VOL VIII

Estudos em Ciências Agrárias e Ambientais

Eduardo Spers
(Organizador)

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2026

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PRÓLOGO

Os desafios contemporâneos relacionados ao uso dos recursos naturais, à conservação da biodiversidade, às mudanças ambientais e à sustentabilidade dos sistemas produtivos exigem abordagens cada vez mais integradas. Nas Ciências Agrárias e Ambientais, essa integração se torna especialmente relevante diante da necessidade de conciliar produção, conservação, desenvolvimento territorial e uso responsável dos recursos, considerando tanto os processos ecológicos quanto as dimensões sociais e econômicas envolvidas.

O oitavo volume de ***Estudos em Ciências Agrárias e Ambientais*** reúne quatorze capítulos organizados em quatro eixos temáticos: **Território, mudanças ambientais e conservação; Solo, biodiversidade e agroecossistemas sustentáveis; Produção sustentável, manejo e organização dos sistemas produtivos; e Economia circular, transformações ambientais e história da agricultura.** Em conjunto, os trabalhos propõem um percurso que parte de questões ambientais e territoriais amplas e avança em direção ao funcionamento dos agroecossistemas, às estratégias de produção sustentável e às transformações históricas das relações entre agricultura, recursos e paisagem.

O primeiro eixo reúne estudos voltados às mudanças ambientais, à vulnerabilidade territorial, à soberania alimentar e à conservação de áreas naturais. As análises destacam como clima, uso da terra, planejamento territorial, políticas de desenvolvimento e participação comunitária interferem diretamente na relação entre sociedade e ambiente. A vulnerabilidade de áreas costeiras diante da elevação do nível do mar, por exemplo, envolve não apenas fatores físicos, mas também infraestrutura, uso do solo, planejamento e capacidade adaptativa. Da mesma forma, a soberania alimentar é discutida a partir das disputas pelo território, pela terra e pela água e das diferentes formas de organização da produção rural.

No segundo eixo, o olhar se volta ao solo, à biodiversidade e ao funcionamento dos agroecossistemas. A agricultura regenerativa é apresentada como uma abordagem sistêmica voltada à recuperação da saúde e da funcionalidade do solo, com princípios relacionados à redução da perturbação, à cobertura permanente, à diversidade e à integração planejada entre componentes do sistema produtivo. Os estudos sobre fungos micorrízicos, bactérias rizosféricas e recursos fitogenéticos ampliam essa discussão ao abordar diferentes dimensões da biodiversidade e de sua importância ecológica. As interações entre organismos e solo, a participação de microrganismos nos processos de transformação da matéria orgânica e a conservação da diversidade vegetal evidenciam a relevância dos recursos biológicos para o funcionamento dos ecossistemas e para o desenvolvimento de estratégias de conservação e uso sustentável.

O terceiro eixo aborda diferentes estratégias de aprimoramento dos sistemas produtivos, considerando aspectos técnicos, ecológicos e organizacionais. São discutidas alternativas como a utilização de microrganismos benéficos para reduzir a dependência da fertilização mineral, o emprego de alimentos vivos na aquicultura, o comportamento e o manejo de bovinos autóctones em sistemas extensivos de montanha e formas coletivas de organização e comercialização entre pequenos produtores. Os trabalhos demonstram que a sustentabilidade da produção depende não apenas da eficiência no uso dos recursos, mas também da adequação das práticas de manejo, da conservação da paisagem e das condições de organização econômica e social dos produtores.

Por fim, o quarto eixo estabelece um diálogo entre aproveitamento de recursos, transformação ambiental e história da agricultura. O estudo sobre a utilização da casca de noz para a produção de carvão ativado examina os requisitos técnicos e de investimento associados à valorização de resíduos agroindustriais, em consonância com os princípios da economia circular. Os dois capítulos seguintes ampliam a perspectiva temporal ao investigar as relações entre agricultura, clima, desmatamento e transformações sociopolíticas nas terras baixas maias, bem como os conhecimentos, as tecnologias de manejo da água e as intervenções sobre a paisagem desenvolvidos no contexto da agricultura andina e inca. Em conjunto, esses trabalhos permitem considerar diferentes formas de utilização e transformação dos recursos naturais, desde experiências históricas de organização agrícola até propostas contemporâneas de valorização de materiais e processos produtivos.

A diversidade dos capítulos reunidos neste volume evidencia que os desafios ambientais e agrícolas contemporâneos não podem ser compreendidos de forma isolada. Solo, água, biodiversidade, território, produção, tecnologia e organização social constituem dimensões interdependentes de sistemas em constante transformação.

Ao integrar estudos sobre conservação, sustentabilidade, produção e história da agricultura, este volume contribui para ampliar o debate sobre formas mais equilibradas de relação entre sociedade, sistemas produtivos e ambiente, valorizando tanto a inovação científica quanto o conhecimento acumulado ao longo do tempo.

Boa leitura!

Eduardo Eugênio Spers

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FUNCTIONAL ROLE OF ARBUSCULAR MYCORRHIZAL FUNGI IN AGGREGATE FORMATION, BIODIVERSITY, AND EDAPHIC FUNCTIONING

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ABSTRACT: The relationships between arbuscular mycorrhizal fungi (AMF) and other microorganisms, and how these microorganisms contribute to aggregate formation and stability, are not yet fully understood. Therefore, the objective of this review is to provide an up-to-date overview of the state of the art regarding AMF and their functionality, using an updated systematic review as the methodology. The research addresses two main questions: 1) What is the functional role of AMF in aggregate formation and stability? and 2) What is the influence of AMF on soil diversity? Arbuscular mycorrhizal fungi play a fundamental role in maintaining soil ecosystem functionality by promoting aggregate formation, enhancing soil biodiversity, and regulating key ecological processes involved in nutrient cycling, carbon sequestration, and ecosystem resilience. Through their extensive interactions with plants, microorganisms, and soil fauna, AMF act as ecosystem engineers that contribute significantly to soil sustainability and the long-term provision of ecosystem services, supporting ecosystem stability, productivity, and adaptation to environmental change.
KEYWORDS: soil biodiversity; hyphae; soil degradation; ecosystem engineers; aggregation.

PAPEL FUNCIONAL DE LOS HONGOS MICORRÍZICOS ARBUSCULARES EN LA FORMACIÓN DE AGREGADOS, BIODIVERSIDAD Y FUNCIONAMIENTO EDÁFICO

RESUMEN: Las relaciones entre los hongos micorrízicos arbusculares (HMA) y otros microorganismos, así como la forma en que estos microorganismos contribuyen a la formación y estabilidad de los agregados, aún

no se comprenden del todo. Por lo tanto, el objetivo de esta revisión es ofrecer una visión general actualizada del estado de la cuestión en relación con los HMA y su funcionalidad, utilizando como metodología una revisión sistemática actualizada. La investigación aborda dos preguntas principales: 1) ¿Cuál es el papel funcional de los HMA en la formación y estabilidad de los agregados? y 2) ¿Cuál es la influencia de los HMA en la diversidad del suelo? Los hongos micorrízicos arbusculares desempeñan un papel fundamental en el mantenimiento de la funcionalidad del ecosistema del suelo al promover la formación de agregados, potenciar la biodiversidad del suelo y regular procesos ecológicos clave relacionados con el ciclo de los nutrientes, el secuestro de carbono y la resiliencia del ecosistema. A través de sus amplias interacciones con las plantas, los microorganismos y la fauna del suelo, los HMA actúan como «ingenieros del ecosistema» que contribuyen de manera significativa a la sostenibilidad del suelo y a la prestación a largo plazo de los servicios ecosistémicos, favoreciendo la estabilidad, la productividad y la adaptación del ecosistema al cambio medioambiental.
PALABRAS CLAVE: biodiversidad del suelo; hifas; degradación del suelo; ingenieros del ecosistema; agregación.

1. INTRODUCTION

Soil is a vital resource for the development of ecosystems and human societies. It constitutes the foundation of agricultural production, supports livelihoods, and accounts for approximately 95% of global food production. Likewise, it provides ecosystem services including biomass production, soil contaminants filtration, plant nutrition, and the regulation of nutrient cycling (Gomiero, 2016; Hu et al., 2023; Tahat et al., 2020). In this context, it is important to highlight that soil properties are affected by both anthropogenic activities and natural events such as droughts and floods, which significantly impact natural processes in the terrestrial ecosystems, causing a global concern about soil health (Chen et al., 2002; Keesstra et al., 2016; Wang et al., 2023). These disruptions can alter the structure and abundance of soil biological communities, negatively influencing their biological and functional diversity; consequently, fundamental ecosystem processes are altered, as edaphic biota play a key role in maintaining soil functions and ecosystem stability (Postma-Blaauw et al., 2010).

Arbuscular mycorrhizal fungi (AMF) are mutualistic root symbionts whose associations are influenced by the functional characteristics established by both organisms. At the same time, their codependent relationship is shaped by environmental conditions and by the biological traits of the interacting species (Davison et al., 2020; Kokkoris et al., 2020). It is widely recognized that, through this association, fungi acquire carbon compounds from their host plants and, in return, provide access to soil nutrients that are often limited, such as N, P, Fe, and S (Almario et al., 2022). Converting this association into a particularly important key to natural nutrient cycles, as well as to soil health and productivity (Fall et al., 2022; Huey et al., 2020).

The presence of these fungi in soil has a notable positive effect on soil diversity, as they produce exudates that play an important role in recruiting bacteria, actinomycetes, and other fungi (Barea et al., 2005; L. Zhang et al., 2022). Likewise, AMF are fundamental to soil multifunctionality, contributing to key processes such as primary production, nutrient cycling, and water and climate regulation across multiple spatial scales: the roots-soil microscale (aggregates formation, carbon transfer, and the creation of micro-habitats); the ecosystemic scale (biomass production increase), and the global scale (reduction of atmospheric CO_2 via its sequestration in soil). In addition to their contributions to disease control, soil and plant health, and the soil microbiome, AMF contribute significantly to the functioning of ecosystem services (Wang & Rengel, 2024).

Many studies have focused on evaluating AMF symbiosis and its function as biofertilizers, limiting themselves to selecting and evaluating the most adaptable morphotypes for agricultural use (Ahammed & Hajiboland, 2024; Azizi et al., 2021; de los Santos-Villalobos & Parra-Cota, 2021; Mahmud & Chong, 2021). Commercially, AMF inoculants are formulated using well-studied AMF species that possess a broad host range and are adapted to a wide variety of soil and environmental conditions (Giovannini et al., 2020).

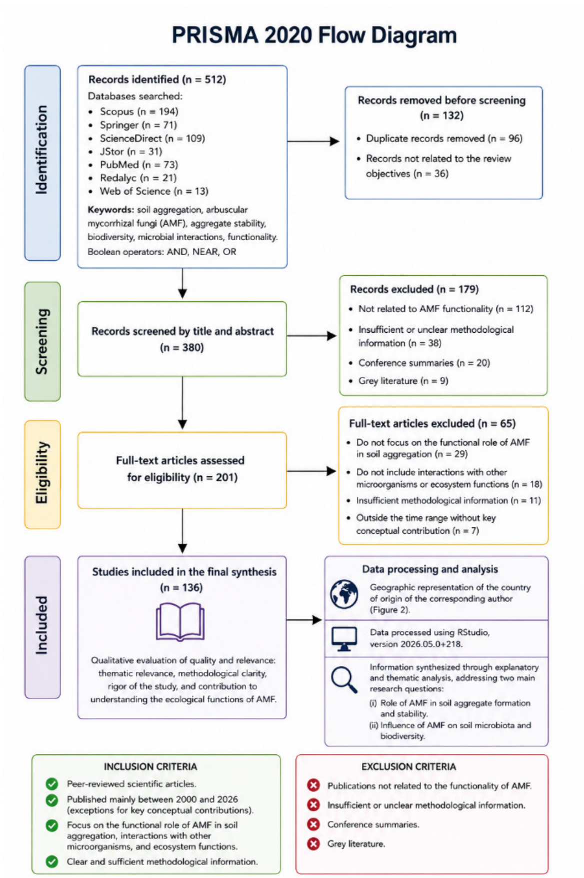
This review focuses on the functional diversity of AMF, addressing biological, physiological, and ecological traits that underline their contributions to plant development, nutrient cycling, and soil ecosystem processes (Rillig & Mummey, 2006). Likewise, their relationships with other soil microorganisms are examined in depth, with which they develop complex interactions that provide a wide range of benefits to plants and soil (Jiang et al., 2020; Netherway et al., 2021). It also describes how the functional diversity of arbuscular mycorrhizal fungi contributes not only to soil fertility but also to the formation and stability of soil aggregates, and how they influence soil diversity.

2. METHODS

The selection of literature was based on a structured review process following the PRISMA 2020 guidelines Fig. 1. Initially, 512 records were identified through searches in Scopus, Springer, ScienceDirect, JStor, PubMed, Redalyc and Web of Science, using keywords such as soil aggregation, arbuscular mycorrhizal fungi (AMF), aggregate stability, biodiversity, microbial interactions and functionality. The searches combined the terms soil aggregation and AMF with other keywords using Boolean operators such as

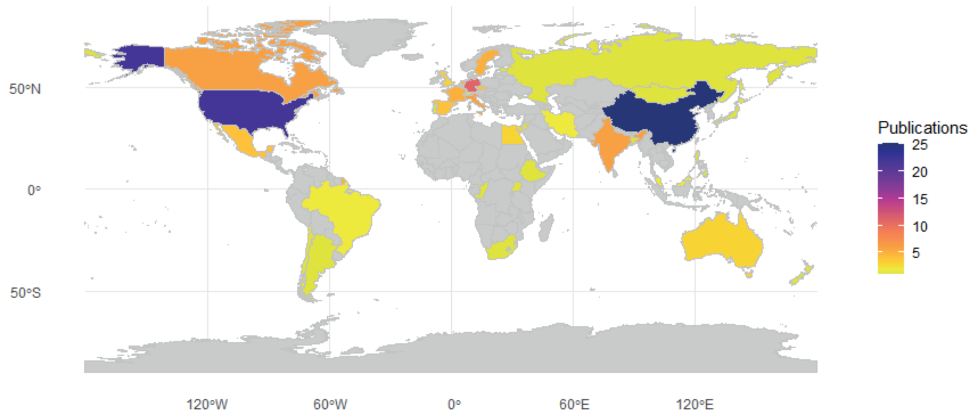
AND, NEAR, and OR. During the initial screening stage, duplicate records and studies not directly related to the review's objectives were excluded. Among the criteria for including peer-reviewed scientific articles was a publication date between 2000 and 2026. Exceptions were made for articles that contained key concepts, in which case the author who originally defined the concept was cited. The publication's focus had to address the functional role of AMF in soil aggregation, their interactions with other microorganisms, and the key ecosystem functions AMF perform in soil.

Figure 1. PRISMA 2020 Diagram. PRISMA methodology for the identification of scientific articles in the systematic review, including criteria for selecting and analyzing scientific literature through a checklist and flow diagrams.



Among the exclusion criteria included publications that were not directly related to the functionality of AMF, those that did not provide sufficiently clear methodological information, likewise scientific conference abstracts and grey literature. The country of origin of the lead author of each reviewed article was represented cartographically Fig. 2. The data were processed using RStudio software, version 2026.05.0+218. After reviewing titles, abstracts, and full texts, 136 articles were selected for the final synthesis. The quality and suitability of the publications were assessed qualitatively based on thematic relevance, clarity of the methodology described, study rigor, and their contribution to understanding the ecological functions of AMF. Selected information was synthesised through an explanatory and thematic analysis, in which the evidence was grouped around two main research questions: (i) the role of AMF in the formation and stability of soil aggregates and (ii) the influence of AMF on soil microbiota and biodiversity.

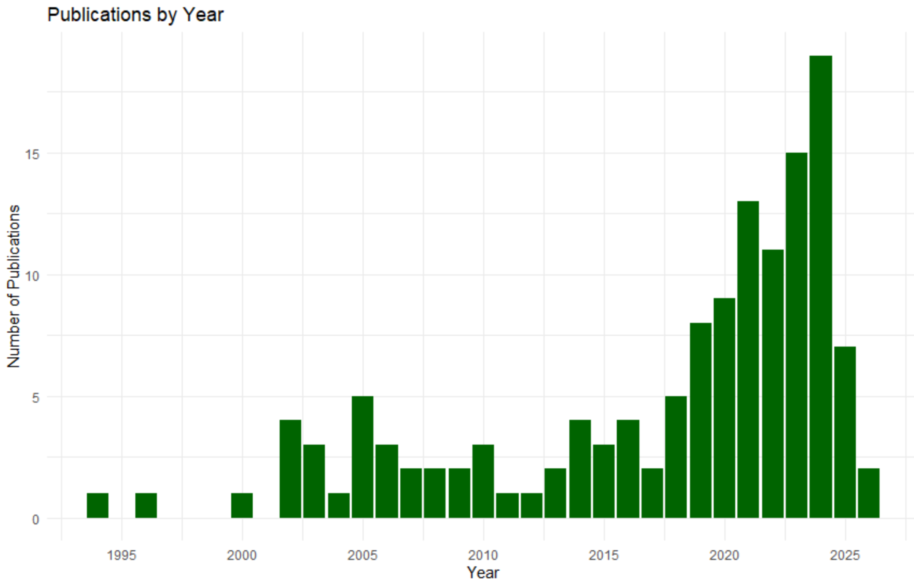
Figure 2. Geographical distribution of publications by the country of the lead author. China and the United States of America had the highest number of publications.



3. RESULTS

The literature review identified 385 documents; of these, 136 papers were selected for inclusion. The publication years are presented in Fig. 3. A total of 2.2% (3 articles) were published before 2000, while 16.9% of the reviewed publications (23 articles) were published from 2000 to 2009. For the decade spanning 2010–2019, the percentage of publications was 24.3% (33 articles), whereas 56.6% (77 articles) corresponded to the period 2020–2025. Special attention was given to the 110 most recent publications (published between 2010 and 2026) to address the objectives of this review. The publications covered a wide range of topics, including the role of AMF in aggregate formation, interactions between AMF and other microorganisms, and the effects of soil disturbance and degradation on AMF.

Figure 3. Number of scientific publications per year related to the objective of this research. An increasing trend in publications was observed, with a higher peak in 2021.



The contribution of the AMF to aggregate formation and stability is under development taking the following question into account:

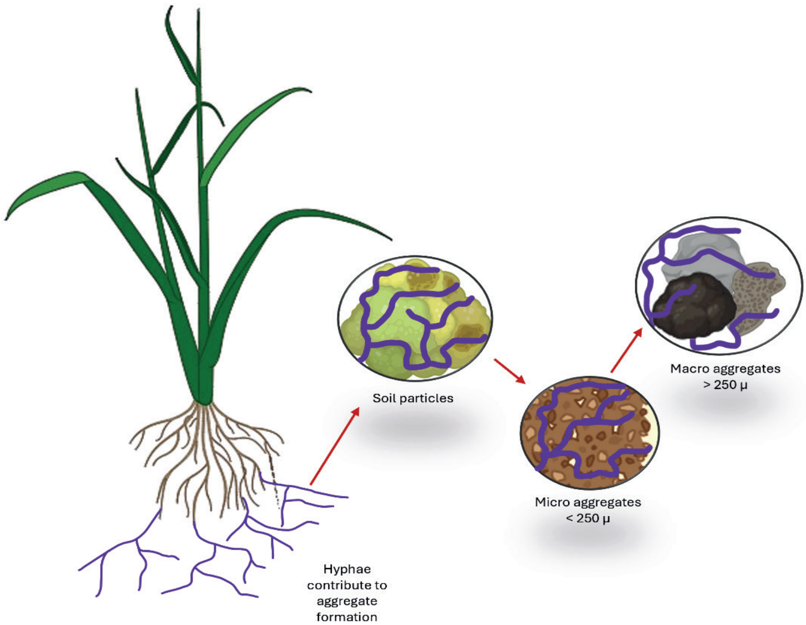
I) The role of AMF in the formation and stability of soil aggregates?

Soil structure, defined as the arrangement or grouping of mineral and organic soil particles into units known as aggregates (Woldemar, 1907), is a crucial characteristic for maintaining soil porosity, gas exchange, water infiltration, erosion resistance, and carbon sequestration (Borie et al., 2008; Guo et al., 2019). This soil characteristic is directly altered by natural and anthropogenic activities such as rainfall regimes, conventional agriculture and deforestation, which directly or indirectly impact its properties, thereby influencing the biotic and abiotic components that regulate soil stability (Barto et al., 2010).

Soil aggregation constitutes a fundamental dynamic component of soil structure formation and stabilization, contributing to the conservation of its physical, chemical and biological properties (Yudina & Kuzyakov, 2023). It is often treated as a static phenomenon, but it is a dynamic cycle in which aggregates are continuously formed and degraded over timescales that can be as short as a few weeks (Morris et al., 2019). Aggregates are an important factor in C sequestration, since the C cycle in soil regulates the quantity and quality of C retained in its principal fractions: humic acid (HA), fulvic acid (FA), and humin, according to their solubility in alkaline and acid solutions (Olk et al., 2019).

The incorporation of carbon into aggregates allows it to remain protected, preventing its rapid release as CO_2 into the atmosphere (Rabbi et al., 2016). The aggregation process is influenced by both abiotic factors, such as rainfall regimes (Spohn & Giani, 2011), and biotic components, such as fungi and bacteria (Lehmann et al., 2017; Lehmann & Rillig, 2015; Morris et al., 2019).

Figure 4. Arbuscular mycorrhizal fungi contribution to the formation, increase in size and stability of soil aggregates. Violet or purple color corresponds to the AMF hyphae.



AMF are among the key actors in the rhizosphere, principally in processes such as the formation and stability of soil aggregates Fig. 4. Their hyphae are one of their most important traits, because they extend to establish networks that are closely associated with the production of glomalin-related soil proteins (GRSP) and interact with soil particles (Zhao et al., 2024). According to Alptekin et al., (2025) this compound is a complex carbohydrate of fungal origin, possibly produced by the cell walls of arbuscular mycorrhizal fungi hyphae, and it plays an important role in soil aggregation and stability by functioning as a cementing agent for soil particles. Recent studies have shown that different AMF taxa differ in extraradical mycelial growth, the GRSP production, and interactions with other soil microorganisms, generating diverse responses in aggregate stability and associated ecosystem processes (Morris et al., 2019; Rillig & Mummey, 2006; Son et al., 2024; Wang & Feng, 2021). GRSP have been studied for their contribution to reducing soil degradation, as they are directly associated with physicochemical parameters such as structural stability, carbon sequestration, water retention, and nutrient cycling (Nagy et al., 2026; Zhou et al., 2024).

Nevertheless, recent advances in the molecular characterization of glomalin have raised questions about its true biochemical identity, challenging the traditional hypothesis that it is a protein produced by AMF and suggesting it may be a predominantly carbohydrate-based compound. In this context, Alptekin et al., (2025), in their research *“From glomalin to glomalose: unravelling the molecular identity of the MAb32B11 antigen”*, indicate that the RiHSP60 protein does not fully explain the nature of glomalin, as it is part of the fungal domain and is not specific to AMF.

Additionally, the authors indicate that this hypothesis lacks experimental support because the MAb32B11 antigen does not recognize the RiHSP60 polypeptide as a protein. Based on their results, the authors propose that the MAb32B11 antigen is associated with a protein-free fraction with higher carbohydrate content, which they term “glomalose”. This molecule is a high-molecular-weight polysaccharide with a size range of 500 to 600 kilodaltons (kDa).

The involvement of AMF in aggregate formation includes: a) biophysical mechanisms, through the direct interaction of hyphae with soil particles (Ji et al., 2024). b) biochemical mechanisms, especially associated with the production of glycoproteins, hydrophobins, and polysaccharides (Li et al., 2023). Finally, c) biological mechanisms, which are its development through AMF interactions with host plants and other soil microorganisms (Gómez-Leyva et al., 2023; Lu et al., 2023).

AMF contributes to aggregate formation through biophysical mechanisms by promoting the growth of extraradical mycelium, which forms an extensive physical network linking particles and microaggregates (Jiménez-Martínez et al., 2024; Richter et al., 2024). Hyphal networks act as physical bridges connecting soil particles and microaggregates, facilitating the movement of water, nutrients, and microorganisms (Faghihinia et al., 2024; Pauwels et al., 2023). Likewise, the extent, thickness, and architecture of hyphae contribute substantially to the mechanical resistance of aggregates against erosion and water degradation (Ji et al., 2024). Through the growth and expansion of these networks, mechanical pressure is generated, bringing soil particles and microaggregates closer together and compacting them, leading to the formation of stable macroaggregates and contributing to pores distribution (Jiménez-Martínez et al., 2024; Richter et al., 2024). Additionally, mycorrhizal networks can connect the roots of different plants via shared hyphae, functioning as a communication network among diverse plants (Luo et al., 2023). Due to their filamentous growth and extensive mycelial networks, AMF can extend beyond the nutrient-depletion zone of the rhizosphere in search of nutrients, reaching distances of up to 14 linear centimeters (Jansa et al., 2003). They also account for 30% of the soil microbial biomass (Kakouridis et al., 2024).

Regarding biochemical mechanisms, studies such as those by Borie et al., (2008); Costa et al., (2018); Lehmann, Zheng, et al., (2017); Morris et al., (2019); Rillig & Mummey, (2006) and Wilkes et al., (2021) indicate that AMF plays an active role in aggregate formation by producing extracellular compounds that act as cementing agents. These exudates enhance adhesion between soil particles and organic matter, creating viscous films around hyphae and roots that contribute to the formation and stability of microaggregates (Agnihotri et al., 2022; Huang et al., 2022; Lanfranco et al., 2016; Řezáčová et al., 2021; Rodriguez-Garcia & Müller, 2026). Additionally, AMF contributes to the stabilization of organic carbon by producing recalcitrant biochemical compounds that protect organic matter within aggregates, reducing rapid decomposition and contributing to the long-term structural integrity of soil (Qin et al., 2023; Tao & Liu, 2024).

AMF contribute to aggregate formation through biological mechanisms by stimulating the growth of bacterial and fungal communities in the mycorrhizosphere, with which they complement processes such as nutrient cycling, carbon sequestration, and aggregate formation (Emmett et al., 2021; Philippot et al., 2024; Yuan et al., 2021; L. Zhang et al., 2022). Their main contribution lies in the creation of microhabitats where associated microorganisms proliferate and contribute to the production of cementing compounds, biofilms, and metabolites that strengthen soil particle cohesion, thereby promoting aggregate formation (Wilpiszeski et al., 2019). Additionally, hyphal necromass is a major source of soil carbon and serves as a substrate for bacterial community development (Liu et al., 2023; Zhou et al., 2024).

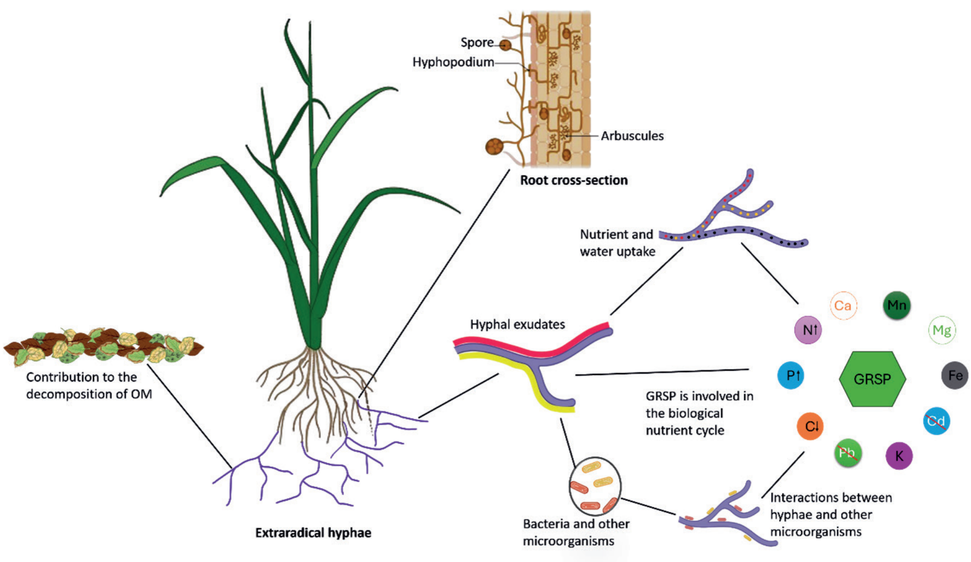
It is important to clarify that the relative contribution of each mechanism can vary considerably across ecosystems or agricultural systems, and that factors such as AMF community structure, the associated microbiome, soil physicochemical characteristics, and environmental disturbance or agronomic management practices must be considered. The community of AMF species present in the soil is related to its aggregation capacity, as different morphotypes can produce hyphae with distinct traits (Klironomos & Hart, 2002; Lehmann, et al., 2017). Studies such as those by Enkhtuya & Vosátka, (2005); Klironomos et al., (2005); Lehmann, et al., (2017) and Piotrowski et al., (2004) provide evidence of differences in soil aggregation capacity among AMF morphotypes, highlighting that the combination of fungal species and host plants is crucial for determining the direction and intensity of the relationship along the mutualism–parasitism continuum.

AMF do not act independently in soil; they develop relationships with a diverse range of microorganisms that influence the formation and maintenance of soil aggregates. This aspect will be further addressed in the second research question, which aims to emphasize the significant role of AMF in soil biodiversity and their positive impact on aggregate formation.

II) What is the influence of AMF on soil biodiversity?

According to Barea et al., (2005), soil biodiversity encompasses a wide range of essential interactions that maintain ecosystem balance and support the productivity of agricultural and natural systems. These microbial interactions are more complex in the rhizosphere and mycorrhizosphere (Wang & Feng, 2021), a dynamic niche that enables complex symbiotic and synergistic relationships among AMF, host plant roots, and the diverse community of soil microorganisms. Fig. 5 illustrates some of the interactions that occur within the mycorrhizosphere.

Figure 5. Main functions of arbuscular mycorrhizal fungi in the soil. Nutrient uptake, interactions with soil microorganisms, heavy-metal immobilization, and nutrient transfer to the plant.



Among the most extensively studied interactions within the mycorrhizosphere are those between AMF and bacteria, known as mycorrhiza helper bacteria (MHB) (Garbaye, 1994). Bacteria belonging to the genera *Bacillus* and *Pseudomonas* play a key role in AMF spore germination (Roesti et al., 2005; Sangwan & Prasanna, 2022; Turrini et al., 2018). Furthermore, bacteria belonging to the genera *Paenibacillus, Pseudomonas, Bacillus, Burkholderia*, and *Streptomyces* can influence hyphal growth (Aspray et al., 2013; Frey-

Klett & Garbaye, 2005), and the establishment of the symbiosis (Nasslahsen et al., 2022; Rigamonte et al., 2010). Table 1 presents several reported cases of bacteria that interact directly with AMF and their effects on the plant-AMF symbiotic association.

Table 1. Literature documenting the types of interactions between AMF and bacteria.

Bacteria	**Type of interaction with AMF**	**Effect in the relation AMF/ Bacteria**	**Scientific reference**
***Pseudomonas* spp.**	Association with spores and roots.	They stimulate spore germination, hyphal growth, and root colonization.	Bharadwaj et al., (2008); Frey-Klett et al., (2007); Xavier & Germida, (2003)
***Azospirillum* spp.**	N fixation and association in the rhizosphere.	Increase in nutrient absorption (N, P, K, etc.).	Bernados et al., (2024)
***Stenotrophomonas* spp.**	Production of phytohormones and enzymes.	They stimulate hyphal growth, improve the establishment of symbiosis, and improve protection against pathogens.	Bharadwaj et al., (2008)
***Burkholderia* spp.**	Association in the mycorrhizosphere.	They stimulate bacterial proliferation, promote root colonization, and enhance mycelial activity.	Akyol et al., (2019)
***Rhizobium* spp.**	Multiple symbiosis with legumes.	Synergy between N fixation and mycorrhization increases the absorption of soluble P.	Artursson et al., (2006)
***Streptomyces* spp.**	Production of antibiotics and bioactive compounds.	They stimulate the spore germination and protect the mycelium against pathogens.	Agnolucci et al., (2019); Pandit et al., (2022)
***Paenibacillus* spp.**	Accelerate hyphal growth.	They induce hyphal branching and improve the mycorrhiza formation.	Frey-Klett et al., (2007); Rigamonte et al., (2010)
***Cellulomonas* spp.**	Associated with the rhizosphere of mycorrhizal plants.	They increase nutrient availability and promote mycelial development.	Akyol et al., (2019)
***Microbacterium* spp.**	They colonize roots and the mycorrhizosphere.	They stimulate AMF colonization and the production of beneficial metabolites.	(Akyol et al., 2019)

The table summarizes bibliographic evidence on the types of interactions between bacteria and arbuscular mycorrhizal fungi, including mechanisms, effects, and references.

These associations promote root colonization and stimulate plant growth, confirming the concept of mycorrhiza as a tripartite association, and framing the symbiosis as a multiscale interaction in which bacterial microorganisms are co-protagonists (Bonfante & Anca, 2009). Likewise, Wang et al., (2022) confirmed that compounds released by AMF hyphae can influence soil pH and aggregation, thereby impacting microbial composition, nutrient availability, and water distribution. In their research, Akyol et al., (2019) demonstrated that AMF inoculation in agricultural soils alters the native microbial community and enriches bacterial genera such as *Burkholderia, Cellulomonas, Microbacterium,* and *Streptomyces*, which can enhance colonization and functioning of the mycelium.

Furthermore, Barea et al., (2002) determined that the mycorrhizosphere of AMF creates a microenvironment where beneficial bacteria act as biocontrol agents, reducing the incidence of phytopathogens and increasing plant tolerance to water and nutrient stress. Additionally, AMF can modify how water affects bacterial communities, leading to changes in plant physiological responses, such as the exudation of organic compounds by roots (Vivas et al., 2003). They also induce changes in the concentrations of plant hormones such as abscisic and jasmonic acids, which serve as signaling molecules that activate induced systemic resistance (ISR), thereby triggering defenses against pathogens and under stress conditions (Ruiz-Lozano et al., 2012). These changes indirectly alter the mycorrhizosphere habitat, potentially promoting the homogenization and loss of bacterial diversity, ultimately modifying multi-kingdom interactions (Debray et al., 2022; Werner et al., 2014). Therefore, AMF act as key determinants of soil microbial community reorganization through plant-mediated mechanisms, highlighting their role in regulating functions in the mycorrhizosphere under stress conditions.

Also, Ansari et al., (2024) indicated that plant growth-promoting bacteria (PGPB) and AMF work together to stimulate acquired systemic immunity and induce resistance, increasing the production of antimicrobial metabolites, promoting competition for nutrients, and modulating hormones, thereby improving plant resistance to pathogens and abiotic stresses. Additionally, AMF act as organizers of soil biodiversity structure and dynamics, functioning as regulators in soil ecological interactions (Yang et al., 2024). These interactions arise from the formation of hyphal networks that enhance the plant´s nutrient and water uptake and create microhabitats that support the growth of bacteria and other fungi (Wang et al., 2024; Zhang et al., 2022). AMF also promote soil biological diversity through the exudation of organic compounds and the release of glomalin, which fosters heterogeneous environments rich in ecological niches for microorganisms and soil mesofauna (Rillig et al., 2015). The presence of HMA increases the structural diversity of the edaphic habitat, allowing colonization by specialized bacterial communities, including PGPR and MHB (Frey-Klett et al., 2007).

Among AMF´s relationships with other microorganisms, the relationship with dark septate fungi (DSF) was also reviewed. DSF is a polyphyletic group of endophytic fungi with melanized cell walls and septa. These fungi cohabit with AMF in the roots of many plants, in both natural and disturbed soils, and both groups can colonize roots simultaneously, forming composite fungal communities (García-Mares et al., 2024; Lugo et al., 2018; Xie et al., 2021). The relationships that develop among these microorganisms are either neutral or synergistic, as observed in cases (Chaudhry et al., 2009; Wang et al., 2024) where the DSF and AMF coexist without apparent antagonism, and in some cases, coinoculation results in additive and synergistic effects on the plant. Researchers such as Bueno de Mesquita et al., (2018) and Gong et al., (2023) have reported competition for niches, space in roots, or resources, which leads to changes in colonization patterns depending on the plant species, fungal species, and soil conditions.

Similarly, plants colonized by AMF can significantly alter their physiological responses to viral infections, often decreasing symptom severity (Ebrahimi et al., 2020; Maffei et al., 2014). The interaction between AMF and plants can induce changes in the expression of defense-related genes, mainly those involved in the synthesis of phenolic and flavonoid compounds, which are essential to the antiviral response (Aseel et al., 2019, 2025; Rashad et al., 2023; Zhang et al., 2013).

On the other hand, soil meso-organisms, such as insects and other mycophagous taxa, play an important role in the ecological dynamics of AMF. Many edaphic arthropods feed on mycorrhizal hyphae, thereby moderating fungal biomass and affecting the capacity for root colonization (Klironomos & Kendrick, 1996). Although mycophagy may decrease symbiotic efficiency, it also allows ecological feedback by breaking hyphae, redistributing propagules in the soil, and increasing the production of biochemical compounds that stimulate other microbial communities (Wardle, 2006). Thus, mycophagous organisms are indirectly involved in AMF activities and in their multi-kingdom interactions in the rhizosphere.

Additionally, larger animals, such as birds and rodents, are also involved in AMF dynamics by dispersing spores (Mangan & Adler, 2000). The AMF dispersal can occur through the accidental ingestion of propagules from roots, soil, or plant material, which are then excreted by animals, providing a safe pathway for the long-distance transport of these organisms (Correia et al., 2019; Stephens et al., 2021). This animal-mediated dispersal (endozoochory and epizoochory) favors the persistence of mycorrhizal symbiosis in fragmented, disturbed, and/or eroded ecosystems, thereby contributing to preserving functional diversity in plant and microbial communities (Paz et al., 2021; Zaharick et al., 2015). Finally, evidence shows that AMF are dispersed through multiple vectors, both biotic (by animals, including humans; Elliott et al., (2022); Mangan & Adler, (2000)), and abiotic (by water or air/wind; Chaudhary et al., (2020)), which helps explain why their presence and colonization do not rely solely on interactions with microbiota and microfauna underground.

Finally, AMF is among the microorganisms that contribute to soil functionality. However, it should be emphasized that symbiosis is driven by multiple ecological factors, including the AMF species or families involved, the host plant´s mycorrhizal dependency, as well as edaphic and climatic conditions, and soil management practices (Enebe & Erasmus, 2023). The contribution of AMF to soil functionality cannot be generalized, as different species or families exhibit distinct ecological traits. As mentioned by Janoušková et al., (2023), AMF respond differently when introduced to new climatic conditions and soil types. A clear example is the use of commercial inoculants, which are industrially produced and often introduced into different regions without considering these natural conditions, resulting in suboptimal functional performance.

4. ANALYSIS

AMF constitute an essential component of soil biota, and their role as mediators of ecological processes in soil has been extensively studied and recognized. Evidence demonstrates that these microorganisms play a determinant role in the formation and stabilization of soil aggregates, a process closely associated with the recovery of soil structure, aeration, and water-holding capacity. This is largely attributed to the growth of their extraradical hyphae, which form extensive networks that bind mineral particles and organic matter, as well as to their ability to produce glomalin and other glycoproteins that act as cementing agents for soil particles (Lehmann et al., 2020; Rillig & Mummey, 2006). Thus, AMF not only contributes to enhancing the structural stability of soil but also increases its resilience to erosion and physical degradation (Morris et al., 2019; Shukla et al., 2025).

Studies such as those by Hossain, (2021); Masebo et al., (2025) demonstrated that glomalin accumulation associated with AMF is correlated with an increase in the percentage of stable organic carbon and improved soil quality in agroecosystems. This function confers a fundamental role on AMF in regulating the carbon and phosphorus biogeochemical cycles, as their hyphal networks promote carbon sequestration in stable soil fractions and enhance nutrient mobilization (Lehmann, et al., 2017; Rillig et al., 2015; Treseder & Allen, 2002).

With respect to edaphic biodiversity, AMF modulates soil microbial communities, influencing the composition of both bacterial and fungal communities (Han et al., 2025; J. Li et al., 2025). Mycorrhizal symbiosis establishes a rhizosphere characterized by diverse microenvironments, through the release of root and fungal derived exudates, which modify physicochemical conditions such as pH, nutrient availability, and colloidal structure, thereby stimulating beneficial microbial activity (Barea et al., 2005; Toljander et al., 2007). AMF establish hyphal networks that act as channels for communication and transfer between roots and microorganisms, generating microhabitats that promote the coexistence of plant growth-promoting bacteria, endophytic fungi, and actinobacteria. Furthermore, they contribute to the functional enrichment of soil microbiomes (Fall et al., 2022; Rillig et al., 2015; Zhang et al., 2014).

The symbiotic and mutualistic interactions established by AMF with plants and other microorganisms expand the soil food web, strengthening the functional resilience of soils to disturbances such as drought, contamination, and intensive land use (Lehmann et al., 2020; Yang et al., 2018). Therefore, AMF act as ecosystem engineers that integrate biological and physicochemical functions within soils, ensuring the continuity of nutrient cycling and sustaining plant productivity (Ndeko et al., 2024; Yang et al., 2018).

Likewise, the presence of AMF is associated with higher functional diversity and soil stability, as well as with the formation and persistence of complex soil food webs (Lethielleux-Juge, 2025). Mycelial networks and their ability to connect plants and microorganisms facilitate the transfer of carbon and nutrients, strengthening interspecific cooperation within the rhizosphere (Fellbaum et al., 2014; Luo et al., 2023). At the same time, the dispersal of AMF through biotic vectors (such as small mammals and birds) and abiotic vectors (water and wind) ensures their persistence in fragmented or degraded ecosystems, thereby contributing to the conservation of genetic diversity and, indirectly, to the ecological functioning and genetic diversity of mycorrhizal communities (Borgmann-Winter et al., 2023; Chaudhary et al., 2020; Luo et al., 2023).

AMF can be considered ecosystem engineers due to their extraordinary capacity to modify soil structure and functioning through physical, biochemical, and biological processes. However, their functionality emerges from complex interactions with host plants and the rhizosphere microbiota. Furthermore, their hyphal networks organize soil microstructure, particularly at the rhizosphere and mycorrhizosphere scales, where they influence carbon dynamics, structural stability through increased aggregation, nutrient distribution, and microbial interactions. The magnitude and persistence of these effects are regulated by spatial and temporal scales determined by the establishment of mycorrhizal associations (plant–fungus–microbiome), as well as by environmental conditions and ecosystem management practices.

Likewise, the ability of AMF to improve soil structure, enrich microbial communities, and mediate trophic interactions makes them essential components of soil sustainability (Ai et al., 2022; Fall et al., 2022; Shukla et al., 2025). Understanding these mechanisms is crucial for promoting agricultural management and ecological restoration practices grounded in soil biology that aim to conserve biodiversity and ecosystem services.

Finally, scientific publications reveal a significant pattern of geographical and ecological biases in the literature on arbuscular mycorrhizal fungi. The largest percentage of studies focuses on temperate agricultural systems and ecosystems in North America, Europe, and China, whereas tropical ecosystems and countries with the highest levels of biodiversity remain comparatively understudied. Consequently, this research imbalance limits the broad applicability of ecological frameworks associated with the functional diversity of AMF, and our understanding of how their functions and contributions to ecosystem processes vary across geographic regions and latitudinal gradients.

5. CONCLUSIONS

AMF plays a fundamental role in the biogeochemical cycles of carbon and phosphorus by promoting carbon sequestration, contributing carbon to stable soil fractions, and optimizing phosphorus mobility and availability to plants, thereby enhancing nutrient availability and long-term soil fertility.

AMF also plays an essential role in the formation and stability of soil food webs by establishing mutualistic relationships with other organisms that strengthen ecosystem resilience. These associations sustain carbon and nutrient fluxes, contributing to biological balance and mitigating the effects of environmental disturbances such as drought, land-use change, and contamination. Within the mycorrhizosphere, symbiotic and cooperative interactions between arbuscular mycorrhizal fungi and other microorganisms promote the development of physical, chemical, and biological processes fundamental to soil sustainability. In this way, their biological activity not only preserves microbial community diversity and the adaptive capacity of the soil–plant system under adverse conditions but also maintains plant productivity and ensures the functional dynamics of ecosystem services.

Despite advances in AMF research, their role in soil structure and function remains poorly understood. Significant knowledge gaps persist regarding the mechanisms by which they influence soil function and the specific processes they mediate. In general, AMF are often treated as a homogeneous functional group, despite limited understanding of the distinctive traits of individual species and families, particularly with respect to exudate production, extraradical hyphal growth, and their roles in processes such as carbon and nutrient transfer. Another important aspect that should be addressed in future research is how AMF interact with their host plants and other soil microorganisms. It is also important to recognize that, given the broad taxonomic diversity of this group, their biological responses to environmental and edaphic factors are not uniform. Furthermore, the molecular nature of glomalin and other AMF-associated glycoproteins remains incompletely understood, particularly regarding their chemical composition and their contribution to soil aggregate formation.

Future research should focus on multiscale, interdisciplinary approaches that integrate observational and experimental studies within the mycorrhizosphere while addressing ecosystem-level functional processes. Comparative studies of diverse AMF species and communities are also needed, incorporating transcriptomic, metabolomic, and functional trait analyses across a range of environmental contexts. Such approaches would provide a clearer understanding of the direct relationship between functional diversity and soil structural stability. Finally, greater emphasis should be placed on studies in tropical agroecosystems and degraded systems, particularly within environmental restoration and agricultural transformation frameworks, where the functional potential of AMF as key contributors to soil sustainability and functional resilience can be more effectively evaluated.

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