sieves had pores of 500–100–50 μm diameter. Most spores were retained on the 45 μm sieve. Spores were purified by re-suspending the sieving in the 60% sucrose solution and centrifugation was carried out at 3000 rpm for 2 min. The spores were taken at the interface between the two liquid phases, then rinsed in a filter of 40 μm pore size with distilled water to remove the sucrose. The top sieve captures large sporocarps and spores associated with roots, and the extracts were washed again from the sieves into 10 cm diameter Petri dishes. The spores were collected using a pipette or needle with the aid of a

dissecting stereoscope (Olympus Corporation, Tokyo, Japan Olympus SZ51) at 10x magnification and counted to determine spore density (number/g dry soil).

Temperature, Precipitation and Soil Physico-Chemical Analyses

The monthly mean temperature and total precipitation data were extracted from the ERA 5 Land dataset with a resolution of approximately 7 km [46]. Data from the last four months prior to sampling (January – April) were used for this analysis, as this period best reflects the accumulated soil moisture and is most relevant for plant development (growing seasons, flowering) in the Mediterranean. Soil physico-chemical properties were measured by sampling the topsoil (0–10 cm) from the immediate surroundings (< 2 m) of the sites where individual plants were collected. Soil samples were air-dried and sieved before analysing SOC (g C kg^{-1}), N (g N kg^{-1}), CEC ($\text{meq } 100 \text{ g}^{-1}$), and pH, following the procedures recommended by the Soil Survey Staff [47].

Literature Review Reporting AMF Symbiosis in the Plant Species

Previous information regarding AMF colonization for the plant species in our study was obtained through a database search on Scopus using as keywords both the genus and plant species, followed by “Myco”, “Mycorrhizae”, “Mycorrhizal”, “AMF”, “Arbuscular”, “Fungi”, “AM”, and “Root”. Inclusion criteria were articles that reported both quantitative (intensity of colonization) and qualitative (presence/absence) data on AMF. We focused on studies analysing at the species level, although we also reported some information at the genus level.

Statistical Analysis

All statistical analyses and figures were produced using R v 4.3.2 [48]. To account for different spatial scales (global and between regions), our analysis employed a two-step approach. First, we ran a global model with all data combined, then we created separate models for each region (excluding Lampedusa due to low variability in soil and climatic variables). To test the effects of soil properties (SOC, pH, TN, and CEC) and climatic variables (temperature and precipitation) on colonization intensity, arbuscule abundance and spores, we used generalised linear mixed models (GLMM, package glmmTMB) in the global models, including site as a random factor to account for spatial variability. In the regional models, random factors were not included due to the limited number of sites per region ($N = 3$). All models employed a backwards procedure, starting from the

full model and selecting the one with the lowest AICc [49], using the *MuMIn* package. Model fit and residual dispersion were evaluated simultaneously with the *performance* and *DHARMA* packages. For colonization intensity and arbuscule abundance (percentages), a beta distribution with a logit link was used [50], while for spores abundance (a count variable), a negative binomial distribution was applied due to high overdispersion in the Poisson and quasi-Poisson models. The same procedure was used to test differences across regions, vegetation cover, and life form. Because of the highly skewed distribution and very low variation in colonization frequency (> 75% of individuals exhibited > 97% colonization), this variable was not included in the environmental/soil GLMMS, and non-parametric tests (Kruskal-Wallis and Dunn post hoc test) were used to assess differences across vegetation cover, life forms, and regions. The R package *emmeans* was used to obtain estimated marginal means from the GLMMs; when significant differences emerged between categorical predictors (vegetation cover and life form), the pairwise function of *emmeans* was used for post-hoc comparisons. Interaction terms in the climatic model were removed if non-significant or if they decreased the model fit (increase in AICc). To account for potential temporal variations, data from both years were pooled for subsequent analyses. All soil and environmental predictors were standardized prior to analysis, and collinearity between predictors was checked by examining VIF

coefficients. Finally, a principal component analysis (PCA) was conducted to explore the relationship and dimensionality of the predictor variables across regions, soil, and environmental gradients.

Results

Patterns of AMF Colonization Frequency, Intensity and Abundance

All the species analysed were mycorrhizal and eleven had never been described as mycorrhizal before, including one endemic species to Lampedusa (*Chiliadenus lopadusanus*). Colonization frequency was generally high, with an average of 96% (± 9.06), ranging from 56.3% to 100%, indicating a potential obligate AMF association (Table 1). All species showed high average frequencies, with the lowest value for *Cistus ladanifer* (69.4%). The average colonization intensity was 54.4% (± 18.5), ranging from 6.1% to 94%. Species-specific values ranged from 12.9% for *Convolvulus lineatus* up to 66.3% for *Artemisia arborescens*. Arbuscule abundance averaged 22.7% (± 21.6), from 0.5% to 72.7%, with a high inter-specific variation, from 1.92% on *Thymelaea hirsuta* to 56.8% on *Artemisia arborescens*. Spore density was also highly variable and averaged 70.3 (± 56.2) spores/g soil, ranging from 4 to 226. Colonization

Table 1 Plant species, life form and number of individuals (N) sampled in our study and respective mean ($\pm$ SD) values of colonization frequency, intensity and arbuscule abundance and spores. The asterisks indicate species that have not been reported as mycorrhizal in the literature, to our knowledge. References reporting previous AM symbiosis observations are reported in table S4 The species indicated with ^c are endemic of the region

Life form	Family	Species	N	Frequency	Col. Intensity	Arbuscule ab.	Spore density
Chamaephyte	Asteraceae	<i>Chiliadenus lopadusanus</i> ^{ac}	6	100 (± 0)	39.58 (± 3.47)	3.28 (± 1.05)	39.17 (± 12.64)
	Convolvulaceae	<i>Convolvulus lineatus</i> [*]	6	96.1 (± 4.18)	12.87 (± 4.84)	2.32 (± 1.7)	10.17 (± 3.54)
	Fabaceae	<i>Cytisus multiflorus</i> [*]	12	99.67 (± 1.15)	61.64 (± 17.68)	10.58 (± 7.89)	22.04 (± 18.23)
	Lamiaceae	<i>Coridothymus capitatus</i>	6	100 (± 0)	49.18 (± 15.43)	5.35 (± 2.73)	56.99 (± 31.76)
Hemicryptophyte	Asteraceae	<i>Reichardia gaditana</i> [*]	6	90.13 (± 17)	60.15 (± 24.25)	47.72 (± 19.21)	142.13 (± 16.69)
	Poaceae	<i>Lygeum spartum</i>	3	100 (± 0)	48.27 (± 8.41)	36.07 (± 6.49)	89 (± 8)
Phanerophyte	Apocynaceae	<i>Periploca angustifolia</i> [*]	3	87.77 (± 4.23)	16.9 (± 4.54)	4.8 (± 2.55)	8 (± 1)
	Asteraceae	<i>Artemisia arborescens</i> [*]	3	100 (± 0)	66.23 (± 14.23)	56.83 (± 18.7)	114.67 (± 29.5)
	Cactaceae	<i>Opuntia ficus-indica</i>	12	92.86 (± 13.91)	55.25 (± 12.32)	16.95 (± 11.94)	58.83 (± 68.57)
	Cistaceae	<i>Cistus ladanifer</i> [*]	6	69.37 (± 9.2)	26.92 (± 6.43)	17.37 (± 3.25)	59.83 (± 9.62)
		<i>Cistus uris</i> [*]	3	94.7 (± 4)	55.03 (± 4.86)	43.23 (± 10.58)	132 (± 19)
	Lamiaceae	<i>Lavandula stoechas</i>	24	95.8 (± 10.11)	53.57 (± 9.69)	25.98 (± 19.77)	70.85 (± 54.94)
	Liliaceae	<i>Asparagus acutifolius</i>	12	98.47 (± 2.89)	57.95 (± 10.52)	27.59 (± 18.28)	40.43 (± 21.11)
	Thymelaeaceae	<i>Thymelaea hirsuta</i>	6	96.08 (± 6.3)	14.52 (± 7.49)	1.92 (± 1.66)	16.5 (± 9.14)
Therophyte	Asteraceae	<i>Andryala integrifolia</i>	36	99.43 (± 1.58)	65.57 (± 11.1)	39.51 (± 21.71)	90.5 (± 69.67)
		<i>Anthemis secundiramea</i> [*]	3	81.1 (± 18.37)	60.83 (± 3.12)	7.13 (± 1.97)	26.33 (± 2.52)
	Brassicaceae	<i>Diplotaxis scaposa</i> [*]	3	92.5 (± 10.61)	36.05 (± 5.16)	5.35 (± 0.78)	17.5 (± 2.12)
	Fabaceae	<i>Lotus edulis</i> [*]	3	98.87 (± 0.98)	45.47 (± 8.91)	27.9 (± 11.81)	87.67 (± 22.74)
	Poaceae	<i>Avena fatua</i>	36	97.12 (± 7.01)	63.1 (± 13.87)	38.09 (± 19.67)	91.64 (± 50.06)
		<i>Hordeum leporinum</i>	3	100 (± 0)	70.07 (± 7.2)	53.93 (± 1.7)	129.33 (± 33.5)
		<i>Lolium multiflorum</i>	3	95.3 (± 4.4)	49.9 (± 5.4)	35.4 (± 4.6)	47.6 (± 12.5)

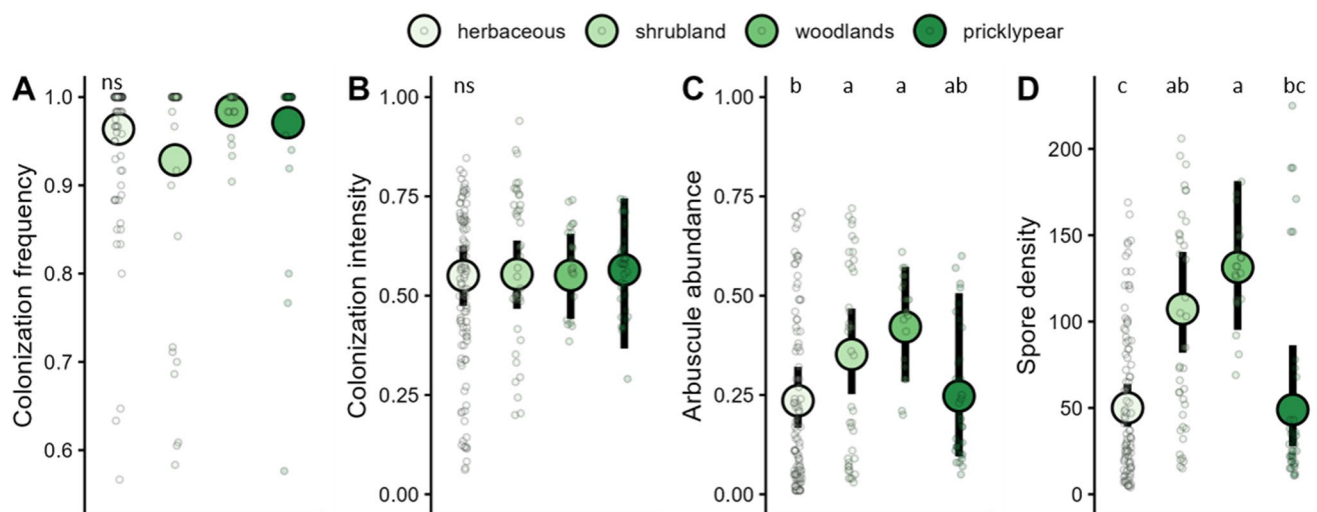


Fig. 2 Patterns of AMF colonization frequency (A) intensity (B), arbuscules abundance (C) and spore density (D) across the four vegetation cover types surrounding the sampled individuals in the study sites of Sicily and Lampedusa (Italy), Extremadura (Spain) and Alentejo (Portugal). Large circles indicate means and bars indicate $\pm 95\%$

CI testing differences between cover types. Means $\pm 95\%$ CI in B, C and D estimated by GLMMs. Small circles show observed values. Different letters indicate significant differences after *emmeans* pairwise comparisons. ns = non-significant

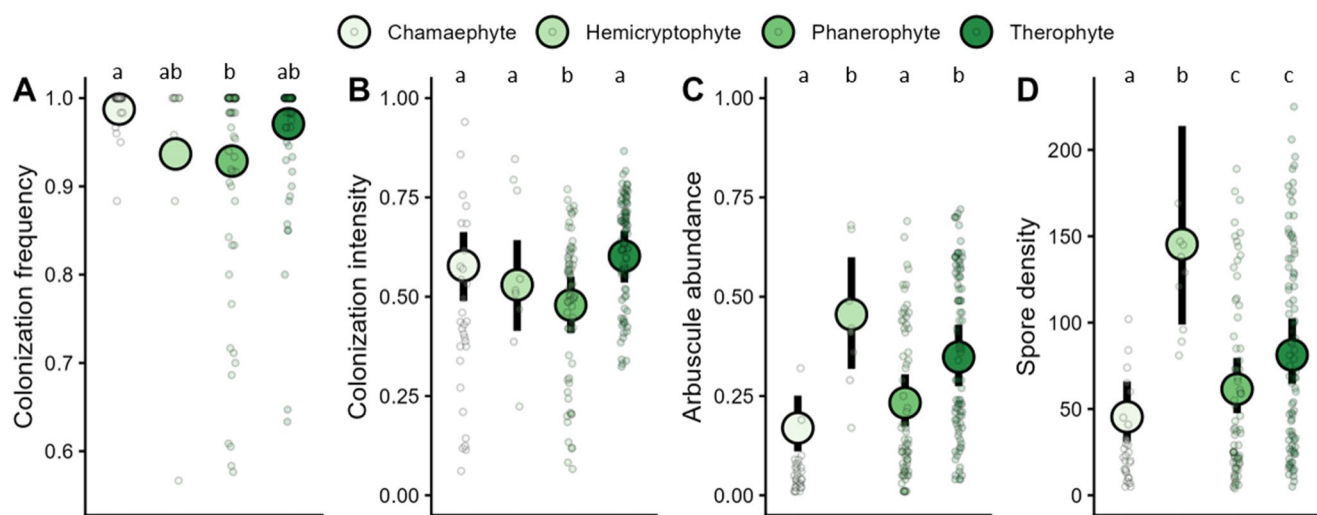


Fig. 3 Patterns of AMF colonization frequency (A) intensity (B), arbuscules abundance (C) and spore density (D) across the four life form types in the study sites of Sicily and Lampedusa (Italy), Extremadura (Spain) and Alentejo (Portugal). Large circles indicate means and bars indicate $\pm 95\%$ CI testing differences between life forms. Means $\pm 95\%$

CI in B, C and D estimated by GLMMs. Small circles show observed values. Different letters indicate significant differences after Dunn test for frequency and *emmeans* pairwise comparisons for colonization intensity, arbuscule abundance and spore density. ns = non-significant. Life forms of the plant species analysed are indicated in Table 1

intensity was positively correlated with frequency, arbuscule abundance, and spore density. Spore density was also highly correlated with arbuscule abundance (Supplementary Figure S2).

Variation Across Vegetation Cover and Life Form

GLMM analysis indicated that AMF colonization frequency and intensity did not differ significantly in plants sampled across the four vegetation types (namely

herbaceous, shrubland, trees, prickly pear crop; $\chi^2 = 0.16$, $p = 0.98$; Fig. 2, Table S5). However, arbuscule abundance ($\chi^2 = 11.1$, $p = 0.011$) and spore density ($\chi^2 = 34.05$, $p < 0.001$) showed higher values in tree- and shrub-dominated areas than in herbaceous zones. Pairwise *emmeans* comparisons showed significant differences in mycorrhizal status among plant life forms (Fig. 3, Table S6). Chamaephytes, that include *Chiliadenus lopadusanus*, *Convolvulus lineatus*, *Cytisus multiflorus* and *Coridothymus capitatus*, showed high colonization frequency

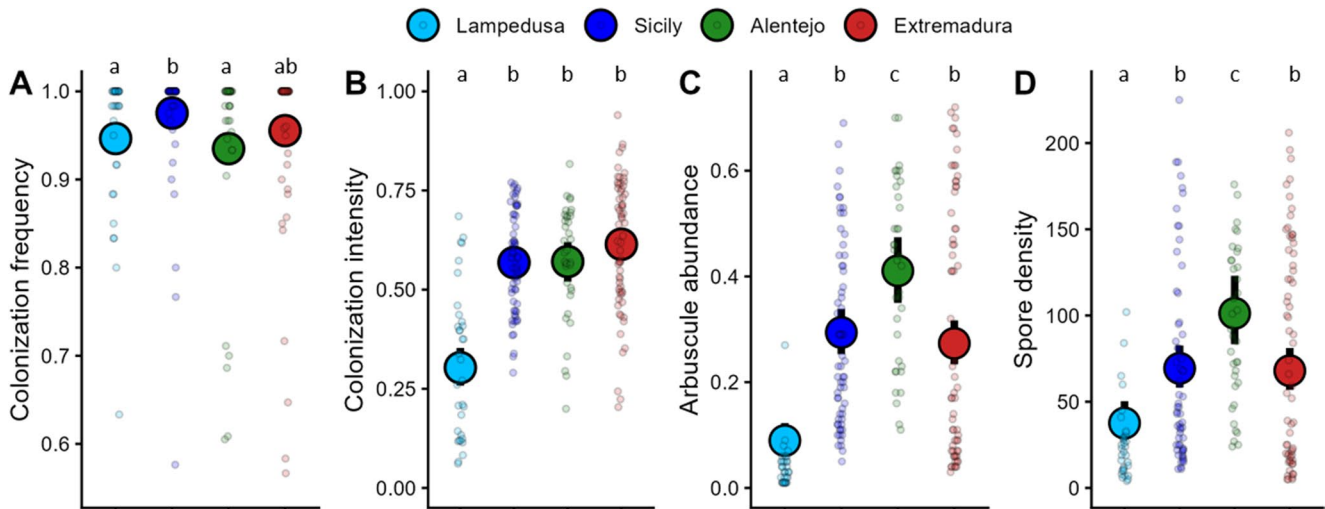


Fig. 4 Patterns of colonization frequency (**A**) intensity (**B**), arbuscules abundance (**C**) and spore density (spore/g soil⁻¹) (**D**) across the study regions of Lampedusa and Sicily (Italy), Extremadura (Spain) and Alentejo (Portugal). Large circles indicate means and bars indi-

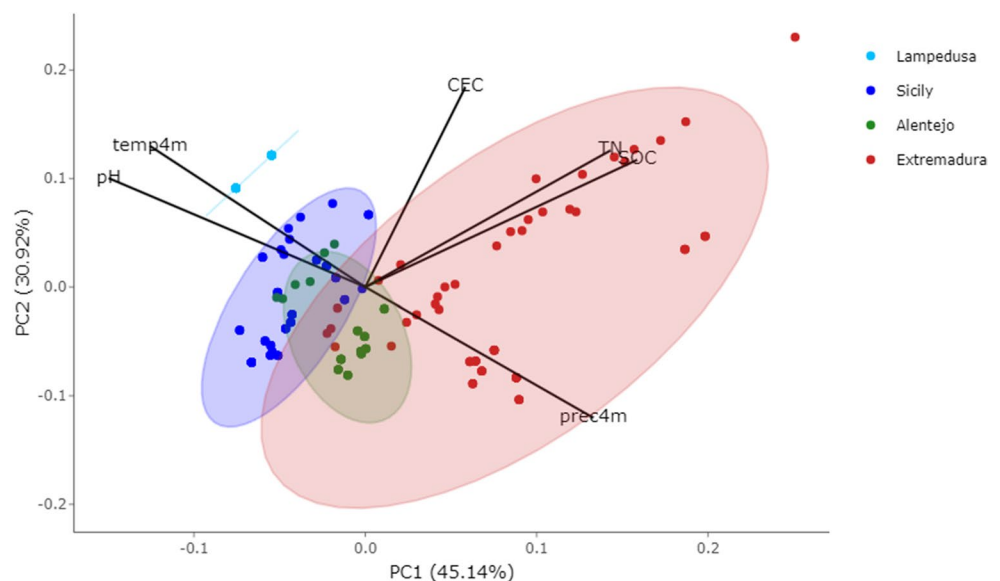
cate $\pm 95\%$ CI testing differences between regions. Means $\pm 95\%$ CI in B, C and D estimated by GLMs. Small circles show observed values. Different letters indicate significant differences after Dunn test for frequency and *emmeans* pairwise comparisons for the others

and intensity but low arbuscule and spore density levels. Hemicryptophyte (including *Reichardia gaditana* and *Lygeum spartum*), conversely, displayed the highest arbuscule abundance and spore density. Phanerophytes (Table 1, including *Periploca angustifolia*, *Artemisia arborecens*, *Opuntia ficus-indica*, *Cistus ladanifer*, *Cistus uris*, *Lavandula stoechas*, *Asparagus acutifolius*, *Thymelaea hirsuta*) had lower colonization values than other groups, with overall lower AMF colonization in woody perennials (Phanerophytes) than in herbaceous annuals plants (Therophytes).

AM Symbiosis Variability Across Regions

Colonization frequency ($\chi^2=12.7$, $p=0.005$), intensity ($\chi^2=90.9$, $p<0.001$), arbuscule abundance ($\chi^2=80.2$, $p<0.001$), and spore density ($\chi^2=32.8$, $p<0.001$) all significantly varied across the four southern Mediterranean regions (Fig. 4, Table S5). The first and second PCA axes, representing soil, precipitation, and temperature, explained 66.28% of the dataset variation, illustrating the broad environmental variability of our sites while showing some overlap even across sites thousands of kilometres apart (Fig. 5).

Fig. 5 Biplot of principal component analyses (PCA) showing the soil (SOC, TN, pH, CEC) and environmental gradient (precipitation and temperature in the last 4 months) sampled across the four regions



However, no clear geographical pattern of AMF colonization was evident. AMF traits values on Portuguese sites differed from both the closer Spanish locations and the more distant Sicilian sites, although Sicily and Alentejo exhibit roughly similar abiotic characteristics (Fig. 5). Lampedusa plants displayed significantly lower intensities of AMF colonization and spore abundances than all other sites (Fig. 4), confirming that the geographic location of Lampedusa also corresponds to a pedoclimatic extreme for Southern Europe, likely representing the conditions found in North Africa.

Effects of Soil Properties, Precipitation and Temperature

GLMM models showed variable and sometimes contradictory relationships between soil properties and fungal traits, both globally and in the three southern European regions. Globally, SOC and TN mainly influenced these traits, but their effects varied: colonization intensity was positively related, while arbuscule abundance and spore density were negatively affected by SOC and TN (Table 2). Spore density was negatively affected by CEC, whereas soil pH showed no significant effect. Regionally, patterns were more diverse, with no single predictor significant for all response variables. For example, SOC positively influenced colonization intensity and arbuscule abundance in Sicily, but negatively impacted them and also spore density in Extremadura, while the effect of SOC was not significant in Alentejo. TN effects were opposite to SOC, while pH negatively affected arbuscule abundance and spore density in more acidic Iberian sites but positively in Sicily, where conditions are more neutral.

The effects of temperature and precipitation on colonization intensity varied in direction and significance —non-significant for precipitation and negative for temperature overall, but positive for both parameters in Extremadura (Table 3).

Precipitation was positively related to arbuscule abundance and spore density across models. The GLMM indicated a significant positive interaction between precipitation and temperature in the global model, suggesting that as temperature increases, precipitation's impact on these traits also increases (Table 3).

Discussion

AMF traits related to root colonization and dispersion (spores) are key indicators of plant-AMF relationships, essential for understanding vegetation dynamics, nutrient cycling, and tracking climate change and desertification effects. Our study advances knowledge of AMF symbiosis

by measuring colonization frequency, intensity, arbuscule abundance, and spore density at the community level and relating these to vegetation type, plant form, soil, temperature, and precipitation across 10 Mediterranean sites. It also expands understanding of the mycorrhizal status of key Mediterranean species, including endemics previously unreported as mycorrhizal, providing a comprehensive base layer to monitor temporal dynamics and the effects of climate change on plant community development in Southern Europe.

Patterns of AMF Colonization Frequency, Intensity, Arbuscule Abundance and Spore Density

All roots of the analysed plant species were colonised by AMF, suggesting a potentially beneficial relationship. AMF colonization and arbuscule abundance detected in this study were generally higher compared to other Mediterranean studies, including herbaceous, shrubs and tree species [16, 25, 36, 51]. Similar levels were observed in a Sicilian endemic tree [52], and even higher values were reported in five woody species on gypsum soils in Spain [53], highlighting context-dependency. Although these previous studies contributed to our understanding of AMF traits in the Mediterranean, none analysed the four traits simultaneously as we did in our study, thus limiting deeper comparisons.

In our study, arbuscule abundance and spore densities were always highly correlated (Supplementary S2), following similar patterns regardless of life form, cover type, or region (Figs. 2, 3 and 4), indicating that increased spore density corresponds with higher colonization and vice versa.

AMF Traits Across Vegetation Cover and Life Form

Our investigation shows variable effects of vegetation cover type on AM symbiosis traits. Colonization frequency and intensity were unaffected, but arbuscule abundance and spore density were higher in plant samples from woodland or shrubland contexts. Shrubs and trees alter soil properties, reduce grazing by large herbivores, moderate temperature, and increase moisture, which positively influence AMF [26, 54–56], although, shaded environments near shrubs and trees may lower photosynthesis and AMF colonization [57]. Mediterranean studies showed shading's limited impact on colonization [51], and the higher arbuscule and spore levels near shrubs and trees in our study suggest greater nutrient exchange, dispersal potential and overall soil benefit by roots. The effect of woody cover (e.g., hedgerows) was reported beneficial not only on AMF colonization but also on AMF diversity in agricultural lands [56, 58, 59]. Given that one consequence of desertification is the gradual loss of vegetation cover, particularly trees, our results suggest

Table 2 Summary of the GLMM (all sites) and GLM (regions) results examining how soil variables influence colonization intensity, arbuscule abundance, and spore density (n. spores g⁻¹ soil dw) across all regions and individually by region. Lampedusa was included exclusively in the all regions analysis

	Colonization intensity				Arbuscule abundance				Spore density			
	Estimate	SE	t	p	Estimate	SE	Z	p	Estimate	SE	Z	p
All sites												
Intercept	0.23	0.15	1.55	0.12	-0.91	0.20	-4.60	< 0.001	4.23	0.13	33.16	< 0.001
SOC	0.33	0.11	2.97	0.003	-0.63	0.20	-3.18	0.001	-0.55	0.17	-3.21	0.001
pH												
TN	-0.34	0.10	-3.35	< 0.001	0.37	0.16	2.32	0.020	0.46	0.14	3.33	< 0.001
CEC									-0.20	0.09	-2.40	0.017
Sicily												
Intercept	0.53	0.16	3.30	< 0.001	-0.73	0.28	-2.62	0.008	3.96	0.22	18.24	< 0.001
SOC	0.73	0.37	1.98	0.048	0.91	0.34	2.65	0.008	0.73	0.14	5.29	< 0.001
pH					0.58	0.15	3.84	< 0.001	0.44	0.20	2.19	0.029
TN	-0.31	0.22	-1.43	0.153	-0.16	0.07	-2.30	0.021	-0.11	0.06	-1.82	0.068
CEC												
Extremadura												
Intercept	0.50	0.09	5.55	< 0.001	-0.66	0.14	-4.67	< 0.001	3.20	0.62	5.15	< 0.001
SOC					-0.62	0.17	-3.72	< 0.001	-0.54	0.16	-3.42	< 0.001
pH									-1.34	0.63	-2.14	0.032
TN					0.45	0.15	2.88	0.004	0.19	0.13	1.49	0.136
CEC	-0.17	0.10	-1.65	0.098								
Alentejo												
Intercept	0.59	0.17	3.54	< 0.001	-0.91	0.29	-3.18	0.001	4.08	0.17	23.60	< 0.001
SOC												
pH					-1.21	0.61	-2.00	0.045	-1.29	0.35	-3.65	< 0.001
TN									1.82	0.33	5.59	< 0.001
CEC	0.39	0.18	2.15	0.032					-0.45	0.13	-3.35	< 0.001

Table 3 Results of the GLMM (all sites) and GLM (regions) showing the overall effects of precipitation, temperature and their interaction on colonization intensity (%), arbuscule abundance and spores (n. spores g⁻¹ soil dw) in all regions and for each region

All sites	Colonization intensity				Arbuscule abundance				Spore density			
	Estimate	SE	t	p	Estimate	SE	Z	p	Estimate	SE	Z	p
Intercept	0.28	0.08	3.52	<0.001	-1.08	0.18	-6.04	<0.001	4.01	0.16	25.20	<0.001
Precipitation	0.12	0.11	1.08	0.28	1.09	0.13	8.32	<0.001	1.13	0.11	10.16	<0.001
Temperature	-0.26	0.10	-2.65	0.008	-0.14	0.16	-0.88	0.38	0.20	0.13	1.55	0.12
Prec*Temp	0.21	0.07	3.01	0.003	0.20	0.10	2.10	0.04	0.16	0.08	2.12	0.034
Sicily												
Intercept	0.04	0.13	0.34	0.73	-0.46	0.17	-2.75	0.006	5.13	0.13	40.26	<0.001
Precipitation	-0.04	0.10	-0.43	0.660	0.81	0.13	6.13	<0.001	3.00	0.35	8.53	<0.001
Temperature	-0.69	0.35	-2.01	0.045	0.12	0.44	0.27	0.791	1.65	0.34	4.83	<0.001
Prec*Temp									5.13	0.87	5.93	<0.001
Extremadura												
Intercept	0.74	0.15	5.04	<0.001	-1.71	0.17	-10.13	<0.001	3.05	0.11	27.21	<0.001
Precipitation	0.35	0.12	2.80	0.005	1.58	0.16	9.68	<0.001	1.27	0.12	10.69	<0.001
Temperature	0.67	0.21	3.25	0.001	0.35	0.31	1.13	0.258	-0.39	0.21	-1.88	0.060
Prec*Temp					0.29	0.19	1.57	0.117	0.40	0.13	3.02	0.003
Alentejo												
Intercept	-1.43	1.40	-1.02	0.309	3.61	2.38	1.51	0.13	3.75	1.00	3.74	0.000
Precipitation	1.83	1.54	1.19	0.234	0.32	1.56	0.20	0.830	2.93	0.65	4.49	<0.001
Temperature	2.23	1.76	1.27	0.205	-10.15	4.50	-2.26	0.024	-1.64	1.90	-0.87	0.386
Prec*Temp					-14.48	5.44	-2.66	0.008	-5.64	2.31	-2.44	0.014

adverse feedback effects on plant-AMF relationships under this scenario.

Finding common trends of AMF traits within plant communities is challenging, as significant differences in AMF colonization can occur along ontogeny and within varieties of the same species [16]. Another issue is that a limited number of AMF traits and plant species are evaluated simultaneously, and there is an overall lack of standardisation in plant grouping criteria. For instance, Navarro-Fernández et al. [36] reported no relation between morphological plant traits and AMF colonization in Mediterranean species, and Mohammad et al. [60] observed no effect of host plant identity on spore density in semi-arid areas.

Different from these studies, in our community analysis, the Raunkiaer life form grouping allowed us to observe some AM patterns. Chamaephytes presented high mycorrhizal frequency and intensity but the lowest values of arbuscule abundance and spore density, while hemicryptophytes maintained a more consistent trend, sharing the highest proportions of arbuscule abundance with therophytes. Interestingly, phanerophytes (i.e. perennial woody plants) had significantly lower values of colonization intensity and arbuscule abundance than therophytes (annuals), regardless of no differences in spore density. Therophytes and chamaephytes are the most common plant life-forms in the Mediterranean, while hemicryptophytes are more common in temperate areas [27]. A recent work has demonstrated that hemicryptophytes are abundant in the understory of forests and woodlands and can influence AMF dynamics considerably in temperate forests [61]; our results indicate that such influence might be also relevant in the Mediterranean, where their arbuscule abundance and soil spore density, could better maintain AMF propagules in soils thus increasing the soil mycorrhizal inoculum potential available for the entire plant community. These evidences are useful for ecological restoration strategies, including soil and vegetation protection. AMF communities generally show low endemism, being dominated by few species or genera, with limited changes over time, especially in arid and semi-arid areas [24, 37, 60, 62]. A recent global study verified that fungal community composition varies across plant functional groups [30], with vegetation cover better predicting fungal functional groups than soil properties and climate in Europe [32]. Our results indicate that the Raunkiaer's plant life forms classification might be an informative community descriptor to be considered in further community wide studies, particularly in regions such as the Mediterranean where plant communities are expected to be highly modulated by seasonal climatic conditions [27]. Moreover, desertification is expected to change plant community composition, so further studies might evaluate how AMF communities and colonization patterns adjust across these changes.

AMF Colonization Variability Across Regions

AMF colonization intensity was similar among all sites except for Lampedusa where the lowest colonization intensity, arbuscule abundance and spore density were observed. Lampedusa is characterized by lower precipitation, higher temperatures and aridity index (Table S1) aligning with the climate trade-off hypothesis that more extreme environments limit AMF colonization [5, 14]. However, Lampedusa plants AMF traits values are comparable to other Mediterranean sites with milder climates [36] and even higher than in semi-arid areas [16, 63], highlighting the complexity of the drivers shaping AMF colonization patterns. Notably, arbuscule abundance and spore density differed significantly between Alentejo and Extremadura, which share most plant species, while plants in Sicily showed similar values to those in Extremadura, indicating a geographical pattern that is worth further investigation.

Effects of Soil Properties, Precipitation and Temperature

AMF-plant relationships are complex and the influence of abiotic factors varies with scale, being less relevant than biotic factors regionally [64]. Additionally, some studies show that soil nutrients and moisture do not affect AMF colonization of Mediterranean tree seedlings [51].

Our study confirms contrasting effects of abiotic variables across scales and AMF traits, with no predictor showing consistent direction or significance (Table 2). For instance, pH, relevant for defining the AMF niche and distribution [21, 65], was irrelevant across all scales despite wide pH variation (4.24 to 8.43). SOC was positively linked to AMF colonization in the Mediterranean [36, 60], and our GLMM supports this overall and in Sicily, although not in Alentejo and Extremadura. Interestingly, SOC was positively associated with soil microbial biomass at the same sites [38], aligning with the overall effects on colonization intensity. Given that high intraradical hyphae colonization generally indicates high extraradical hyphae development, future research could explore the extent to which, under our field conditions, high AMF intraradical colonization is contributing or not to increasing overall SOC in such a feedback loop. Conversely, SOC was negatively associated with arbuscule abundance and spore density overall, suggesting a potential threshold along the functional equilibrium gradient.

The AMF–SOC relationship remains complex and possibly nonlinear in some contexts. For example, SOC proportions have been found to affect the dynamics of other nutrients in our sites [18], and other unexamined soil properties may also have a significant impact [36]. Additionally, AMF may even directly contribute to soil carbon storage by

improving soil structure through glomalin production [66, 67].

We observed contrasting effects of N on AMF traits. TN was negatively related to colonization but positively related to arbuscule abundance and spore density. AMF influences N cycling and supports plant N uptake [68], and negative relationship between soil N and AMF colonization might be expected because abundant N allows plants to absorb it directly, as recently reported in meta-analysis on N addition experiments [6, 10]. The GLMM revealed that arbuscule abundance and spore density, which are linked to AMF nutrient exchange and dispersal, increased with N levels—a pattern also observed in smaller-scale studies [21]. CEC is a variable that reflects soil micronutrient content and potential nutrient flow, but variable effects of CEC were seen in Mediterranean AMF communities [21]. Moreover, the effects of soil predictors varied significantly across regions, highlighting the complex and context-dependent nature of AMF-plant relationships, as different species react differently to soil properties even in similar habitats [10, 64]. Finally, since nutrient acquisition by AMF may be influenced by soil bacterial communities [33], future research could attempt to link the previously characterised microbial communities [38] with AMF-plant functional outcomes in our sites.

Our results show that temperature and precipitation significantly influence AMF traits, albeit with variable effects. Temperature was a better predictor of colonization intensity but had weak and regionally variable links with arbuscule abundance and spore density. Among the three main regions, Alentejo sites showed the highest mean temperatures over the last four months, yet positive temperature effects were likely influenced by higher precipitation. This aligns with Mediterranean studies where temperature affected colonization and spore density broadly, but varied locally [16]. Conversely, precipitation resulted non-significant for colonization intensity (with the exception of Extremadura). In turn, precipitation strongly predicted arbuscule abundance and spore density, in line with studies made globally [62, 66] and in Europe [32], including the Mediterranean [16, 36].

In conclusion variability in model results reflects the context-dependent nature of AMF relationships across scales and the complex interactions among abiotic/biotic factors, and AMF communities [64]. Finally, further research could include genetic analysis to identify the community composition, AMF guilds, and ecological strategies responsible for the widespread colonization pattern observed in our study, while also considering other factors not evaluated here, e.g. grazing pressure [69]. Our study provides a unique contribution to understanding AMF plant-root colonization traits at various scales in the Mediterranean, along with how biotic and abiotic

factors influence these traits and their dependence on context. Climate change impacts temperature and precipitation patterns, while desertification gradually alters plant species composition, reduces woody vegetation cover, and decreases soil organic matter. Consequently, our research establishes a foundational framework that can improve indicators used to monitor, compare, and predict the effects of climate change and desertification, as well as to assess the effects of restoration efforts.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

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References

- Mirzabaev A, Wu J, Evans J, Garcia-Oliva F, Hussein IAG, Iqbal MH, Kimutai J, Knowles T, Meza F, Nedjroaoui D, Tena F, Türkeş M, Vázquez RJ, Weltz M (2019) Desertification. In: Shukla, PR, Skeg, J, Calvo Buendia, E, Masson-Delmotte, V, Pörtner, HO, Roberts, DC, Zhai, P, Slade, R, Connors, S, van Diemen, S, Ferrat, M, Haughey, E, Luz, S, Pathak, M, Petzold, J, Portugal Pereira, J, Vyas, P, Huntley, E, Kissick, K, Belkacemi, M, Malley, J (eds.) Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems
- Reynolds JF, Smith DMS, Lambin EF, Turner BL, Mortimore M, Batterbury SPJ, Downing TE, Dowlatabadi H, Fernández RJ, Herrick JE, Huber-Sannwald E, Jiang H, Leemans R, Lynam T, Maestre FT, Ayarza M, Walker B (2007) Global desertification: Building a science for dryland development. *Science* 316:847–851. <https://doi.org/10.1126/science.1131634>
- Meng Y, Davison J, Clarke JT, Zobel M, Gerz M, Moora M, Öpik M, Bueno CG (2023) Environmental modulation of plant mycorrhizal traits in the global flora. *Ecol Lett* 26:1862–1876. <https://doi.org/10.1111/ele.14309>
- Cavagnaro TR, Bender SF, Asghari HR, Heijden, MGAvd (2015) The role of arbuscular mycorrhizas in reducing soil nutrient loss. *Trends Plant Sci* 20:283–290. <https://doi.org/10.1016/j.tplants.2015.03.004>
- Hu H, He L, Ma H, Wang J, Li Y, Wang J, Guo Y, Ren C, Bai H, Zhao F (2022) Responses of AM fungal abundance to the drivers of global climate change: A meta-analysis. *Sci Total Environ* 805:150362. <https://doi.org/10.1016/j.scitotenv.2021.150362>
- Han Y, Feng J, Han M, Zhu B (2020) Responses of arbuscular mycorrhizal fungi to nitrogen addition: A meta-analysis. *Global Change Biol* 26:7229–7241. <https://doi.org/10.1111/gcb.15369>
- Barceló M, van Bodegom PM, Tedersoo L, den Haan N, Veen GF, Ostonen I, Trimbos K, Soudzilovskaia NA (2020) The abundance of arbuscular mycorrhiza in soils is linked to the total length of roots colonized at ecosystem level. *PLoS ONE* 15:e0237256. <https://doi.org/10.1371/journal.pone.0237256>
- Augé RM, Toler HD, Saxton AM (2015) Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. *Mycorrhiza* 25:13–24. <https://doi.org/10.1007/s00572-014-0585-4>
- Hawkins H-J, Cargill RIM, Van Nuland ME, Hagen SC, Field KJ, Sheldrake M, Soudzilovskaia NA, Kiers ET (2023) Mycorrhizal mycelium as a global carbon pool. *Curr Biol* 33:R560–R573. <https://doi.org/10.1016/j.cub.2023.02.027>
- Bennett AE, Groten K (2022) The costs and benefits of Plant–Arbuscular mycorrhizal fungal interactions. *Annu Rev Plant Biol* 73:649–672. <https://doi.org/10.1146/annurev-arplant-102820-124504>
- Brundrett MC, Tedersoo L (2018) Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytol* 220:1108–1115. <https://doi.org/10.1111/nph.14976>
- Staddon PL, Thompson K, Jakobsen I, Grime JP, Askew AP, Fitter AH (2003) Mycorrhizal fungal abundance is affected by long-term Climatic manipulations in the field. *Global Change Biol* 9:186–194. <https://doi.org/10.1046/j.1365-2486.2003.00593.x>
- Kim Y-C, Gao C, Zheng Y, He X-H, Yang W, Chen L, Wan S-Q, Guo L-D (2015) Arbuscular mycorrhizal fungal community response to warming and nitrogen addition in a semiarid steppe ecosystem. *Mycorrhiza* 25:267–276. <https://doi.org/10.1007/s00572-014-0608-1>
- Soudzilovskaia NA, Douma JC, Akhmetzhanova AA, van Bodegom PM, Cornwell WK, Moens EJ, Treseder KK, Tibbett M, Wang Y-P, Cornelissen JHC (2015) Global patterns of plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. *Glob Ecol Biogeogr* 24:371–382. <https://doi.org/10.1111/geb.12272>
- Ma X, Geng Q, Zhang H, Bian C, Chen HYH, Jiang D, Xu X (2021) Global negative effects of nutrient enrichment on arbuscular mycorrhizal fungi, plant diversity and ecosystem multifunctionality. *New Phytol* 229:2957–2969. <https://doi.org/10.1111/nph.17077>
- Meddad-Hamza A, Hamza N, Neffar S, Beddiar A, Gianinazzi S, Chenhoumi H (2017) Spatiotemporal variation of arbuscular mycorrhizal fungal colonization in Olive (*Olea Europaea* L.) roots across a broad mesic-xeric Climatic gradient in North Africa. *Sci Total Environ* 583:176–189. <https://doi.org/10.1016/j.scitotenv.2017.01.049>
- Alguacil MM, Schlaeppi K, López-García Á, van der Heijden MGA, Querejeta JI (2022) Contrasting responses of arbuscular mycorrhizal fungal families to simulated climate warming and drying in a semiarid shrubland. *Microb Ecol* 84:941–944. <https://doi.org/10.1007/s00248-021-01886-6>
- Grilli E, Carvalho SCP, Chiti T, Coppola E, D’Ascoli R, La Mantia T, Marzaioli R, Mastrocicco M, Pulido F, Rutigliano FA, Quatrini P, Castaldi S (2021) Critical range of soil organic carbon in Southern Europe lands under desertification risk. *J Environ Manage* 287:112285. <https://doi.org/10.1016/j.jenvman.2021.112285>
- Johnson NC (2010) Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytol* 185:631–647. <https://doi.org/10.1111/j.1469-8137.2009.03110.x>
- Rog I, van der Heijden MGA, Bender F, Bousageon R, Lambach A, Schlaeppi K, Bodenhausen N, Lutz S (2025) Mycorrhizal inoculation success depends on soil health and crop productivity. *FEMS Microbiol Lett* 372. <https://doi.org/10.1093/femsle/fnaf031>
- Avio L, Njeru EM, Oehl F, Turrini A, Bocci G, Barberi P, Giovannetti M, Sbrana C (2020) Small-scale soil heterogeneity affects the distribution of arbuscular mycorrhizal fungal species in a hot-spot field in a mediterranean site. *Appl Soil Ecol* 154:103631. <https://doi.org/10.1016/j.apsoil.2020.103631>
- Clark RB (1997) Arbuscular mycorrhizal adaptation, spore germination, root colonization, and host plant growth and mineral acquisition at low pH. *Plant Soil* 192:15–22. <https://doi.org/10.1023/A:1004218915413>
- Alguacil MM, Torres MP, Montesinos-Navarro A, Roldán A (2016) Soil characteristics driving arbuscular mycorrhizal fungal communities in semiarid mediterranean soils. *Appl Environ Microbiol* 82:3348–3356. <https://doi.org/10.1128/AEM.03982-15>
- Ferrol N, Calvente R, Cano C, Barea J-M, Azcón-Aguilar C (2004) Analysing arbuscular mycorrhizal fungal diversity in shrub-associated resource Islands from a desertification-threatened semiarid mediterranean ecosystem. *Appl Soil Ecol* 25:123–133. <https://doi.org/10.1016/j.apsoil.2003.08.006>
- Martínez-García LB, Armas C, Miranda JD, Padilla FM, Pugnaire FI (2011) Shrubs influence arbuscular mycorrhizal fungi communities in a semi-arid environment. *Soil Biol Biochem* 43:682–689. <https://doi.org/10.1016/j.soilbio.2010.12.006>
- Bueno RS, Badalamenti E, Gristina L, Novara A, La Mantia T (2023) The role of Almond-Leaved Pear *pyrus spinosa* Forssk. In mediterranean pasturelands carbon storage and woodlands restoration. *Land* 12:135

27. Midolo G, Axmanová I, Divíšek J, Dřevojan P, Lososová Z, Večeřa M, Karger DN, Thuiller W, Bruehlheide H, Aćić S, Attorre F, Biurrun I, Boch S, Bonari G, Čarni A, Chiarucci A, Čuštrevska R, Dengler J, Dziuba T, Garbolino E, Jandt U, Lenoir J, Marcenò C, Růsina S, Šibík J, Škvorec Ž, Stančić Z, Stanišić-Vujačić M, Svenning J-C, Swacha G, Vassilev K, Chytrý M (2024) Diversity and distribution of Raunkiaer's life forms in European vegetation. *J Veg Sci* 35:e13229. <https://doi.org/10.1111/jvs.13229>
28. Alguacil MM, Díaz G, Torres P, Rodríguez-Caballero G, Roldán A (2019) Host identity and functional traits determine the community composition of the arbuscular mycorrhizal fungi in facultative epiphytic plant species. *Fungal Ecol* 39:307–315. <https://doi.org/10.1016/j.funeco.2019.02.002>
29. López-García Á, Azcón-Aguilar C, Barea JM (2014) The interactions between plant life form and fungal traits of arbuscular mycorrhizal fungi determine the symbiotic community. *Oecologia* 176:1075–1086. <https://doi.org/10.1007/s00442-014-3091-7>
30. Davison J, García de León D, Zobel M, Moora M, Bueno CG, Barceló M, Gerz M, León D, Meng Y, Pillar VD, Sepp S-K, Soudzilovskaia NA, Tedersoo L, Vaessen S, Vahter T, Winck B, Öpik M (2020) Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. *New Phytol* 226:1117–1128. <https://doi.org/10.1111/nph.16423>
31. Bueno CG, Moora M, Gerz M, Davison J, Öpik M, Pärtel M, Helm A, Ronk A, Kühn I, Zobel M (2017) Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Glob Ecol Biogeogr* 26:690–699. <https://doi.org/10.1111/geb.12582>
32. Labouyrie M, Ballabio C, Romero F, Panagos P, Jones A, Schmid MW, Mikryukov V, Dulya O, Tedersoo L, Bahram M, Lugato E, van der Heijden MGA, Orgiazzi A (2023) Patterns in soil microbial diversity across Europe. *Nat Commun* 14:3311. <https://doi.org/10.1038/s41467-023-37937-4>
33. Martin FM, van der Heijden MGA (2024) The mycorrhizal symbiosis: research frontiers in genomics, ecology, and agricultural application. *New Phytol* 242:1486–1506. <https://doi.org/10.1111/nph.19541>
34. Lutz S, Mikryukov V, Labouyrie M, Bahram M, Jones A, Panagos P, Delgado-Baquerizo M, Maestre FT, Orgiazzi A, Tedersoo L, van der Heijden MGA (2025) Global richness of arbuscular mycorrhizal fungi. *Fungal Ecol* 74:101407. <https://doi.org/10.1016/j.funeco.2024.101407>
35. Embury EL, Romero-Olivares AL (2025) Fungi follow Flora, bacteria track the seasons: A Tale of a changing landscape. *Microb Ecol* 88:68. <https://doi.org/10.1007/s00248-025-02568-3>
36. Navarro-Fernández CM, Pérez-Ramos IM, de la Riva EG, Vera JR, Roumet C, Villar R, Maraňón T (2016) Functional responses of mediterranean plant communities to soil resource heterogeneity: a mycorrhizal trait-based approach. *J Veg Sci* 27:1243–1253. <https://doi.org/10.1111/jvs.12446>
37. Sánchez-Castro I, Ferrol N, Cornejo P, Barea J-M (2012) Temporal dynamics of arbuscular mycorrhizal fungi colonizing roots of representative shrub species in a semi-arid mediterranean ecosystem. *Mycorrhiza* 22:449–460. <https://doi.org/10.1007/s00572-011-0421-z>
38. Catania V, Bueno RS, Alduina R, Grilli E, La Mantia T, Castaldi S, Quatrini P (2022) Soil microbial biomass and bacterial diversity in Southern European regions vulnerable to desertification. *Ecol Indic* 145:109725. <https://doi.org/10.1016/j.ecolind.2022.109725>
39. Dřevojan P, Čeplová N, Štěpánková P, Axmanová I (2023) FloraVeg.EU – Database of European Vegetation, Habitats and Flora. Accessed may 2024. <https://floraveg.eu>
40. Bueno RS, Badalamenti E, Sala G, La Mantia T (2024) A crop for a forest: opuntia ficus-indica as a tool for the restoration of mediterranean forests in areas at desertification risk. *Front Forests Global Change* 7. <https://doi.org/10.3389/ffgc.2024.1343069>
41. Phillips JM, Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans Br Mycological Soc* 55:158–1118. [https://doi.org/10.1016/S0007-1536\(70\)80110-3](https://doi.org/10.1016/S0007-1536(70)80110-3)
42. Trouvelot A, Kough J, Gianinazzi-Pearson V (1986) Mesure du Taux de mycorrhization VA d'un système racinaire. Recherche de methods d'estimation ayant une signification fonctionnelle. In: Gianinazzi-Pearson V, Gianinazzi S (eds) *Physiological and genetical aspects of mycorrhizae*. INRA, Paris, pp 101–109
43. Mercy L (2017) INOQ calculator Advanced. Evaluate the mycorrhizal rate according to a modified trouvelot method. <https://doi.org/10.3389/fpls.2024.1385245>
44. Gerdemann JW, Nicolson TH (1963) Spores of mycorrhizal endogone species extracted from soil by wet Sieving and decanting. *Trans Br Mycological Soc* 46:235–244. [https://doi.org/10.1016/S0007-1536\(63\)80079-0](https://doi.org/10.1016/S0007-1536(63)80079-0)
45. Furlan V, Bartschi H, Fortin JA (1980) Media for density gradient extraction of endomycorrhizal spores. *Trans Br Mycological Soc* 75:336–338. [https://doi.org/10.1016/S0007-1536\(80\)80102-1](https://doi.org/10.1016/S0007-1536(80)80102-1)
46. Muñoz Sabater J (2019) ERA5-Land monthly averaged data from 1950 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). Accessed 05/ 2024
47. Soil Survey Staff (2014) Survey investigations report No. 42, version 5.0. U.S. Department of Agriculture, Natural Resources Conservation Service
48. R Core Team (2021) R: A Language and Environment for Statistical Computing. Version 4.1.2. R Foundation for Statistical Computing, Vienna, Austria
49. Burnham KP, Anderson DR (2002) Model selection and multi-model inference: A practical Information-Theoretic approach. Springer, New York
50. Douma JC, Weedon JT (2019) Analysing continuous proportions in ecology and evolution: A practical introduction to beta and dirichlet regression. *Methods Ecol Evol* 10:1412–1430. <https://doi.org/10.1111/2041-210X.13234>
51. Ibáñez B, Gómez-Aparicio L, Ávila JM, Pérez-Ramos IM, García LV, Maraňón T (2015) Impact of tree decline on Spatial patterns of seedling-mycorrhiza interactions: implications for regeneration dynamics in mediterranean forests. *Ecol Manage* 353:1–9. <https://doi.org/10.1016/j.foreco.2015.05.014>
52. Badalamenti E, Catania V, Sofia S, Sardina MT, Sala G, La Mantia T, Quatrini P (2021) The root mycobiota of betula aetnensis Raf., an endemic tree species colonizing the lavas of Mt. Etna (Italy). *Forests* 12:1624
53. Cera A, Duplat E, Montserrat-Martí G, Gómez-Bolea A, Rodríguez-Echeverría S, Palacio S (2021) Seasonal variation in AMF colonisation, soil and plant nutrient content in gypsum specialist and generalist species growing in P-poor soils. *Plant Soil* 468:509–524. <https://doi.org/10.1007/s11040-021-05140-3>
54. Birhane E, Aregawi K, Giday K (2017) Changes in arbuscular mycorrhiza fungi spore density and root colonization of Woody plants in response to enclosure age and slope position in the highlands of Tigray, Northern Ethiopia. *J Arid Environ* 142:1–10. <https://doi.org/10.1016/j.jaridenv.2017.03.002>
55. Azcón-Aguilar C, Palenzuela J, Roldán A, Bautista S, Vallejo R, Barea JM (2003) Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened mediterranean shrublands. *Appl Soil Ecol* 22:29–37. [https://doi.org/10.1016/S0929-1393\(02\)00107-5](https://doi.org/10.1016/S0929-1393(02)00107-5)
56. Ambrosino ML, Torres YA, Garayalde AF, Armando LV, Lorda GS, Velázquez MS (2025) Shrub effect in semiarid Monte range-lands: variation of arbuscular mycorrhizal fungi communities

- associated with different functional groups of plants. *Appl Soil Ecol* 209:106000. <https://doi.org/10.1016/j.apsoil.2025.106000>
57. Konvalinková T, Jansa J (2016) Lights off for arbuscular mycorrhiza: on its symbiotic functioning under light deprivation. *Front Plant Sci* 7. <https://doi.org/10.3389/fpls.2016.00782>
 58. González Fradejas G, García de León D, Vasar M, Koorem K, Zobel M, Öpik M, Moora M, Rey Benayas JM (2022) Hedgerows increase the diversity and modify the composition of arbuscular mycorrhizal fungi in mediterranean agricultural landscapes. *Mycorrhiza* 32:397–407. <https://doi.org/10.1007/s00572-022-01090-5>
 59. Yang H, Yuan Y, Zhang Q, Tang J, Liu Y, Chen X (2011) Changes in soil organic carbon, total nitrogen, and abundance of arbuscular mycorrhizal fungi along a large-scale aridity gradient. *CATENA* 87:70–77. <https://doi.org/10.1016/j.catena.2011.05.009>
 60. Mohammad MJ, Hamad SR, Malkawi HI (2003) Population of arbuscular mycorrhizal fungi in semi-arid environment of Jordan as influenced by biotic and abiotic factors. *J Arid Environ* 53:409–417. <https://doi.org/10.1006/jare.2002.1046>
 61. Zubek S, Rola K, Rożek K, Błaszowski J, Stanek M, Chmolewska D, Chowaniec K, Zalewska-Gałosz J, Stefanowicz AM (2022) Experimental assessment of forest floor geophyte and hemicryptophyte impact on arbuscular mycorrhizal fungi communities. *Plant Soil* 480:651–673. <https://doi.org/10.1007/s11104-022-05610-2>
 62. Tedersoo L, Bahram M, Pölme S, Kõljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME, Sharp C, Saluveer E, Saitta A, Rosas M, Riit T, Ratkowsky D, Pritsch K, Pöldmaa K, Piepenbring M, Phosri C, Peterson M, Parts K, Pärtel K, Otsing E, Nouhra E, Njouonkou AL, Nilsson RH, Morgado LN, Mayor J, May TW, Majuakim L, Lodge DJ, Lee SS, Larsson K-H, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo L-d, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, De Kesel A, Dang T, Chen X, Buegger F, Brearley FQ, Bonito G, Anslan S, Abell S, Abarenkov K (2014) Global diversity and geography of soil fungi. *Science* 346:1256688. <https://doi.org/10.1126/science.1256688>
 63. Robin-Soriano A, Maurice K, Boivin S, Bourceret A, Laurent-Webb L, Youssef S, Nespoulous J, Boussière I, Berder J, Damasio C, Vincent B, Boukcim H, Ducouso M, Gros-Balthazard M (2024) Absence of gigasporales and rarity of spores in a hot desert revealed by a multimethod approach. *Mycorrhiza* 34:251–270. <https://doi.org/10.1007/s00572-024-01160-w>
 64. Alzarhani AK, Clark DR, Underwood GJC, Ford H, Cotton TEA, Dumbrell AJ (2019) Are drivers of root-associated fungal community structure context specific? *ISME J* 13:1330–1344. <https://doi.org/10.1038/s41396-019-0350-y>
 65. Davison J, Moora M, Semchenko M, Adenan SB, Ahmed T, Akhmetzhanova AA, Alatalo JM, Al-Quraishy S, Andriyanova E, Anslan S, Bahram M, Batbaatar A, Brown C, Bueno CG, Cahill J, Cantero JJ, Casper BB, Cherosov M, Chideh S, Coelho AP, Coghill M, Decocq G, Dudov S, Fabiano EC, Fedosov VE, Fraser L, Glassman SI, Helm A, Henry HAL, Hérault B, Hiiesalu I, Hiiesalu I, Hozzein WN, Kohout P, Kõljalg U, Koorem K, Laanisto L, Mander Ü, Mucina L, Munyampundu J-P, Neuenkamp L, Niinemets Ü, Nyamukondiwa C, Oja J, Onipchenko V, Pärtel M, Phosri C, Pölme S, Püssa K, Ronk A, Saitta A, Semboli O, Sepp S-K, Seregin A, Sudheer S, Peña-Venegas CP, Paz C, Vahter T, Vasar M, Veraart AJ, Tedersoo L, Zobel M, Öpik M (2021) Temperature and pH define the realised niche space of arbuscular mycorrhizal fungi. *New Phytol* 231:763–776. <https://doi.org/10.1111/nph.17240>
 66. Wang Y-J, He X-H, Meng L-L, Zou Y-N, Wu Q-S (2023) Extraradical mycorrhizal hyphae promote soil carbon sequestration through difficultly extractable Glomalin-Related soil protein in response to soil water stress. *Microb Ecol* 86:1023–1034. <https://doi.org/10.1007/s00248-022-02153-y>
 67. Choreño-Parra EM, Treseder KK (2024) Mycorrhizal fungi modify decomposition: a meta-analysis. *New Phytol* 242:2763–2774. <https://doi.org/10.1111/nph.19748>
 68. Basiru S, Mhand KAS, Hijri M (2025) Deciphering the mechanisms through which arbuscular mycorrhizal symbiosis reduces nitrogen losses in agroecosystems. *Appl Soil Ecol* 206:105799. <https://doi.org/10.1016/j.apsoil.2024.105799>
 69. Faghihinia M, Zou Y, Bai Y, Dudáš M, Marrs R, Staddon PL (2022) Grazing intensity rather than host plant's palatability shapes the community of arbuscular mycorrhizal fungi in a steppe grassland. *Microb Ecol* 84:1062–1071. <https://doi.org/10.1007/s00248-021-01920-7>

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