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Land cover shapes arbuscular mycorrhizal fungal communities in the Maros-Pangkep karst landscape

Gusmiaty[1,2], Muhammad Restu[2,3*], Siti Halimah Larekeng[2,4],
Retno Prayudyaningsih[4,5], Mukrimin[2], Muhammad Akhsan Akib[6],
Fajri Ansari[4,7], Nilam Sari[2], Lisa Tandi[2], Nur Padli[2],

[1] Doctoral Program of Forestry, Faculty of Forestry, Hasanuddin University, Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, South Sulawesi, Indonesia
[2] Department of Forestry, Faculty of Forestry, Hasanuddin University, Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, South Sulawesi, Indonesia
[3] Forest Tree Breeding and Genomic Research Group, Faculty of Vocational Studies, Hasanuddin University, Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, South Sulawesi, Indonesia
[4] Research Collaboration Center for Karst Microbes, BRIN–UNHAS, Hasanuddin University, Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, Indonesia
[5] Research Center for Applied Microbiology, National Research and Innovation Agency, Jl. Raya Jakarta-Bogor, West Java, Indonesia
[6] Study Program of Agrotechnology, University of Muhammadiyah Parepare, Jl. Jend. Ahmad Yani Km. 6, Parepare 91112, South Sulawesi, Indonesia
[7] Research Center for Ecology, National Research and Innovation Agency, Jl. Raya Jakarta-Bogor, West Java, Indonesia
* Corresponding author's e-mail: muhrestu@unhas.ac.id

ABSTRACT

The Maros-Pangkep Karst Area, a UNESCO Global Geopark, is a globally significant ecosystem threatened by environmental degradation. Arbuscular mycorrhizal fungi (AMF) are key soil microorganisms that enhance plant nutrient uptake and stress tolerance, yet information on their communities in karst environments is limited. This study aims to determine how different land cover types former mining land, scrubland, mixed gardens, and secondary forests shape AMF community composition, diversity, and root colonization patterns. Four dominant AMF genera Glomus, Acaulospora, Gigaspora, and Entrophospora were identified, and their abundance and distribution were strongly influenced by land cover type. Mixed gardens exhibited the highest spore density (62.7 spores/50 g of soil) and genus diversity, dominated by Acaulospora, whereas secondary forests showed the lowest densities (11.4 spores/50 g of soil). Former mining areas were enriched in the stress-tolerant genus Entrophospora, while Glomus was cosmopolitan across all sites. Root colonization trends reflected these patterns. These results reveal that land cover is a major driver of AMF community structure in the Maros-Pangkep karst area and identify taxa adapted to degraded habitats, providing new insights into microbial ecology in karst landscapes.

Keywords: Maros Pangkep Karst Area, AMF, association, identification.

INTRODUCTION

The Maros-Pangkep Karst Area (MPKA) in South Sulawesi is a globally significant ecosystem, recognized as the second-largest karst landscape in the world and designated a UNESCO Geopark in 2022. Unlike karst areas in other parts of Indonesia, the MPKA is dominated by limestone, which is mainly composed of the Tonasa Formation (Fatinaware, et al., 2019). MPKA stretches from Maros Regency to Pangkep and covers an area of 46,200 ha, of which

22,800 ha (49.35%) is under the management of Bantimurung Bulusaraung National Park, while the remaining 23,400 ha are located outside the conservation area and are affected by mining and development activities (Achmad and Hamzah, 2016). As a unique ecosystem, the MPKA boasts distinct flora and fauna diversity, particularly since it is located in the Wallacea region. However, the beauty and uniqueness of the Maros-Pangkep karst does not mean that this area is well preserved. Despite its ecological and biological significance, the composition and ecological roles of soil microorganisms, particularly arbuscular mycorrhizal fungi (AMF), in this karst system remain largely unexplored.

Karst topography is formed by the dissolution of bedrock, generally carbonate rock, creating fragile structures and making ecosystems in karst areas vulnerable to disturbance (Parise and Pascali, 2003). Ecologically fragile karst systems are characterized by aridity, limited phosphorus, high calcium, low alkalinity, low primary productivity, soil erosion, surface collapse, and soil degradation, which make vegetation recovery even more difficult (Wang et al., 2004). Human activity in karst areas can also cause degradation. Limestone and marble mining activities accelerate the degradation of karst areas. Mining activities, particularly marble mining, have led to significant environmental degradation, including soil structure disruption, loss of natural vegetation, and a decline in soil microbial diversity. Former mining land generally has soil that is poor in organic matter, low in nutrients, and has poor water retention. In addition to former mining land, other land cover types in the MPKA area, such as mixed gardens, shrubs, and secondary forests, also present very different ecological conditions in terms of vegetation diversity and soil microorganisms. These contrasting ecological conditions across land cover types suggest that soil microbial communities, including arbuscular mycorrhizal fungi, may respond differently to habitat quality and disturbance, highlighting the need to systematically investigate their diversity and distribution in the MPKA.

Soil microorganisms play a vital role in restoring degraded karst ecosystems by promoting plant growth and nutrient uptake and by enhancing soil nutrient availability (Chen et al., 2012; Richardson and Simpson, 2011; Wang et al., 2018; Liu et al., 2007). Among them, arbuscular mycorrhizal fungi (AMF) are particularly important functional groups in karst soils. Forming symbiotic associations with approximately 80% of terrestrial plants (Kardol and Wardle, 2010), AMF enhance plant growth, facilitate the uptake of phosphorus, nitrogen, sulfur, and micronutrients (He et al., 2017; Ferrol et al., 2019; Augé et al., 2015; Prayudyaningsih, 2014), and improve drought tolerance and soil structure (Smith et al., 2003; Noyd and Pfleger, 1996). AMF also contribute to early plant colonization (O'Connor et al., 2002), drought resistance (Augé, 2001), and overall ecosystem stability. Their application in ecological restoration has been shown to support plant establishment in degraded soils and enhance soil quality and health (Straker et al., 2008; Cuenca and Lovera, 1992; Prayudyaningsih et al., 2015). Initial plantings inoculated with arbuscular mycorrhizal fungi function as a strong catalyst for the restoration of ecosystems in areas of severe land degradation including limestone post-mining sites (Prayudyaningsih et al., 2026). Despite the recognized importance of soil microorganisms in karst restoration, the diversity and distribution of arbuscular mycorrhizal fungi (AMF) across different land cover types in the Maros-Pangkep Karst Area remain poorly understood, particularly in disturbed versus semi-natural habitats. This knowledge gap limits our ability to develop targeted microbial-based restoration strategies, underscoring the need for a systematic assessment of AMF communities across former mining sites, mixed gardens, shrublands, and secondary forests.

Although land cover is known to influence soil microbial community structure (Pérez-Redondo et al., 2025) and vegetation diversity can significantly affect AMF density and composition (Díaz et al., 2025), these relationships have not been systematically evaluated in the Maros-Pangkep Karst Area. In particular, the responses of AMF communities in disturbed habitats such as former mining sites and shrublands where soil properties and host plant assemblages differ markedly remain largely uncharacterized, leaving a gap in understanding how land cover gradients influence AMF diversity, abundance, and plant associations across this karst landscape (Shen et al., 2020; Pérez-Redondo et al., 2025; Díaz et al., 2025).

Several studies have shown that vegetation cover characteristics influence AMF communities. For example, Pérez-Redondo et al. (2025)

reported that vegetation diversity significantly affects AMF density and community structure, while Díaz et al. (2025) demonstrated that AMF–host plant associations produce distinct fungal assemblages across vegetation types. However, to date, no systematic assessment has been conducted to compare AMF diversity, spore density, and plant associations across multiple contrasting land cover types in the Maros-Pangkep Karst Area, particularly between disturbed systems (former mining land, shrublands) and seminatural systems (secondary forests, mixed gardens).

Given the recognized role of AMF in supporting plant growth, nutrient cycling, and soil stability in degraded ecosystems (Richardson and Simpson, 2011; Wang et al., 2018), and the current lack of comprehensive data on their distribution across karst land cover gradients, this study aims to determine how land cover types shape AMF community composition, diversity, spore density, and root colonization patterns in the Maros-Pangkep Karst landscape. We hypothesize that (i) land cover variation is associated with significant differences in AMF community structure and abundance, with seminatural cover types supporting higher diversity than disturbed sites; and (ii) specific AMF taxa will be indicative of particular land cover conditions, with stress-tolerant genera being more prevalent in degraded habitats. By addressing these hypotheses, this work fills a critical gap in understanding how land cover gradients influence AMF ecology in karst ecosystems.

METHODOLOGY

Research location and time

The research was conducted from November 2024 to January 2025. The research began with the collection of soil and plant root samples in the Maros-Pangkep karst area on several types of land cover, including former mining sites, scrubland, mixed garden, and secondary forest in three villages, namely, Balleanging Village, Balocci Baru Village, and Tonasa Village, Balocci District, Pangkep Regency, South Sulawesi (Figure 1 and Figure 2). The isolation, identification, and preparation of AMF inoculum will be conducted

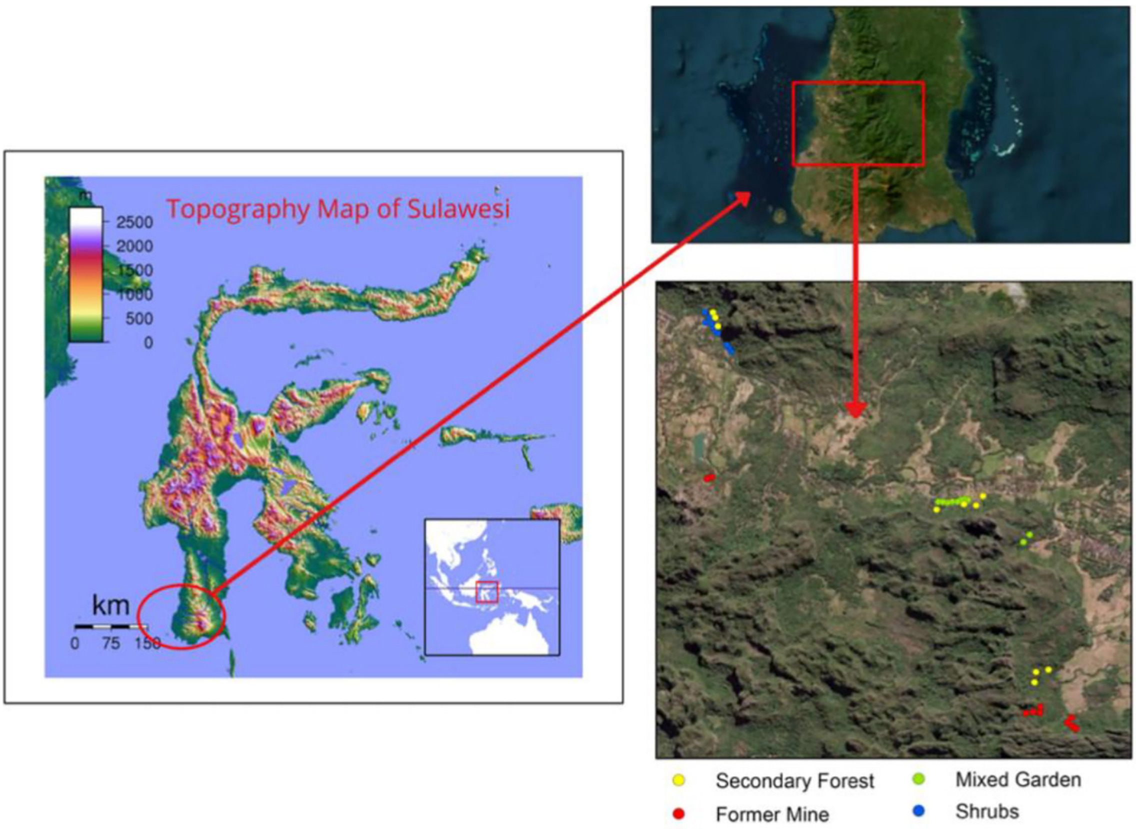

Figure 1. Location of soil and root sample collection

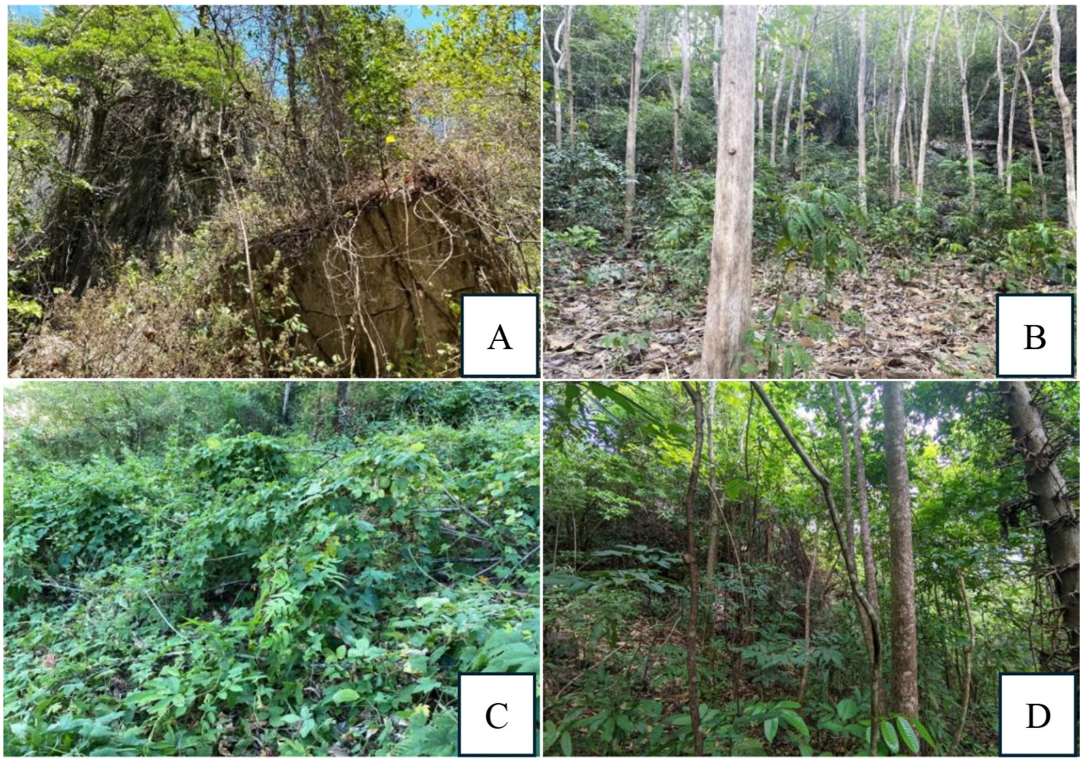

Figure 2. Four land cover types in the Maros Pangkep Karst Area: Former Mine (A); Mixed Garden (B); Scrubland (C); Secondary Forest (D)

at the Microbiology Laboratory of the Karst Microbe Research Collaboration Center for Karst Microbe, the Research and Community Service Institute, Hasanuddin University.

Research procedures

Sampling

Soil and root sampling were conducted using a purposive sampling method across four land cover types: former mine, mixed gardens, scrubland, and secondary forests. For each land cover type, ten sampling plots were established at intervals of approximately 50–100 m. Each plot measured 20 × 20 m. GPS coordinate points for each plot for each land cover are presented in Table 1.

- Soil sampling:

At each plot, soil was collected from the top 0–20 cm layer at five points: four corners and the plot center. Soil samples were combined per plot to form a composite sample. Furthermore, for the purposes of soil chemical analysis, soil samples are composited based on the sampling location. Samples were placed in labeled, sterile plastic bags and transported to the laboratory on the same day. The samples were stored at room temperature (27–28 °C) and air-dried for approximately 1 week.

- Root sampling:

Roots were collected from naturally occurring plants within each plot to assess AMF colonization. Root samples were taken from each type of plant in the plot (3 root samples each). Root samples were taken from four points around the plant roots and selected from young roots (lateral roots), avoiding damaged or senescent tissues (Figure 3). Roots were washed gently with tap water, placed in labeled bags, and transported to the laboratory. For unknown plant species, herbarium vouchers should be prepared and deposited, with species identification provided.

Extraction and identification of AMF spores in soil

Soil samples collected from the four land cover types were processed in the laboratory to extract and isolate AMF spores. Extraction was performed using a modified wet sieving and decanting method (Pacioni, 1992) combined with centrifugation (Brundrett et al., 1996) as follows:

- Preparation of soil suspension:

Table 1. GPS coordinates of plots in several land covers in the Maros-Pangkep Karst Area

Land cover types	Plot	Latitude	Longitude
Former mine	1	4.93166421231 S	119.676650446 E
	2	4.9310947182 S	119.676693215 E
	3	4.93155856798 S	119.67595624 E
	4	4.9317150239 S	119.675254074 E
	5	4.93211265489 S	119.679733715 E
	6	4.93258430795 S	119.67930312 E
	7	4.93298921319 S	119.679737232 E
	8	4.93315934607 S	119.680125351 E
	9	4.90899048325 S	119.644997888 E
	10	4.90915472014 S	119.644602092 E
Mixed garden	1	4.91454333918 S	119.675662947 E
	2	4.9152507359 S	119.675035075 E
	3	4.9111784775 S	119.66968496 E
	4	4.91112569979 S	119.669324353 E
	5	4.9111992563 S	119.669009298 E
	6	4.91135410757 S	119.668703576 E
	7	4.91134716223 S	119.668180972 E
	8	4.91145758644 S	119.667685864 E
	9	4.91139591504 S	119.667289181 E
	10	4.91138864426 S	119.666847664 E
Scrubland	1	4.89693660212 S	119.646878559 E
	2	4.89650372066 S	119.646651608 E
	3	4.89634191149 S	119.646434734 E
	4	4.8952247167 S	119.645574401 E
	5	4.89483730377 S	119.645275552 E
	6	4.89453954758 S	119.645157253 E
	7	4.89415174237 S	119.644957512 E
	8	4.89357351997 S	119.6449192 E
	9	4.89316910032 S	119.64434999 E
	10	4.89414480662 S	119.644425901 E
Secondary forest	1	4.912063 S	119.666775 E
	2	4.911684 S	119.669342 E
	3	4.911873 S	119.670673 E
	4	4.910926 S	119.671243 E
	5	4.928651 S	119.675896 E
	6	4.927718 S	119.676096 E
	7	4.927518 S	119.677233 E
	8	4.894673 S	119.645604 E
	9	4.893807 S	119.645336 E
	10	4.893074 S	119.645136 E

50 g of composite soil per plot was suspended in 1000 mL of distilled water in a 2 L beaker. The suspension was stirred continuously for approximately 2 minutes to break soil aggregates and release AMF spores. The suspension was allowed to settle for 15 minutes to remove large soil particles.

- Sieving:

The supernatant was carefully decanted and sequentially passed through sieves with pore sizes of 425 μm, 250 μm, and 45 μm. The procedure

Figure 3. Soil sampling (A), root sampling (B)

was repeated three times per sample to maximize spore recovery. Material retained on the 250 µm and 45 µm sieves was combined and rinsed into a 15 mL centrifuge tube.

- Centrifugation and sugar flotation:

Tubes were centrifuged at 2000 rpm for 5 minutes. The supernatant was discarded, and the pellet was resuspended in a sucrose solution (2× volume of water) for density-based separation of spores. Samples were centrifuged again at 2000 rpm for 1 minute, and the supernatant containing spores was filtered through a 45 µm filter. Filtrate was rinsed with distilled water to remove sugar residues. The remaining sediment on the filter was collected into a Petri dish for spore counting and identification.

- Identification and counting of spores:

AMF spores were observed using a stereo microscope (magnification 8x–40x), and a compound microscope (magnification 100x–400x).

Counting and morphotyping of AMF spores

The AMF spores obtained after extraction were processed to determine spore density and classify spores by morphotype as follows:

- Observation:

Filtered sediment was carefully transferred into Petri dishes (60 × 15 mm). Spores were examined under a stereo microscope at 40x magnification to identify individual spores.

- Morphotyping:

Spores were sorted and placed on filter paper marked with vertical and horizontal grids to facilitate counting and avoid double-counting. Each morphotype was documented based on size, shape, color, and wall structure, with reference to the database of the International Collection of AMF Cultures (INVAM, https://invam.ku.edu/). Representative spores from each morphotype were photographed to provide visual confirmation.

Spore observation

AMF spores that have been isolated on the basis of their morphotypes are then prepared for morphological identification. Spore preparations were made using PVLG and Melzer's solutions separately on a single glass slide. Spores that had been counted and separated by morphotype were placed on a glass slide, with PVLG solution applied to the left side and Melzer's solution to the right; then each was covered with a cover slip. The spores were broken by pressing the surface of the cover slip using a pin. A color change in spores in Melzer's solution is one indicator of the type of spores present (Brudrett et al., 1996). The identification of AMF spore types was based on the morphology, size, color, and subcellular structure of the spores (INVAM, https:// invam. ku. edu/).

Observation of AMF colonization and identification of Mycorrhiza types

The association between AMF and natural plants across different land cover types in the Maros-Pangkep Karst Area was assessed by determining root colonization rates using a modified root staining technique (Kormanik and McGraw, 1982). The procedure was as follows:

- Root sample preparation:

Young lateral roots were carefully cleaned of soil and debris. Root samples were preserved in 50% ethanol until processing.

- Clearing:

Root pieces were soaked in 10% KOH solution for 24 hours to clear cytoplasmic contents and facilitate dye penetration. If roots remained pigmented, they were further treated with 10% H_2O_2 until a lighter color was achieved.

- Neutralization:

Cleared roots were rinsed with running water and soaked in 2% HCl solution for 24 hours to neutralize residual KOH or H_2O_2.

- Staining:

Roots were immersed in an appropriate staining solution (Trypan Blue) for 24 hours. After staining, roots were transferred to a destaining solution to remove excess dye and enhance visibility of fungal structures.

- Microscopic examination:

AMF colonization was systematically assessed by taking 10 random 1 cm-long sections of stained root hairs and arranging them on a microscope slide for observation. One type of tree studied used a single microscope slide containing 10 1 cm-long root hair sections, with 6 fields of view. AMF structures (arbuscules, vesicles, hyphae) were observed under a light microscope at 100x to 400× magnification. Root colonization was quantified as the percentage of root length colonized, following standard gridline-intersect methods (Giovannetti and Mosse, 1980). Fields of view showing signs of colonization (the presence of hyphae, vesicles, arbuscules, or spores) were markedly positive (+), whereas those without signs of colonization were markedly negative (-). The number of microscope slides showing signs of colonization was counted. The percentage of colonized roots can be calculated using the formula developed by Brundrett et al. (1996) as follows:

$$\textit{AMF colonization percentage} = \frac{\textit{Number of colonized fields of view}}{\textit{Number of fields view}} \times 100\% \quad (1)$$

Data analyst

The results of AMF spore identification were analyzed on the basis of the methods of Shi et al. (2006), namely, by observing spore density, spore diversity, spore abundance, and spore frequency. Each parameter was calculated using the following formula:

$$\text{Spore density} = \textit{Number of spores in } 50\text{ g } \textit{soil sample} \quad (2)$$

$$\textit{Spore diversity} = \textit{Number of AMF genera in } 50\text{ g } \textit{soil sample} \quad (3)$$

$$\textit{Relative abundance } (\%) = \frac{\textit{Number of spores from a genus (species) of AMF}}{\textit{Total spores}} \times 100\% \quad (4)$$

$$\text{Genus frequency } (\%) = \frac{\textit{Number of samples found in genus (species)}}{\textit{Total sample}} \times 100\% \quad (5)$$

The data obtained from laboratory observations were tabulated and analyzed using Excel software and then presented in tables and histograms. The percentage of root colonization can be calculated using the formula developed by Brundrett et al. (1996) as follows:

$$\textit{AMF colonization percentage} = \frac{\textit{Number of colonized fields of view}}{\textit{Number of fields view}} \times 100\% \quad (6)$$

The percentage of AMF root colonization was then classified according to O'Connor et al. (2001): 0 (no colonization), <10% (low colonization), 10–30% (moderate colonization), and >30% (high colonization).

The AMF spore density was analyzed by ANOVA in SPSS 25. One-way analysis of variance was used to compare the means across different treatments (area). Means separation tests were performed using the Duncan multiple range test (DMRT) at the $P<0.05$ level after significant F values were obtained. The edaphic data from all observation plots were first averaged across plots. Prior to multivariate analysis, all edaphic variables were standardized to ensure consistency between different measurement scales. Principal component analysis (PCA) was then performed in Minitab 22 using the correlation matrix to identify the main patterns and explain the relationships between edaphic variables and the number of FMA spores on land in former mining areas, secondary forests, mixed gardens, and shrublands.

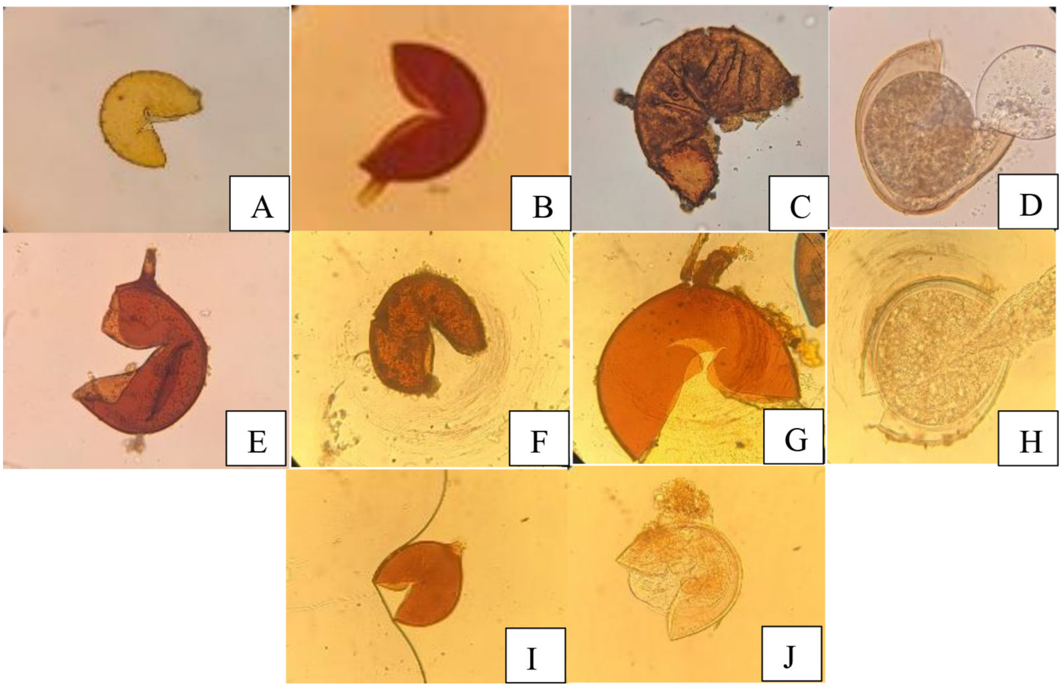

Figure 4. AMF genera isolated from four land cover types in the Maros Pangkep Karst Area: Former Mine (*A. Entropospora, B. Glomus*); Mixed Garden (*C. Acaulospora, D. Entropospora, E. Glomus*); Scrubland (*F. Glomus, G. Gigaspora, H. Acaulospora*); Secondary Forest (*I. Glomus, J. Acaulospora*)

RESULTS AND DISCUSSION

Results of AMF spore identification

Observations and identification of the morphotypes of AMF spores from four types of land cover in the Maros Pangkep karst area revealed the presence of four AMF genera, namely, *Entrophospora*, *Glomus*, *Acaulospora*, and *Gigaspora*. As shown in Figure 4, the composition of the AMF genera varied across the four land cover types, namely, former mines, mixed gardens, shrubbery, and secondary forests, reflecting the different ecological conditions of each land type.

On former mining land, only two AMF genera were found, namely, *Entrophospora* (Figure A) and *Glomus* (Figure B). The presence of these two genera indicates the ability to adapt to extreme and disturbed conditions. Glomus is known as a common genus that is tolerant to environmental stress, whereas *Entrophospora* indicates the initial regenerative potential of the soil. The mixed garden contained three genera, namely, *Acaulospora* (Figure C), *Entrophospora* (Figure D), and *Glomus* (Figure E). Compared with the former, the former reflects more stable and heterogeneous soil conditions, supporting a more complex AMF community. In the shrub cover, three genera were identified, namely, *Glomus* (Figure F), *Gigaspora* (Figure G), and *Acaulospora* (Figure H). The presence of *Gigaspora,* which tends to be more sensitive to disturbance, indicates improved ecological conditions and enhanced mycorrhizal habitat quality in this area, whereas in secondary forests, two genera were found, namely, *Glomus* (Figure 4) and *Acaulospora* (Figure J). Although the number of genera identified was the same as that in the former mine, the dominance of *Acaulospora* and *Glomus* reflects a relatively stable ecosystem that supports efficient mycorrhizal symbiotic relationships. A study conducted by Gusmiaty et al. (2025) showed that observations of AMF spores in rubber plants in agroforestry systems identified two AMF genera, namely *Glomus* and *Acaulospora*.

Density of AMF spores

Spore density is the number of mycorrhizal spores found in an ecosystem in the soil sample analyzed. The study was conducted by counting the number of spores present in 50 g of the soil sample in each plot. The spore density of AMF differed significantly across land cover types (Figure 5). This reflects the close relationships among plant communities, soil conditions, and the presence of

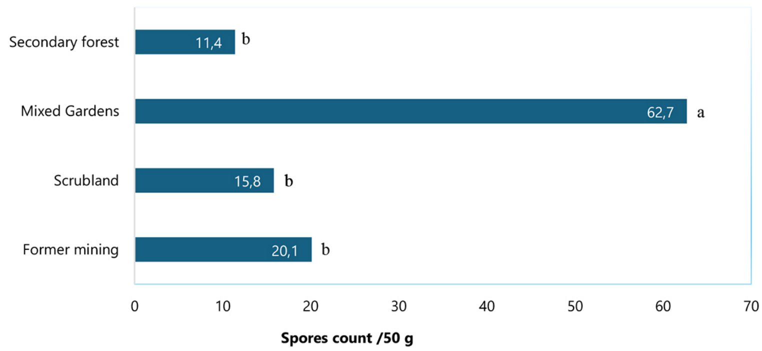

Figure 5. Graph of AMF spore density on several land cover types in the Maros-Pangkep Karst Area

these soil symbionts. The results of Duncan's new multiple range test revealed the highest spore density in mixed gardens (62.7 spores/50 g of soil), which significantly differed from that in former mines (20.1), shrubs (15.8), and secondary forests (11.4). The results of research conducted by Pérez-Redondo et al. (2025) revealed that vegetation cover strongly influences the spore density of AMF, with densely vegetated areas having a spore density of up to 10 spores/g of soil and degraded areas having a spore/g density of <1.

Spore dominance in mixed gardens results from plant diversity and high root activity, which are the main factors driving the formation of symbiotic relationships with AMF. Chaudhary et al. (2025) emphasized that structurally and biologically diverse agroecosystems can support AMF communities through organic matter enrichment, enhanced soil aggregate stability, and the support of other beneficial microbes, such as phosphate-solubilizing bacteria. These findings indicate that agroforestry not only increases the number of spores quantitatively but also enriches their communities both functionally and ecologically. Conversely, low spore densities in secondary forests and shrublands indicate ecological constraints. Vázquez-Santos et al. (2025) reported that AMF communities are highly sensitive to host plant identity and abiotic conditions such as pH, phosphorus availability, and soil moisture. Secondary forests with dense canopies and acidic soils may inhibit sporulation, whereas shrublands may be dominated by plants that do not form intensive symbioses with AMF.

Interestingly, the spore density at former mining sites was moderate (20.1 spores/50 g), indicating early biological recovery. Although previously disturbed, the presence of pioneer plants during revegetation can promote early AMF colonization. Pandey et al. (2025) suggested that, in restoration systems, strategies using locally available, phylogenetically diverse plants are effective at facilitating AMF propagation and soil improvement. This finding reinforces the argument that the success of former mining ecological restoration is highly dependent on vegetation design that supports soil symbionts.

Relationships between land cover and edaphic factors

The results of the principal component analysis (PCA) shown in Figure 6 reveal that each land cover type has a distinct relationship with edaphic factors (soil properties). The organic C content, Mg content, and C/N ratio of mixed gardens are correlated, indicating that high organic matter and nutrient contents support a high density of mycorrhizal spores. Secondary forests are associated with organic N (%), which comes from litter decomposition and plays a dominant role in spore growth. Shrubs are associated with Ca and CEC, indicating sufficient cation exchange capacity and calcium even when their organic matter content is lower. Moreover, former mining sites are associated with Na, K, Ca, and KB, reflecting unstable soil chemistry and low organic matter content; thus, these factors are dominant but negatively correlated with mycorrhizal spore density.

Diversity of AMF types

The condition of an ecosystem affects the presence of AMF on a plot of land. This study was conducted by identifying spores based on their morphological characteristics. The results of AMF spore diversity identification across the entire land cover (Figure 4) revealed four genera: *Gigaspora*, *Acaulospora*, *Glomus*, and *Entropospora*.

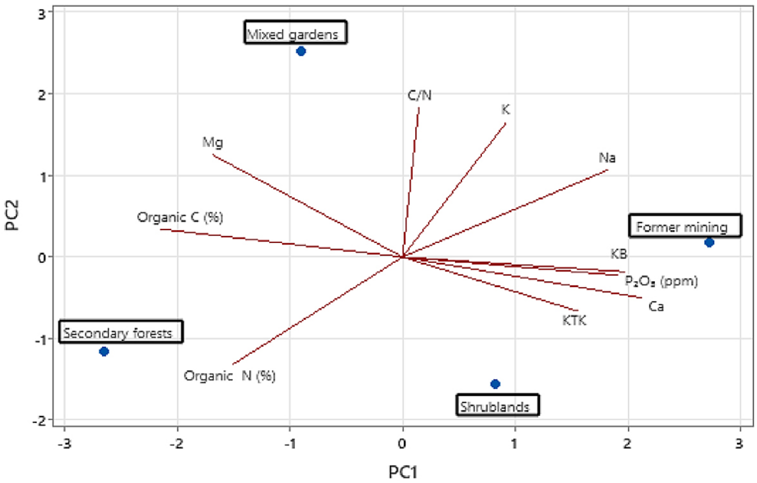

Figure 6. PCA of the effects of edaphic factors on land cover

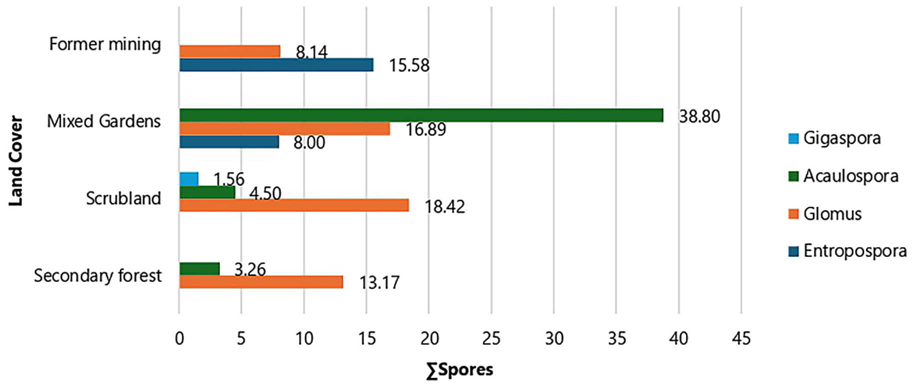

Figure 7. Graph of AMF spore diversity across several land cover types in the Maros-Pangkep karst area

Analysis of AMF spore genus diversity among the four land cover types revealed that mixed gardens presented the greatest diversity of the genera *Acaulospora*, *Entropospora*, and *Glomus*, which were dominated by *Acaulospora* (Figure 7). In contrast, former mines and secondary forests contained only two genera, and shrublands contained three genera, with lower total spore values. The high diversity in mixed gardens reflects the positive effect of mixed vegetation on mycorrhizal communities, where host plant diversity increases the likelihood of colonization by various AMF species. This is reinforced by the findings of Pérez-Redondo et al. (2025), who reported that permanent vegetation and plant phylogenetic diversity significantly increase the density and propagation of AMF spores. Former mining sites exhibit low genus diversity but are dominated by *Entropospora*, which rarely appears in other land types. These findings suggest that some AMF genera may tolerate or adapt ecologically to high-stress conditions, such as nutrient-poor soils and early revegetation. The results of research by Manga et al. (2025) show that extreme environments, such as saline or disturbed soils, can give rise to unique and taxonomically unidentified AMF communities, with the potential for certain genera to specialize in these conditions. Glomus emerged as the most common genus across all land cover types. The presence of Glomus in secondary forests, shrublands, mixed gardens, and former mining sites indicates its broad adaptability to various environmental conditions.

Overall, the results of this study indicate that the complexity and diversity of land cover play important roles in determining the structure of AMF communities at the genus level. Agroforestry systems, such as mixed gardens, have great potential for preserving AMF diversity, both in terms of quantity and quality of symbiont genera. Conversely, secondary forests and shrublands may be less supportive due to vegetation homogeneity or suboptimal

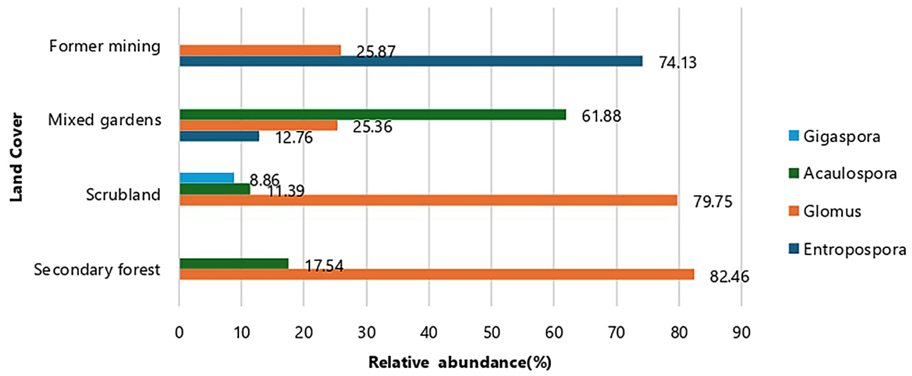

Figure 8. Graph of the relative abundance of FMA spores across several land cover types in the Maros Pangkep karst area

soil conditions. These findings reinforce the strategic role of plant diversity in maintaining soil ecosystem sustainability and providing important ecological services through root symbionts.

Relative abundance

The presence of AMF on a plot indicates that there is interaction between AMF spores and environmental conditions. Relative abundance is the percentage of spores of a particular genus out of the total spores found in the sample observed. Based on the relative abundance graph (Figure 8), the Glomus species had the widest distribution and were found across all land cover types.

Analysis of the relative abundance of AMF spores revealed clear differences in terms of genus dominance across land cover types. In former mining areas, *Entropospora* was significantly dominant, with a relative abundance of 74.13%, while Glomus contributed only 25.87%. This dominance of *Entropospora* most likely reflects the genus's ability to adapt to nutrient-poor soil conditions and to high environmental stress, such as extreme pH or heavy metal content. A study by Manga et al. (2025) revealed that some less common AMF genera can become dominant in marginal or extreme environments because of specific ecological advantages, such as salinity tolerance and the ability to colonize the roots of pioneer plants.

In mixed gardens, *Acaulospora* was predominant at 61.88%, followed by *Glomus* (25.36%) and *Entropospora* (12.76%). The high abundance of *Acaulospora* in this agroforestry system indicates that this genus has an affinity for mixed farming systems with high host plant diversity, abundant organic matter, and environments that are not highly disturbed. According to Pérez-Redondo et al. (2025), dense and phylogenetically heterogeneous vegetation cover greatly contributes to the propagation and dominance of certain genera in AMF communities, especially those that are strongly mutualistic, such as *Acaulospora*, in agroecological systems.

In the scrublands, *Glomus* was again the dominant genus (79.75%), while *Gigaspora* (8.86%) and *Acaulospora* (11.39%) were present at lower proportions. The dominance of *Glomus* in ecosystems with low diversity and limited vegetation cover demonstrates its ecological flexibility. *Glomus* is known for its ability to survive and dominate under diverse environmental conditions.

Similar conditions were also observed in secondary forests, where *Glomus* dominated (82.46%) and *Acaulospora* (17.54%) was the minority. This dominance is likely influenced by the dense forest canopy, minimal host plant root dynamics, and limited light penetration and soil air circulation, which can restrict other genera. Under these conditions, *Glomus*, known for its widespread propagules and short life cycle, becomes more competitive. The study by Chaudhary et al. (2025) also highlights that intensive agricultural systems and natural forests tend to support the survival of genera with aggressive colonization strategies, which can persist despite microhabitat disturbances or resource limitations.

Relative frequency

The relative frequency is a percentage that describes the distribution rate of AMF types in the observed sample. The relative frequency of AMF spores in all land cover types in the Maros Pangkep Karst area is shown in Figure 9.

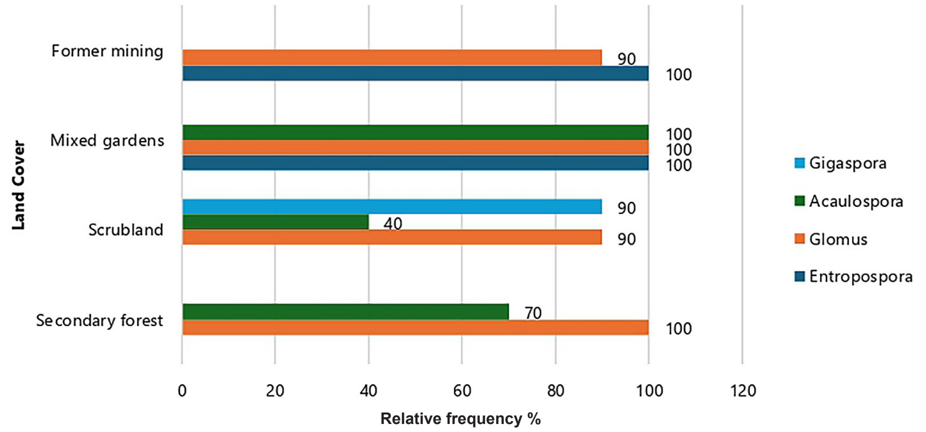

Figure 9. Relative frequency graph of FMA spores in several land cover types in the Maros Pangkep karst area

Relative frequency data indicate that the genus *Glomus* is widely distributed and is predominant in almost all types of land cover, with a frequency of 90–100%. These findings indicate that *Glomus* is a highly cosmopolitan and competitive genus capable of forming symbioses under diverse edaphic and vegetative conditions. A study by Pérez-Redondo et al. (2025) supported this, showing that *Glomus* is a dominant genus in both permanent and marginal vegetated environments due to its short life cycle and high propagule production via spores, vesicles, and hyphae.

On former mining land, *Entropospora* was found to have a frequency of 100%, which is even higher than that of *Glomus* (90%). These findings suggest that *Entropospora* may have a specific colonization strategy for degraded habitats, such as nutrient-poor substrates and high environmental stress. A study by Manga et al. (2025) demonstrated that less common genera can become dominant in extreme environments and that numerous mycorrhizal taxa remain unidentified due to limitations in current genetic sequence databases. This suggests that *Entropospora* is an indicator of a stressed ecosystem or plays a unique role in early restoration.

Moreover, mixed gardens contained three main genera (*Acaulospora*, *Entropospora*, and *Glomus*), each with a frequency of 100%. These findings indicate the high stability and diversity of the ecological functions of the AMF community under agroforestry conditions. This ecosystem offers a diverse range of host plants, fluctuating nutrient levels, and dynamic root systems that encourage various AMF taxa to establish stable colonies. Kajihara et al. (2025) emphasized that, in complex microbial communities, the relationship between taxonomic diversity and ecosystem functional stability indicates the presence of "keystone taxa" that maintain system integrity, a pattern consistent with that observed in mixed gardens.

In scrublands and secondary forests, *Glomus* remains dominant (90–100%), but there is a striking difference in the presence of *Acaulospora*. In shrublands, its frequency is only 40%, whereas in secondary forests, it increases to 70%. These differences can be attributed to variations in canopy cover, soil moisture, and host plant community dynamics. More open and unstable shrub vegetation may not support genera with more specific requirements, such as *Acaulospora*. A study by Chaudhary et al. (2025) revealed that the intensity of land disturbance and vegetation composition directly affect the ability of AMF genera to form persistent symbiotic networks. Thus, relative frequency can be a crucial indicator for assessing the stability of underground ecosystems and the suitability of land for mycorrhiza-based restoration.

Arbuscular mycorrhizal fungi (AMF) colonization

The level of AMF colonization can be determined by observing the degree of infection that occurs on plant roots. Root infection is a form of association between AMF and plant roots in which AMF produces special structures such as hyphae, arbuscules, and vesicles. Observations of root colonization revealed the presence of both uninfected and infected samples. Some of the AMF structures found in the root samples included hyphae, spores, and vesicles. For more details, see Figure 10.

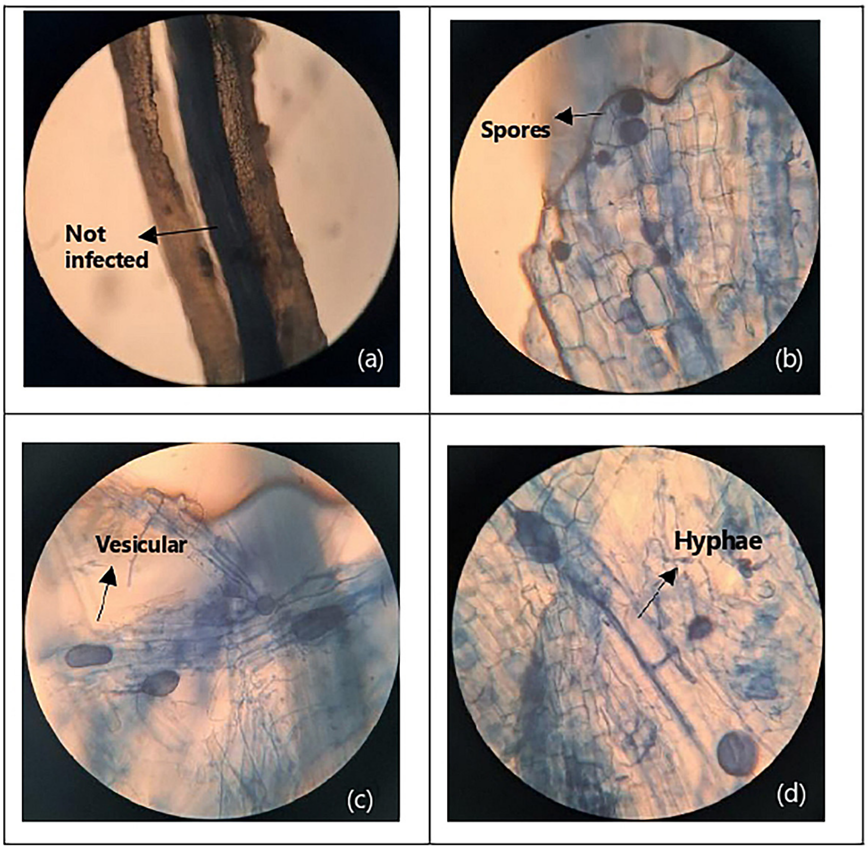

Figure 10. Arbuscular mycorrhizal fungal structure viewed at 10x magnification: Uninfected *Syzygium cumini* root (a), Spores on *Neolamarckia cadamba* root (b), Vesicles on *Arenga pinnata* root (c), Hyphae on *Psidium guajava* L. plant root (d)

The data show that AMF colonization levels on plant roots vary widely across land cover types and host plant species (Table 2). On former mining land, most plants showed low to moderate colonization rates, with only three plant species – the grass *Gigantochloa atter* (71.67%), the herb *Blumea lacera* (42.78%), and the tree *Ficus glanduivera* (41.67%) – showing high rates. This finding is consistent with the initial characteristics of revegetation, in which the soil remains nutrient-poor, root structures are not yet stable, and the AMF community is still in the early stages of colonization. A study by Wang et al. (2025) revealed that in dry and disturbed ecosystems, AMF colonization increases over time and depends on the stress tolerance of the host plant and the adaptation of AMF hyphae to edaphic factors such as pH, nitrogen, and phosphate content (Wang et al., 2025).

Conversely, in mixed gardens, most plants, including those associated with 12 tree species and 3 herb species, were colonized. The high diversity of host plants, intensive root interactions, and more stable, organic soil conditions supported the successful colonization by mycorrhizal symbionts. These findings are reinforced by previous studies (Melo et al., 2025), which show that the colonization rate of melon roots by AMF can reach more than 70% under favorable environmental conditions (especially with specific inoculations such as *Acaulospora longula*) and that this colonization contributes significantly to growth and water-use efficiency.

In scrubland, colonization rates vary from very low (e.g., *Cyrtococcum oxyphyllum*, 0.56%) to high (*Leea indica*, 66.67%; *Drocontomelon dao*, 81.67%). This finding indicates the heterogeneity of microhabitats within shrublands, where some species can establish intensive symbioses, whereas others cannot, possibly because of root structural constraints, invasive plant dominance, or interspecific competition. A study by Yarwood et al. (2025) revealed that aboveground vegetation quality is correlated with soil microbiome health and AMF root colonization, especially in seminatural ecosystems such as urban forests, where plant species dominance and

Table 2. AMF colonization levels in several land covers in the Maros-Pangkep karst area

No	Species	Habitus	AMF colonization level (%)			
			Former mining	Mixed gardens	Scrublands	Secondary forest
1	*Tectona grandis*	Tree	2.78 L	49.05 H	28.33 M	-
2	Alstonia scholaris	Tree	16.67 M	56.67 H	-	8.89 L
3	*Ficus nervosa*	Tree	3.33 L	-	-	-
4	*Lithocarpus celebicum*	Tree	3.33 L	28.33 M	8.89 L	-
5	*Syzygium cumini*	Tree	10.56 L	21.67 M	-	-
6	*Arthophylum sp*	Tree	16.67 M	-	-	-
7	*Ficus glandulifera*	Tree	26.67 M	-	-	-
8	*Mallotus mollissimus*	Tree	18.33 M	-	-	-
9	*Pterocarpus indicus*	Tree	10.56 L	-	-	-
10	*Chormolaena odorata* L.	Herb	18.89 M	-	-	-
11	Unidentified_1	Tree	21.11 M	-	-	-
12	*Nauclea orientalis*	Tree	11.67 M	-	-	-
13	*Gigantochloa atter*	Grass	71.67 H	-	-	-
14	*Blumea lacera*	Herb	42.78 H	-	-	-
15	*Cassia timorensis*	Tree	22.5 M	-	-	-
16	*Neolitsea* sp.	Tree	15 M	-	-	-
17	*Ficus benjamina*	Tree	15.83 M	-	19.45 M	-
18	*Ficus glanduivera*	Tree	41.67 H	-	-	-
19	*Arenga pinnata*	Tree	-	86.67 H	-	0 NA
20	*Neolamarckia cadamba*	Tree	-	82.5 H	-	8.33 L
21	*Psidium guajava* L.	Tree	-	58.89 H	-	-
22	*Stachytarpheta Jamaicensis*	Herb	-	76.11 H	26.11 M	-
23	*Mangifera indica*	Tree	-	52.78 H	-	-
24	*Lamtana camara* L.	Shrub	-	20.56 M	-	-
25	*Swietenia mahagoni*	Tree	-	42.22 H	-	-
26	*Pennisetum purpureum*	Grass	-	5.56 L	-	-
27	*Artocarpus heterophyllus*	Tree	-	36.67 H	-	-
28	*Cocos nucifera* L.	Tree	-	30 M	-	-
29	*Bambusa sp*	Grass	-	38.33 H	-	13.33 M
30	*Gmelina arborea Roxb*	Tree	-	53.89 H	28.34 M	-
31	*Leea indica*	Tree	-	54.58 H	66.67 H	-
32	*Choromolaena odorata* L.	Herb	-	65.56 H	26.11 M	20 M
33	*Melicope lunu-ankeda*	Tree	-	98.33 H	-	-
34	*Garcinia balica*	Tree	-	93.33 H	-	-
35	*Mucuna* sp.	Herb	-	37.78 H	-	-
36	*Ficus oppositifolia*	Tree	-	-	8.33 L	-
37	*Ficus vargata*	Tree	-	-	13.89 M	-
38	*Calopogium sp*	Liana	-	-	17.78 M	-
39	*Acacia auriculuformis*	Tree	-	-	12.22 M	-
40	*Mimosa pudica Linn*	Herb	-	-	9.45 L	-
41	*Arthophyllum* sp.	Tree	-	-	14.44 M	1.67 L
42	*Centrosema pubescens*	Liana	-	-	4.44 L	-
43	*Drocontomelon dao*	Tree	-	-	81.67 H	-
44	*Gliricidia sepium*	Tree	-	-	42.22 H	-
45	*Merremia vitifolia (Burm.f.) Hallier f.*	Liana	-	-	51.67 H	-
46	*Cyrtococcum oxyphyllum Stapf*	Grass	-	-	0.56 L	-

No	Species	Habitus	AMF colonization level (%)			
			Former mining	Mixed gardens	Scrublands	Secondary forest
47	*Cananga odorata*	Tree	-	-	15 M	-
48	*Chioantahus* sp.	Tree	-	-	5.56 L	-
49	*Ficus* sp.	Tree	-	-	-	2.22 L
50	*Cassia siamea Lamk.*	Tree	-	-	-	7.78 L
51	*Caryota mitis*	Tree	-	-	-	6.11 L
52	*Mallotus floribundus*	Tree	-	-	-	5 L
53	*Adiantum cuneatum*	Herb	-	-	-	13.34 M
54	*Strobilanthes* sp.	Herb	-	-	-	43.89 H
55	*Salvia officinalis* L.	Herb	-	-	-	5 L
56	*Piper* sp.	Liana	-	-	-	11.67 M
57	*Kleinhovia hospita*	Tree	-	-	-	25 M
58	*Sapatholobus* sp.	Liana	-	-	-	39.45 H
59	*Strebius aper*	Tree	-	-	-	2.22 L
60	*Unidentified_2*	Tree	-	-	-	13.34 M
61	*Tamarindus indica*	Tree	-	-	-	4.45 L
62	*Flacourtia inermis Roxb*	Tree	-	-	-	7.78 L
63	*Vitex cofassus*	Tree	-	-	-	3.33 L

Note: L – low; M – moderate; H – high; NA – no colonization.

soil quality determine the proportion of mycorrhizal associations.

Moreover, in secondary forests, AMF colonization is generally low. The majority of plants colonized <20%, except for several herbaceous and liana species, such as *Strobilanthes* sp. (43.89%) and *Sapatholobus* sp. (39.45%). This is likely due to the dense forest canopy, lack of root dynamics below the surface, and the possible dominance of other symbionts, such as ectomycorrhizal fungi or dark septate endophytes (DSEs). Wang et al. (2025) reported that DSEs tend to dominate under extreme or closed environmental conditions and can compete or interact complexly with AMF in plant roots, resulting in reduced AMF colonization in habitats such as mature forests.

CONCLUSION

This study revealed four main genera of AMF in the Maros-Pangkep karst area, namely, *Glomus, Acaulospora, Gigaspora,* and *Entrophospora*, with different distributions in each land cover type. The highest spore density was found in mixed gardens, while secondary forests had the lowest density. Spore diversity was also highest in mixed plantations, whereas only two dominant genera were detected in former mines and secondary forests. In terms of relative abundance, former mining sites were dominated by *Entrophospora*, mixed gardens were dominated by *Acaulospora*, and shrublands and secondary forests were dominated by *Glomus*. Relative frequency analysis revealed *Glomus* to be the most cosmopolitan genus, with a frequency of almost 100% in all land types, although *Entrophospora* was more dominant in former mining sites. In terms of plant root colonization, mixed plantations had high colonization rates for most species; however, the colonization rates of shrublands varied from very low to high, and secondary forests generally had low colonization rates, whereas former mining sites were dominated by low to moderate colonization rates, with only a few pioneer species showing high colonization rates.

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