aeet
ASOCIACIÓN ESPAÑOLA DE ECOLOGÍA TERRESTRE

Ecosistemas 34(2): 2821 [May - August / mayo- agosto, 2025]
https://doi.org/10.7818/ECOS.2821

Associate editor / Editor asociado: Daniel Montagud Tarrasó

REVIEW ARTICLE / ARTÍCULO DE REVISIÓN

ecosistemas

ISSN 1697-2473

www.revistaecosistemas.net

Arbuscular mycorrhizal fungi: a multifunctional soil biotic component

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> Received / Recibido: 25/07/2024 – Accepted / Aceptado: 08/04/2025

How to cite / Cómo citar: Vázquez-Santos, Y., Castillo-Argüero, S., Jiménez-Martínez, A. 2025. Arbuscular mycorrhizal fungi: a multifunctional soil biotic component. *Ecosistemas* 34(2): 2821. https://doi.org/10.7818/ECOS.2821

Arbuscular mycorrhizal fungi: a multifunctional soil biotic component

Abstract: Arbuscular mycorrhizal fungi (AMF) are soil microorganisms that play an important role in terrestrial ecosystems. This review highlights the diverse functions of AMF and emphasizes their potential as biological tools to address current and future environmental challenges. They contribute to organic matter decomposition, with evidence that AMF enhance soil microbial activity and nutrient cycling in organic-rich soils. AMF also improve soil structure by increasing aggregate stability. In plant communities, AMF influence reproductive phenology, and promoting higher germination rates and biomass accumulation in different species, especially herbs and shrubs. These fungi are involved in climate change mitigation by enhancing carbon sequestration and buffering environmental stressors such as prolonged drought. Despite these well-documented functions, research on AMF has primarily focused on their role in nutrient transport, overlooking their broader ecological implications. Key ecological filters, such as elevation, nutrient availability, host identity, and anthropogenic activities, modulate AMF community structure and functionality. In conclusion, AMF are a multifunctional biotic component of soils because they are involved in a variety of ecological processes. Future research should address the multifunctionality of AMF in soil quality, their interactions with other soil microbiota, and their potential applications in large-scale ecological restoration.

Keywords: ecosystems; biotic interactions; arbuscular mycorrhiza; multifunctionality; mutualism; resilience

Hongos micorrícicos arbusculares: un componente biótico multifuncional del suelo

Resumen: Los hongos micorrízicos arbusculares (HMA) son microorganismos del suelo que desempeñan un papel fundamental en los ecosistemas terrestres. Esta revisión destaca la multifuncionalidad de los HMA y resalta su potencial como herramienta biológica para enfrentar los desafíos ambientales actuales y futuros. Los HMA contribuyen a la descomposición de la materia orgánica, ya que se ha demostrado que aumentan la actividad microbiana del suelo y el reciclaje de nutrientes en suelos ricos en materia orgánica. Además, mejoran la estructura del suelo al aumentar la estabilidad de los agregados. En las comunidades vegetales, los HMA influyen en la fenología reproductiva, y promueven la germinación y acumulación de biomasa, principalmente herbáceas y arbustivas. Asimismo, estos hongos participan en la mitigación del cambio climático, al favorecer el secuestro de carbono y actuar como reguladores de estrés ambiental como las sequías. A pesar de estas funciones ampliamente documentadas, el estudio sobre HMA se ha centrado en su función de transporte de nutrientes, dejando de lado otras funciones ecológicas. Diversos filtros ecológicos, como la elevación, disponibilidad de nutrientes, identidad del hospedero y actividades antropogénicas, modulan la estructura y función de las comunidades de HMA. En conclusión, los HMA son un componente biótico multifuncional del suelo, ya que participan en una amplia variedad de procesos ecológicos. Futuras investigaciones deben abordar la multifuncionalidad de los HMA en la calidad del suelo, sus interacciones otros microorganismos edafícos y sus aplicaciones potenciales en la restauración ecológica a gran escala.

Palabras clave: ecosistemas; interacciones bióticas; micorriza arbuscular; multifuncionalidad; mutualismo; resiliencia

Introduction

Soil microorganisms are essential components of ecosystem function and resilience (Graham et al. 2014). These microorganisms play fundamental roles in key ecological processes such as biogeochemical cycling, organic matter (OM) decomposition, carbon (C) sequestration, net primary productivity, and natural regeneration (Zheng et al. 2019; Creamer et al. 2022). Among the great diversity of soil microorganisms, arbuscular mycorrhizal fungi (AMF) play a crucial ecological role as widespread symbionts, forming mutualistic associations with approximately 75% of plant species (Brundrett and Tedersoo 2018).

Traditionally, the assumed primary function of AMF has been to enhance the uptake of water and macronutrients from the soil, primarily phosphorus (P) and nitrogen (N), thereby benefiting the survival and growth of their host plants (Smith and Read 2008; Smith and Smith 2011). This has led to extensive studies on the beneficial effects of native AMF inoculum on growth indicators such as seedling height and biomass production of agriculturally important crops such as *Triticum* spp. *Zea mays*, *Solanum lycopersicum*, *Solanum tuberosum* and *Coffea arabica* (Vosátka and Gryndler 2000; Zhu et al. 2001; Al-Karaki 2006; Begum et al. 2019; Perea-Rojas et al. 2019; Abrar et al. 2024). Likewise, this paradigm has overlooked the deeper exploration of other functions of this fungal group in various ecological processes of ecosystems, such as OM decomposition, soil structure, reproductive phenology of wild plants, and seed germination. These processes become particularly relevant in the current scenario of global changes such as climate change and soil desertification.

Through nutrient transport, AMF influences the nutritional status of the host plant and its physiological ability to respond to adverse environmental conditions. Therefore, these fungi are recognized as buffers against environmental stress and protectors against pathogen attack (Pozo et al. 2008). A meta-analysis by Veresoglou and Rillig (2012), which analyzed 106 previous studies, found that AMF can reduce the severity of disease, and that the efficacy of this suppression is highly dependent on the specific identity of the AMF involved. For example, *Funneliformis mosseae* is particularly effective in protecting against fungal pathogens, whereas *Rhizoglomus intraradices* is particularly effective in protecting against plant-parasitic nematodes. This perspective has promoted the study of AMF in systems where environmental conditions are challenging, such as agricultural areas, arid and semi-arid zones (Varela-Fregoso et al. 2017). In contrast, AMF have been poorly studied in temperate forests, for example, because it has long been assumed that the characteristic tree species of these forests are exclusively associated with ectomycorrhizal fungi. This claim has been challenged in recent studies, for example, Bueno et al. (2017) showed that arbuscular mycorrhizal associations vary according to environmental gradients, such as latitude and elevation, suggesting that our understanding of these associations is still incomplete. Likewise, the involvement of AMF in the early stages of the life cycle of tree species (Olivera-Morales et al. 2011) and in ecological succession (Zobel and Öpik 2014; Krüger et al. 2017) is now recognized.

The study of the multifunctionality of AMF should be considered in future research, not only considering their role in soil nutrient uptake and transport, but also their influence on other ecological processes. This review aims to: i) deepen and highlight the functions of AMF in key processes of terrestrial ecosystems, such as OM decomposition, soil structuring and plant ecology (reproductive phenology and seed germination), and ii) propose some ecological filters that influence the composition of AMF. The study of the multifunctionality of these soil microorganisms is urgent given the current conditions of deforestation and soil desertification and the unprecedented alteration of terrestrial ecosystems.

Information search

For the review on the multifunctionality of AMF, a literature search was conducted in interdisciplinary databases such as Web of Science, Scopus and EBSCO. Specific keywords combined with Boolean operators (AND, OR) were used to optimize the retrieval of relevant studies in five main axes: (1) organic matter decomposition; (2) soil structure, highlighting their influence on aggregate formation; (3) reproductive phenology, evaluating their influence on flowering and fruiting of host plants; (4) seed germination, considering their contribution to early root colonization and mycorrhizal resistance; and (5) ecological filters regulating AMF activity, such as elevation gradients, nutrient availability, host identity, and anthropogenic disturbance. This strategy provides a comprehensive approach to understanding the contribution of AMF to soil dynamics.

The search was conducted between March and June 2024 and included publications from 1990 to 2024. A total of 208 articles were initially retrieved. After applying inclusion and exclusion criteria, 117 articles were selected for detailed analysis. Inclusion criteria included peer-reviewed articles in English or Spanish that presented empirical data or comprehensive reviews that directly addressed at least one of the five axes of AMF functionality. Exclusion criteria included duplicate entries, non-peer-reviewed sources, publications with insufficient methodological information, or studies focused exclusively on ectomycorrhizal fungi. This process ensured a rigorous selection of literature

Arbuscular mycorrhizal fungi in OM decomposition

Early research on AMF suggested that they had saprophytic activity, as they were found to colonize litter and proliferate in various types of OM (Nicolson 1959; Gerdemann and Trappe 1974). This led to the formulation of the 'direct mineral cycling' hypothesis proposed by Went and Stark (1968), which postulated the direct involvement of AMF in OM decomposition and subsequent transport of nutrients to their host. However, this hypothesis was rejected for lack of convincing evidence.

AMF lack the enzymatic machinery necessary to degrade organic molecules (Tisserant et al. 2013), so they only transport inorganic forms of nutrients from soil to plants. This has been the paradigm for nutrient flow from fungi to plants in the arbuscular mycorrhizal association. However, this model is currently being challenged by studies using in vitro systems showing that species of the genus *Glomus* assimilate organic forms of N (Hodge et al. 2001; Hodge and Storer 2015) and P (Koide and Kabir 2000). The role of AMF extracellular enzymes in OM degradation is unclear, and recent findings on access to organic forms of nutrients have been seriously questioned due to lack of reproducibility and heterogeneity in the results obtained (Koide and Kabir 2000; Jansa et al. 2013). Furthermore, most experiments have focused on two specific species, *Rhizoglomus irregulare* and *Simiglomus hoi* (Leigh et al. 2011), which limits inferences to higher taxonomic categories, as it is unknown whether other species or genera exhibit similar behavior.

The colonization of AMF in litter (Bunn et al. 2019; Kemmelmeier et al. 2022) and the proliferation of these fungi in some forms of OM (Gavito and Olsson 2003; Hodge and Fitter 2010; Barrett et al. 2011; Paterson et al. 2016) clearly indicate that AMF

somehow intervene in decomposition and even transfer some of the released nutrients to their host (**Fig. 1**) (Bunn et al. 2019). However, the exact mechanisms remain unknown, as it is complex to establish the direct involvement of these microorganisms, considering that they are completely dependent on their host for C acquisition (Smith and Read 2008).

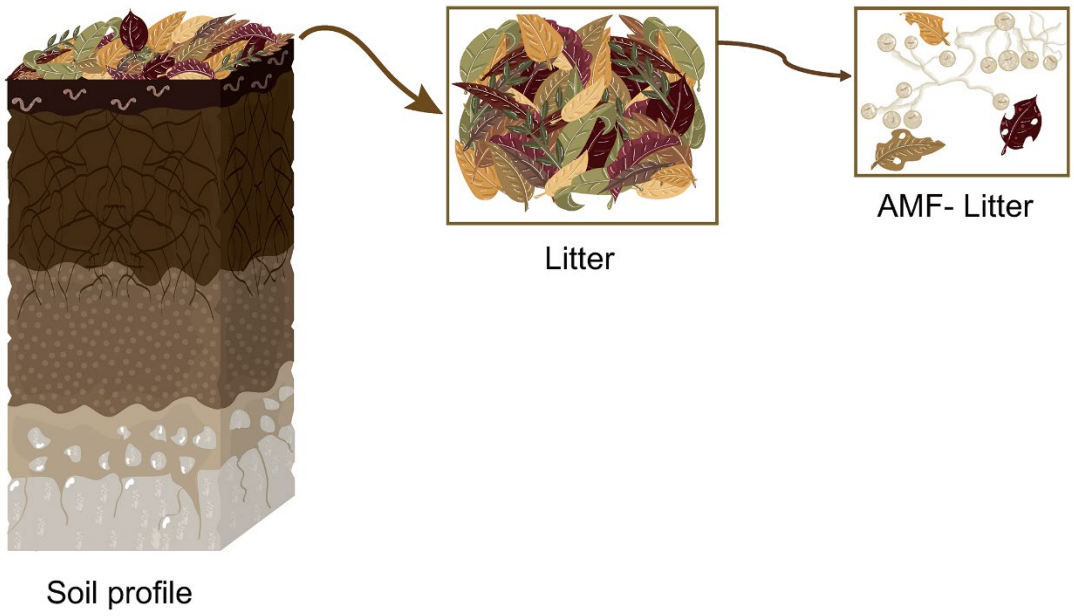

Figure 1. Schematic representation of a hypothetical soil profile highlighting the litter layer and its progressive transformation, including colonization by AMF (Arbuscular mycorrhizal fungi). The figure shows the decomposition of plant litter and its interaction with AMF structures. Elaborated by Vázquez-Santos LM (2024).

Figura 1. Representación de un perfil de suelo hipotético en el que se resalta el mantillo y su transformación progresiva, incluida la colonización por HMA (hongos micorrízicos arbusculares). Se muestra la descomposición del tejido vegetal y su interacción con las estructuras de HMA. Elaborado por Vázquez-Santos LM (2024).

The rapid growth of AMF extraradical mycelium in OM patches can be interpreted as 'direct foraging' of these fungi towards nutrient-rich sites (Welc et al. 2010; Hodge 2014). It has been suggested that AMF biochemically recognize nutrient patches and grow towards them through chemical signaling mechanisms, similar to the pre-symbiotic recognition signals between plant and fungus (Barrett et al. 2011). However, it is also likely that the hyphae randomly locate the patches and, once there, branch out into the nutrient-rich zone (Barrett et al. 2011).

While the direct involvement of these microorganisms in OM decomposition is inconclusive, indirect mechanisms of their involvement have been proposed. AMF hyphae can penetrate sites of mineralization activity within the decomposing substrate (Jansa et al. 2013), facilitating the intervention of other decomposer microorganisms such as bacteria. It has been suggested that 'hyper-symbionts' are transported at the hyphal tips, physically decomposing the organic substrate and forming a 'secondary symbiosis' with the AMF (Jansa et al. 2013). At the same time, fungi release C through hyphal exudates, stimulating microbial activity associated with the hyphosphere, the zone of interaction between the hyphae and the soil (Toljander et al. 2007).

The colonization of different soil habitats may be an important ecological strategy of these fungi to increase their exploration area, especially in topographically heterogeneous sites with low P availability. Indeed, a recent study suggests that there is habitat selection by certain AMF families. It was observed that Archeosporaceae were found exclusively in litter, Paraglomeraceae in plant roots and Ambisporaceae in mineral soil (Kemmelmeier et al. 2022). The authors do not provide a conclusive explanation for this pattern, but speculate that it is related to the morphological (e.g., spore size, hyphal architecture, and root colonization strategies) and functional traits (e.g., nutrient exchange efficiency, response to environmental stress, and host specificity) of AMF that are conserved at the family level (Hart and Reader 2002; Powell et al. 2009).

Arbuscular mycorrhizal fungi in soil structure

OM improves the stability, porosity, and water-holding capacity of soils because its presence promotes the formation and stability of aggregates by acting as a cementing agent (Six et al. 2000). Likewise, the mycelium of AMF acts as a cementing agent, binding soil particles and promoting the formation of aggregates (macro [>250 µm] and micro [< 250 µm]) that are more resistant to erosion and increase porosity, which means an increase in soil solution infiltration and gas exchange, and a decrease in soil bulk density, which is crucial for the maintenance of agroecosystems because it contributes to increasing the physical fertility of the soil (**Fig. 2**) (Lehmann et al. 2017; Fall et al. 2022; Wang et al. 2022).

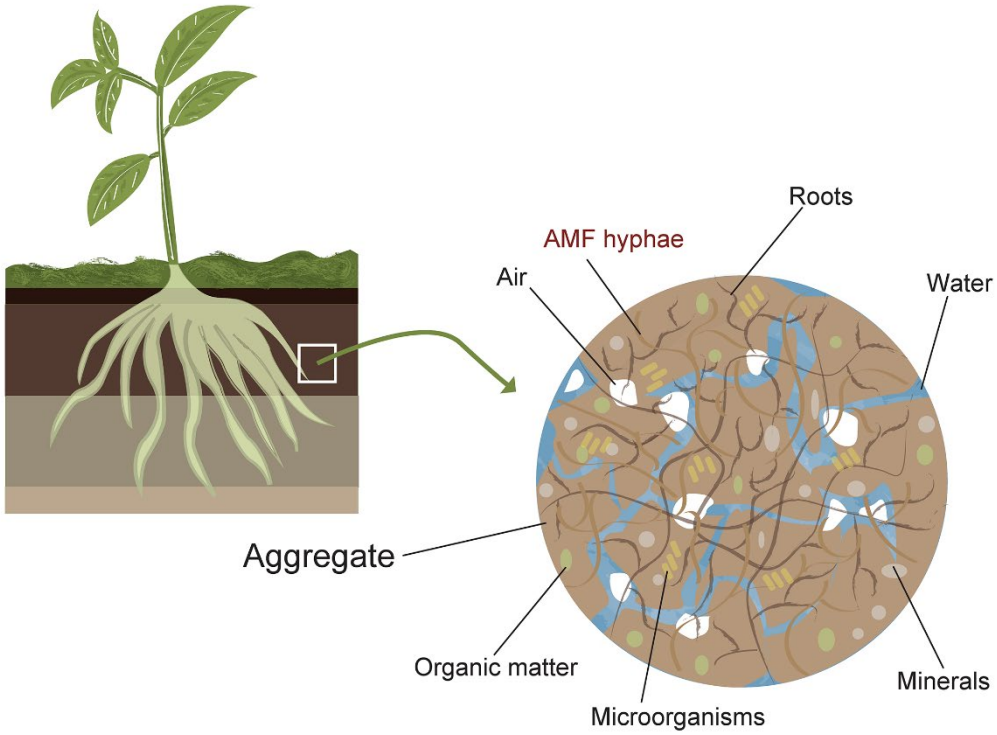

Figure 2. Example of AMF (arbuscular mycorrhizal fungi) distribution in soil aggregates. The figure illustrates the spatial organization of AMF within soil micro- and macroaggregates, highlighting their hyphal networks, spore localization, and potential interactions with soil organic matter and mineral particles. Elaborated by Vázquez-Santos LM (2024).

Figura 2. Ejemplo de distribución de HMA (hongos micorrícicos arbusculares) en los agregados del suelo. Se ilustra la organización espacial de los HMA dentro de los microagregados y macroagregados, destacando sus redes hifales, localización de esporas, y potenciales interacciones con la materia orgánica del suelo y partículas minerales. Elaborado por Vázquez-Santos LM (2024).

AMF have different strategies to colonize the soil, which is reflected in the production of extraradical mycelium as a result of the search for nutrients (Hart and Reader 2002, 2005). As well as they have different extraradical mycelial architecture and thickness (Dodd et al. 2000; Drew et al. 2003; Beck et al. 2007), which affects differently in the aggregates 'construction. On the other hand, it has been reported that the process of soil aggregate formation depends on the mycorrhizal species as well as the interaction with its host plant (Piotrowski et al. 2004).

Because studies of AMF and saprophytic fungi and their interactions with soil particles and other components of the biota have been conducted destructively or in isolated photographs showing soil aggregates and only one AMF species, various models have been proposed for how the process of soil aggregate formation occurs (Rillig and Mummey 2006; Lehmann and Rillig 2015; Jeewani et al. 2021). However, as mentioned above, many species of AMF have distinct traits that are not represented in such schemes. On the other hand, the stability of aggregates in water as a product of mycorrhizal interactions is also carried out in a disruptive manner, thus altering the relationship between hyphae, macro- and microaggregates, and porous space (Kemper and Rosenau 1986; Jiménez-Martínez et al. 2024).

Jiménez-Martínez et al. (2024) showed through micromorphological studies, image analysis (with thin sections) and destructive techniques how *Funneliformis mosseae*, *Rhizophagus intraradices* and *Gigaspora gigantea* contribute differently to the formation of stable aggregates in water (modified system) and how through thematic maps with high resolution mosaics (unmodified system) they showed for one year how these mycorrhizal fungi contribute differently to the formation of aggregates.

Therefore, it has been proposed as a complementary technique to study the interactions between mycorrhizal fungi and other components of the biota, such as bacterial communities (biofilms), as well as processes of OM decomposition and how it relates to the processes of formation of soil aggregates (Gutiérrez-Castorena et al. 2018; González-Vargas and Gutiérrez-Castorena 2022; Jiménez-Martínez et al. 2024).

Arbuscular mycorrhizal fungi in the reproductive phenology of the host

Experimental studies have shown that AMF significantly improve nutrient uptake efficiency, particularly for P and N, both of which are essential for plant metabolism and reproductive success (Derelle et al. 2015; Vosnjak et al. 2021). Wang and Tang (2022) highlight that AMF influence key reproductive traits, including flowering time, seed production, and fruit set, ultimately enhancing the functional fitness of host plants. Their findings suggest that AMF-mediated nutrient acquisition directly contributes to higher reproductive efficiency, especially under nutrient-limited conditions.

In addition to their role in nutrient uptake, AMF actively modulate plant phenology by modulating flowering and fruit production (Vázquez-Santos 2019; Bennett and Meek 2020). Field studies in temperate forests indicate that AMF colonization varies with the nutrient requirements of plants during their reproductive stages, with significant correlations between AMF root colonization and fruiting in species such as *Acaena elongata*, *Ageratina glabrata*, and *Solanum pubigerum* (Vázquez-Santos 2025). Similarly, Vega-Frutis and Guevara (2009) reported that higher AMF colonization during the dry season was associated with increased flower and fruit production in *Carica papaya*, suggesting that AMF play an important role in maintaining reproductive success under water-limited conditions.

AMF affect flower and fruit production by modifying hormone levels, promoting the accumulation of gibberellins and cytokinins, and increasing nutrient and water uptake by the plant (Roman-García et al. 2004; Ludwig-Müller 2010). The study of reproductive phenology in relation to AMF has hardly been addressed in wild plant species. However, increased intraradical colonization of these fungi during the reproductive period of their host has been observed in agriculturally important plant species and semi-arid ecosystems (Bennett and Meek 2020). This suggests that these fungi indirectly contribute to the reproductive success of plants and may be a key component in the reproductive plasticity of their hosts in different environments.

Mountains are ideal systems for comparing the responses of organisms to the environment because of the presence of an elevation gradient that produces variation in abiotic factors. In plant populations established at lower elevations, the onset of the reproductive period (flower bud burst) occurs earlier, and reproductive maturity is reached more slowly, whereas in populations growing at higher elevations, flower bud burst is delayed and flowers and fruits develop rapidly (Laiolo et al. 2015). Early flowering results in reduced reproductive output due to frost damage to developing floral tissues, a decrease in pollinators, intense herbivory, and lack of sufficient resources (Hegland et al. 2009). At the same time, late flowering individuals are unable to complete their reproductive cycles before the onset of adverse conditions such as drought or frost (Anderson et al. 2012). In this context, by increasing nutrient uptake and water transport, AMF would allow the plant to buffer adverse environmental conditions during its reproductive period along the elevation gradient.

Variation in plant reproductive response along the elevation gradient triggers changes in C metabolism and microenvironmental conditions that affect AMF activity in roots and soil. Patterns indicate that intraradical colonization and AMF diversity are negatively correlated with elevation (Lugo et al. 2008; Gai et al. 2012; Vázquez-Santos et al. 2019). Thus, we can conclude that at higher elevations, the high allocation of plant resources to the production of reproductive structures, together with low temperature, high humidity and acidic pH, limit intraradical colonization and AMF spore production. At the same time, the low availability of nutrients at higher elevations favors the maintenance of the association. At lower elevations, the colonization and sporulation of a greater number of AMF species is favored by high plant C transfer, low water availability, and warmer temperatures, which favor soil microbial activity and, consequently, OM decomposition. The relationship between reproductive phenology, AMF and elevation has not been proven and represents an excellent field of study that would allow predicting the variability of the arbuscular mycorrhizal association in the face of future severe environmental changes, especially under the scenario of climate change.

Arbuscular mycorrhizal fungi in seed germination

The AMF can directly and indirectly influence seed germination by modulating soil conditions and biochemical signals that trigger the germination process. It has been observed that seed germination is higher in substrates with the presence of AMF propagules (**Fig. 3**) (spores, previously infected roots). Their role goes beyond creating 'optimal' microenvironmental conditions, as they also release signaling molecules and secondary metabolites, such as strigolactones, that can stimulate seed germination in certain plant species (Akiyama et al. 2005; Besserer et al. 2006). Strigolactones act as chemical signals in the rhizosphere that promote hyphal branching in AMF and influence plant root architecture, thereby facilitating early root colonization and enhancing seedling establishment (Akiyama et al. 2005). This suggests that these fungi may induce seed germination (Koide 2000).

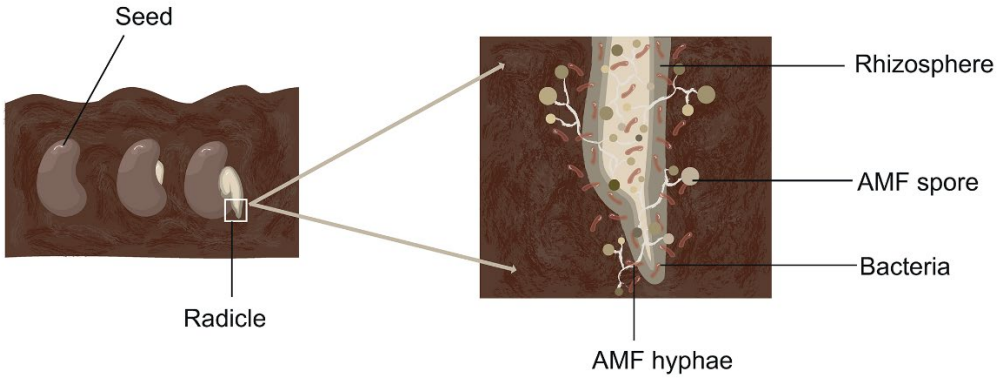

Figure 3. Illustration of the early stages of root colonization by AMF (arbuscular mycorrhizal fungi) in the rhizosphere. The image shows a germinating seed with its radicle surrounded by AMF hyphae, spores, and associated rhizosphere bacteria. Elaborated by Vázquez-Santos LM (2024).

Figura 3. Ilustración de las primeras etapas de la colonización intra-radical por AMF (hongos micorrícicos arbusculares). La imagen muestra una semilla en germinación con su radícula rodeada de hifas de HMA, esporas y bacterias asociadas a la rizosfera. Elaborado por Vázquez-Santos LM (2024).

The germination stage is crucial for the establishment of an individual and is one of the most vulnerable in the plant life cycle (Jurado and Flores 2005). Therefore, the rapid establishment of the arbuscular mycorrhizal association will allow the seedling to obtain the necessary nutrients for its survival, growth and development. Experimental studies have shown that AMF have a positive effect on seed germination. Vázquez-Santos et al. (2024) found that species such as *Acaena elongata*, *Ageratina glabrata*, and *Solanum pubigerum* exhibited higher germination percentages when inoculated with AMF. Similarly, Olivera-Morales et al. (2011) reported that AMF inoculation increased germination and seedling establishment of *Quercus rugosa* in a temperate forest in Mexico. Research by Ballina-Gómez et al. (2017) demonstrated that the interaction between AMF and light availability significantly increased germination rates in tree species from tropical dry forests, such as *Tecoma stans*, *Sapindus saponaria*, and *Bauhinia forficata*. Additionally. These findings suggest that the presence of AMF not only facilitates germination but also enhances seedling establishment and survival, making them a key biotic factor in plant recruitment and restoration strategies.

The role of AMF in seed germination and seedling establishment can also be analyzed from another perspective: their contribution to plant defense through mycorrhizal-induced resistance (MIR), a priming effect that enhances the ability of seedlings to respond more efficiently to biotic and abiotic stresses (Pozo and Azcón-Aguilar 2007). This priming effect may play an important role in seed germination by modulating signaling pathways such as jasmonic acid and salicylic acid, which are crucial for plant stress responses. Activation of these pathways could increase the likelihood of successful germination and early seedling establishment by enhancing pathogen resistance and optimizing resource allocation during this critical developmental stage (Pozo and Azcón-Aguilar 2007). These findings highlight the potential dual role of AMF, not only as facilitators of optimal germination conditions, but also as biological enhancers that prepare the seedling for environmental challenges, ultimately improving plant recruitment and survival under dynamic ecological conditions.

Bacteria and other organisms associated with the AMF hyphosphere (Jansa et al. 2013) could act as scarifying agents for seeds, thus enhancing their germination in association with these fungi. Understanding the role of AMF in seed germination is an important step that will elucidate the function of these fungi in forest natural regeneration. In addition, it is important to understand whether these microorganisms represent an adaptive strategy of plants that favors their germination and establishment in topographically heterogeneous sites.

Ecological filters that affect arbuscular mycorrhizal fungi

AMF are subject to various ecological filters that influence their distribution, diversity and functionality within ecosystems. These filters can be natural, such as elevation gradients, the availability of essential nutrients and the biological identity of the host plant, or anthropogenic, resulting from human activities such as deforestation, agricultural intensification, and land-use change that alter the composition and structure of AMF communities (Chagnon et al. 2021). On a global scale, climate change is altering temperature and precipitation patterns, affecting the functionality of these fungi and their interactions with plants (Alguacil et al. 2021). Ecological filters act as selection mechanisms that determine which species colonize a given habitat, a concept extensively explored by Zobel (2016), who analyzes the interaction between species, environmental filters, and functional traits in community structuring. Future research on ecological filters is essential to predict how AMF will respond to environmental change, and to develop conservation and management strategies that ensure their ecological role in ecosystems.

Natural filters: elevation gradient

Along the elevation gradient, there are changes in temperature and precipitation that result in differences in soil properties. As elevation increases, temperature and pH decrease and soil moisture increases (Chen et al. 2017). Nutrient availability is deficient at higher elevations due to low enzymatic and mineralization activity caused by low temperatures, resulting in an apparent accumulation of litter (Fahey et al. 2015; Laiolo et al. 2015). An inverse pattern is found at lower elevations where temperature is warmer, pH is less acidic, soil moisture decreases, and microbial activity increases (Fahey et al. 2015; Laiolo et al. 2015).

AMF respond significantly to these elevation changes. Studies conducted in different mountains have shown that AMF diversity and colonization tend to decrease with increasing elevation due to harsher conditions and lower nutrient availability (Guo et al. 2020). At lower elevations, where conditions are more favorable for microbial activity, AMF colonization and diversity tend to be higher. For example, on Mount Taibai in China, AMF diversity peaked at intermediate elevations and declined at the highest and lowest elevations, suggesting optimal adaptation to the edaphic conditions of intermediate elevations (Zhang et al. 2022). Another study on Mt. Helen in the UU EE showed that the structure of the AMF community varied significantly with elevation and was influenced by factors such as soil pH, organic matter content, and nutrient availability (Guo et al. 2020). Therefore, the effect of elevation gradient on AMF activity is governed by the microenvironmental changes resulting from the interaction of climate, topography, relief, and elevation.

Nutrient availability

Soil nutrient availability has a significant impact on AMF colonization and diversity (Johnson 2010). P is a key nutrient that directly affects AMF colonization. In soils with low phosphorus availability, plants tend to rely more on AMF for the uptake of this nutrient. This is because AMF have the ability to explore larger volumes of soil than roots to access P reserves. One study showed that under low P conditions, mycorrhizal colonization and extraradical mycelium length increased significantly, thereby improving plant nutrition (Akter et al. 2024; Xiao et al. 2023).

Nitrogen availability also plays a critical role. However, the effect of N can be twofold. Studies have shown that high N availability can reduce plant dependence on AMF, thereby reducing mycorrhizal colonization. This occurs because plants can obtain sufficient N directly from the soil without the need to establish energetically costly symbiotic associations. However, in soils with limited N, plants increase their dependence on AMF, which can increase the colonization and diversity of these fungi in the soil (Fall et al. 2022).

It is important to clarify that this interaction is not always beneficial for the plant. Johnson (2010) proposes the functional equilibrium model, which suggests that a high concentration of N and P in the soil can have an antagonistic effect on the plant-fungus relationship. In this model, a high concentration of N and low P strengthens the mycorrhizal association because plants are more dependent on fungi for P uptake. On the other hand, a low N and high P can turn the interaction into a commensal one, where the benefits to the plant are significantly reduced.

The consideration of other macronutrients besides P and N, such as potassium (K), is essential in the study of the arbuscular mycorrhizal association. The K is essential for osmotic regulation and enzyme activation in plants, but the role of AMF in potassium transfer is poorly understood. Plants also take up these essential nutrients for growth and development. Similarly, micronutrients such as zinc (Zn) and iron (Fe) are essential for many enzymatic and structural functions in plants (Xiao et al. 2023). The transfer of these other nutrients by AMF remains largely unexplored and an active area of research.

Plant biological identity

Plant biological traits, such as root structure, leaf area, and life form, have a significant impact on AMF colonization and function (Davison et al. 2011). Plant biological identity acts as an important ecological filter, determining the degree of "functional compatibility" between fungi and plants through specific biochemical and physiological interactions (Chagnon et al. 2013). Recent studies suggest that these associations are not random but rather regulated by factors that influence the efficiency and specificity of the symbiosis.

Root architecture strongly influences AMF colonization. Plants with fine, highly branched roots, such as grasses, tend to support higher AMF diversity and colonization rates than species with thicker, less branched roots (Morris et al. 2013; Li et al. 2023). Studies in temperate and subtropical grasslands have shown that species with fibrous root systems have more colonization sites, allowing for greater diversity of AMF taxa (Garrido et al. 2023). In addition, root longevity and turnover rates influence the persistence and structure of AMF networks, reinforcing the role of plant functional traits in symbiotic efficiency (Sepp et al. 2009).

Leaf traits, particularly plant leaf area and photosynthetic capacity, also influence the AMF interactions. Plants with larger leaf areas and higher photosynthetic rates allocate more carbohydrates to AMF, supporting higher colonization rates and improved nutrient uptake (Li et al. 2023). A study conducted in a subtropical forest found that plant species with larger leaf areas and higher photosynthetic rates had more intense AMF colonization in their roots (Li et al. 2023).

Plant life form, whether trees, shrubs, herbs, or epiphytes, also plays an important role in the diversity and structure of AMF communities. Trees, for example, tend to host a more diverse AMF assemblage than herbs and shrubs due to their longer root life, deeper rooting systems, and more stable microenvironmental conditions (Chen et al. 2020). Recent research using multilayer network analysis has shown that plant-AMF interactions follow specific structural patterns, with plant species differentially filtering AMF based on their functional traits (Garrido et al. 2023). These findings highlight the importance of understanding plant functional diversity is crucial for predicting AMF community structure and ecosystem functioning.

Anthropogenic filters

Nutrient availability, plant community structure, and AMF activity in soils are affected by anthropogenic activities (Dickie et al. 2013). The magnitude of these changes depends on the intensity, frequency, and type of disturbance (Teste and Dickie 2017; van der Heyde et al. 2017). Low-intensity disturbances, such as selective weeding, minimally alter the physical properties (e.g., structure and bulk density) and chemical properties (e.g., nutrient availability and pH), while promoting gradual changes in plant community composition that largely preserve native plant species (Sánchez-Fuente 2019). However, even mild disturbance can lead to shifts in AMF community structure, decreasing species richness and favoring the proliferation of AMF taxa that are less sensitive to environmental changes in soil properties (Schnoor et al. 2011; Brundrett and Ashwath 2013). Changes in richness may not be observed, but there may be changes in abundance of some AMF species (**Fig. 4**) (Violi et al. 2008).

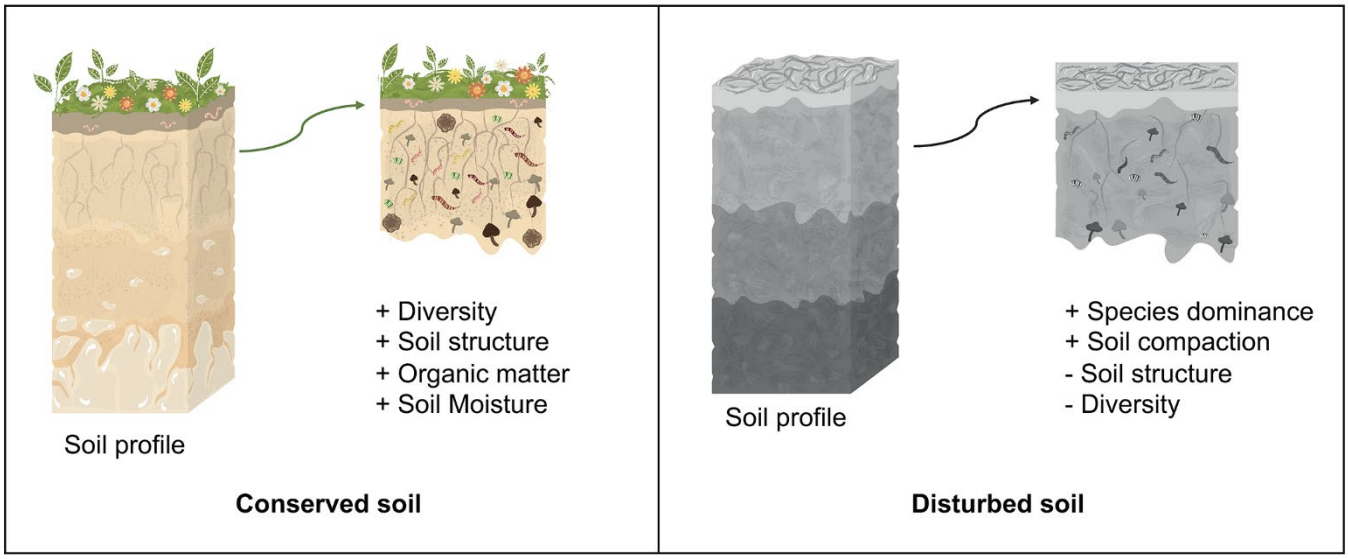

Figure 4. Arbuscular mycorrhizal fungi in a preserved soil *vs*. a disturbed soil. Prepared by Vázque-Santos LM (2024).

Figura 4. Hongos micorrícicos arbusculares en un suelo conservado frente a un suelo alterado. Elaborado por Vázque-Santos LM (2024).

High-intensity disturbances, such as intensive agriculture and deforestation, exert strong selective pressures on AMF communities, leading to phylogenetic and trait-based filtering (Chagnon et al. 2022). Long-term agricultural practices tend to favor AMF species with specific functional traits, particularly those adapted to disturbed environments, while reducing overall community diversity. These findings are consistent with the evolutionary framework proposed by Verbruggen and Kiers (2010), which suggests that anthropogenic management practices drive selection for AMF species with traits that enhance their persistence in intensively managed soils.

Chronic disturbance also shapes plant community dynamics, favoring species with disturbance-tolerant traits that dominate ecosystems (Mayfield et al. 2010). As a result, physical, chemical, and biological properties of soil are negatively altered, leading to functional degradation (Mayfield et al. 2010). Plants that successfully colonize degraded soils tend to be strong competitors for resources (Ramos-Zapata et al. 2013), and their mycorrhizal associations can significantly influence local AMF composition. Frequently, more degraded sites have lower alpha and beta diversity compared to less affected areas, highlighting the cascading effects of ecosystem degradation on AMF networks (García et al. 2018). Furthermore, prolonged disturbance may weaken the mutualistic balance of the symbiosis, reducing the benefits provide by AMF to plant hosts and shifting interactions towards more neutral or even parasitic associations (Verbruggen and Kiers 2010).

The life history strategies of both AMF species and their plant hosts determine the colonization success and persistence of species in degraded sites. Chagnon et al. (2013) propose that severe anthropogenic disturbance favors the presence of generalist AMF species, which tolerate high levels of disturbance and have rapid growth and early investment in the formation of large numbers of small spores. The family Glomeraceae has been classified as predominantly generalist (Klironomos and Hart 2002; Hart and Reader 2005). However, recent studies indicate a significant diversity of life history traits within Glomeraceae, comparable to the variation observed in other AMF families (Horsch et al. 2023). In this context, Davison et al. (2011) suggest that plant species with similar functional traits associate with functionally analogous AMF taxa, i.e., generalist plants tend to form symbioses with generalist AMF species. However, more evidence is needed to support this hypothesis.

Arbuscular mycorrhizal fungi in climate change

Rising temperatures, shifts in precipitation regimes, and elevated carbon dioxide (CO_2) concentrations are well recognized abiotic factors that influence plant reproductive phenology (Beaubien and Hamann 2011; Zhang et al. 2021). These extreme weather events characteristics of global climate change are expected to drive local changes in plant phenology, species distributions, extinctions, and disruptions in above- and belowground biotic interactions (Alberton et al. 2005). For example, earlier flowering and fruiting may negatively affect plant-pollinator and plant-disperser interactions, leading to cascading effects on ecosystem functionality (Haggerty and Galloway 2011).

Plant species will need to adapt in situ to climate change, and their association with AMF may provide a key advantage due to their roles in nutrient and water transfer, organic matter decomposition, pathogen protection, and temperature tolerance. AMF can also adapt rapidly to environmental changes, helping both fungi and their host plants to mitigate the effects of climate change. Experimental studies indicate that elevated CO_2 levels increase intraradical colonization and AMF biomass in soils, as plants allocate more photosynthates to fungal symbionts (Alberton et al. 2005). This suggests that AMF symbiosis may increase soil carbon sequestration because these fungi contribute to carbon storage through the production of glomalin, a highly recalcitrant, carbon-rich protein (Drigo et al. 2010).

However, climate change is not uniformly beneficial to AMF communities. Increased temperatures and altered precipitation patterns can reduce soil phosphorus (P) availability (Hou et al. 2018), limiting nutrient exchange in AMF-host interactions. In this scenario, AMF may enhance plant tolerance to heat stress and improve phosphorus uptake (Zhu et al. 2017). However, when climatic conditions exceed AMF tolerance thresholds, fungal biomass, intraradical colonization, and spore production decrease, negatively affecting plant-mycorrhizal mutualisms (Zhu et al. 2017).

Further evidence suggests that the effects of climate change on AMF communities are highly context dependent. Weber et al. (2019) found that AMF responses to simultaneous drivers of global change-including increases in temperature, CO_2 levels, and nitrogen deposition-were highly variable. Their study highlighted species-specific and ecosystem-dependent differences in AMF functional traits, suggesting that some AMF taxa may be more resilient to climate change than others. Similarly, Alguacil et al. (2021) examined AMF responses to simulated climate warming and drying and demonstrated contrasting effects among AMF families, with some taxa benefiting from warmer conditions while others declined. In addition, Solaiman (2024) emphasized that AMF plays a critical role in organic matter decomposition and soil carbon sequestration, reinforcing their potential role in climate change mitigation.

These findings highlight the need for a deeper understanding of how AMF diversity, functional traits, and ecological roles shift under climate stressors. Given the complex responses of AMF to multiple drivers of global change, future research should focus on identifying resilient AMF species, exploring their functional plasticity, and assessing their potential for ecosystem restoration in climate-altered landscapes.

Main challenges in the study of arbuscular mycorrhizal fungi

The SARS-CoV-2 pandemic in 2019 has affected the production of scientific research, including studies on AMF. As result, there is urgent need to integrate and synthesize existing data to compensate for research gaps and provide a clear understanding of AMF ecology. However, beyond pandemic-related disruptions, several key challenges persist in AMF research.

One major challenge is understanding how global climate change affects AMF functionality. These fungi play an important role in plant adaptation to stress conditions such as prolonged drought, high temperatures, and soil degradation. Additionally, AMF enhance carbon capture and sequestration, contributing to climate change mitigation. However, it is unknown how increased temperatures, changes in precipitation regimes, and changes in soil factors will affect the functionality of AMF. Moreover, the functional diversity of AMF across ecosystems is still poorly understood, making it difficult to predict how these fungi will respond to environmental stressors and ecosystem disruptions.

To address these gaps, meta-analysis serves as a powerful tool to synthesize results from multiple studies, increase statistical power and sample size, and identify consistent ecological patterns across diverse environments. By integrating data from independent studies, meta-analyses can provide stronger evidence of causal relationships and offer deeper insights into how AMF respond to climate change and anthropogenic pressures. In the context of AMF research, meta-analyses can clarify the effects of environmental variables on colonization, diversity, and functionality, helping to provide a stronger foundation for future studies and practical applications in ecosystem management.

Conclusions

Arbuscular mycorrhizal fungi are multifunctional soil microorganisms that play a crucial role in ecological processes. They facilitate the OM decomposition, mediate vegetation structure, enhance nutrient transport, and mitigate environmental stress during the reproductive period of their host plants. They also promote seed germination and contribute to soil formation and stability by forming and strengthening aggregates.

Arbuscular mycorrhizal symbiosis is a key ecological strategy that enables plants to adapt to environmental change, from localized disturbances such as soil degradation to broader challenges such as global climate change.

Despite significant advances in the understanding of AMF ecology and function, several knowledge gaps remain. Future research should focus on quantifying AMF contributions to carbon sequestration, elucidating their interactions with other soil microbiota, and exploring their potential in large-scale ecological restoration projects. In addition, investigating the functional diversity of AMF under different environmental conditions will provide valuable insights into their adaptability and effectiveness in addressing emerging ecological challenges.

Author contributions

Yasmin Vázquez: Conceptualization, Investigation; Yasmin Vázquez, Silvia Castillo and Arturo Martínez: writing-original draft, writing – review and editing

Data accesibility

Requests for data can be made directly to the author for correspondence by mail.

Financing, required permits, potential conflicts of interest and acknowledgments

This research did not receive any specific grants from funding agencies in the public, commercial or non-profit sectors. We declare that we have no conflicts of interest.

This research is part of the doctoral studies of Y. Vázquez-Santos in the Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México. Y. Vázquez-Santos acknowledges the Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI)-Mexico (No. 818569) for scholarships to pursue her doctoral studies. Vázquez-Santos LM for the preparation of the illustrative material. Martínez-Orea Y for revision and translation.

References

Abrar, M., Zhu, Y., Rehman, M.M.U., Batool, A., Duan, H.X., Ashraf, U., Xiong, Y.C. 2024. Functionality of arbuscular mycorrhizal fungi varies across different growth stages of maize under drought conditions. *Plant Physiology and Biochemistry* 213, 108839. https://doi.org/10.1016/j.plaphy.2024.108839

Akiyama, K, Matsuzaki, K.I., Hayashi, H. 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* 435(7043), 824-827. http://doi.org/10.1038/nature03608

Akter, S., Kamruzzaman, M., Sarder, M.P., Amin, M.S., Joardar, J.C., Islam, M.S, Halder, M. 2024. Mycorrhizal fungi increase plant nutrient uptake, aggregate stability and microbial biomass in the clay soil. *Symbiosis* 1–14. https://doi.org/10.1007/s13199-024-00994-4

Al-Karaki, G.N. 2006. Nursery inoculation of tomato with arbuscular mycorrhizal fungi and subsequent performance under irrigation with saline water. *Scientia Horticulturae* 109(1):1–7. https://doi.org/10.1016/j.scienta.2006.02.019

Alberton, O., Kuyper, T.W., Gorissen, A. 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. *New Phytologist* 167(3):859–868. https://doi.org/10.1111/j.1469-8137.2005.01458.x

Alguacil, M.M., Schlaeppi, K., López-García, Á., van der Heijden, M.G.A., Querejeta, J.I. 2021. Contrasting Responses of Arbuscular Mycorrhizal Fungal Families to Simulated Climate Warming and Drying in A Semiarid Shrubland. *Microbial Ecology* 0123456789: 1–4. https://doi.org/10.1007/s00248-021-01886-6

Anderson, J.T., Inouye, D.W., McKinney, A.M., Colautti, R., Mitchell-Olds, T. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society* 282:3843–3852. https://doi.org/10.1098/rspb.2012.1051

Ballina-Gómez, H.S., Ruiz-Sánchez, E., Ambriz-Parra, E., Alvarado-López, C.J. 2017. Efecto de la luz y micorrizas en la germinación de semillas de árboles de selvas secas. *Madera y bosques* 23(3):29-37. https://doi.org/10.21829/myb.2017.2331531

Barrett, G., Campbell, C.D., Fitter, A.H., Hodge, A. 2011. The arbuscular mycorrhizal fungus *Glomus hoi* can capture and transfer nitrogen from organic patches to its associated host plant at low temperature. *Applied Soil Ecology* 48:102–105. https://doi.org/10.1016/j.apsoil.2011.02.002

Beck, A., Haug, I., Oberwinkler, F., Kottke, I. 2007. Structural characterization and molecular identification of arbuscular mycorrhiza morphotypes of Alzatea verticillata (Alzateaceae), a prominent tree in the tropical mountain rain forest of South Ecuador. *Mycorrhiza* 17:607-625. https:/doi.org/10.1007/s00572-007-0139-0

Beaubien, E., Hamann, A. 2011. Spring flowering response to climate change between 1936 and 2006 in Alberta, Canada. *Bioscience* 61:514–524. https://doi.org/10.1525/bio.2011.61.7.6

Begum, N., Ahanger, M.A., Su, Y., Lei, Y., Mustafa, N.S.A., Ahmad, P., Zhang, L. 2019. Improved drought tolerance by AMF inoculation in maize (*Zea mays*) involves physiological and biochemical implications. *Plants 8*(12):579. https://doi.org/10.3390/plants8120579

Bennett, A.E., Meek, H.C. 2020. The influence of arbuscular mycorrhizal fungi on plant reproduction. *Journal of chemical ecology* 46(8):707–721. https://doi.org/10.1007/s10886-020-01192-4

Besserer, A., Puech-Pagès, V., Kiefer, P., Gomez-Roldan, V., Jauneau, A., Roy, S., Séjalon-Delmas, N. 2006. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. *PLoS biology* 4(7):e226. https://doi.org/10.1371/journal.pbio.0040226

Brundrett, M.C., Ashwath, N. 2013. Glomeromycotan mycorrhizal fungi from tropical Australia III. Measuring diversity in natural and disturbed habitats. *Plant Soil* 370:419–433. https://doi.org/10.1007/s11104-013-1613-4

Brundrett, C.M., Tedersoo, L. 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist* 220:1108–1115. https://doi.org/10.1111/nph.14976

Bueno, C.G., Moora, M., Gerz, M., Davison, J., Öpik, M., Pärtel, M., Zobel, M. 2017. Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Global Ecology and Biogeography* 26(6):690-699. https://doi.org/10.1111/geb.12582

Bunn, R. A., Simpson, D.T., Bullington, L.S., Lekberg, Y., Janos, D.P. 2019. Revisiting the 'direct mineral cycling' hypothesis: arbuscular mycorrhizal fungi colonize leaf litter, but why? *ISME J*ournal 13:1891–1898. https://doi.org/10.1038/s41396-019-0403-2

Chagnon, P.L., Bradley, R.L., Maherali, H., Klironomos, J.N. 2013. A trait-based framework to understand life history of mycorrhizal fungi. *Trends in plant science* 18(9):484–491. https://doi.org/10.1016/j.tplants.2013.05.001

Chagnon, P.-L., Bradley, R.L., Lafond, J., Maxime, Paré, C., Penaud, V., Bradley, R.L., Penaud, V., Lafond, J., Paré, M.C. 2021. Trait-based and phylogenetic filtering of arbuscular mycorrhizal fungal communities under long-term agricultural practices. *Plant and Soil.* https://doi.org/10.1007/s11104-021-05155-w

Chagnon, P.L., Bradley, R.L., Lafond, J., Paré, M.C., Penaud, V. 2022. Trait-based and phylogenetic filtering of arbuscular mycorrhizal fungal communities under long-term agricultural practices. *Plant and Soil* 1-15. https://doi.org/10.1007/s11104-021-05155-w

Chen, D., Yu, M., González, G., Zou, X., Gao, Q. 2017. Climate impacts on soil carbon processes along an elevation gradient in the tropical Luquillo experimental forest. *Forests* 8:90. https://doi.org/10.3390/f8030090

Chen, W., Koide, R.T., Eissenstat, D.M. 2020. Topographic and Host Effects on Arbuscular Mycorrhizal and Ectomycorrhizal Fungal Communities in a Forested Watershed. *Ecosystems*, *23*:1537–1546. https://doi.org/10.1007/s10021-020-00486-8

Creamer, R.E., Barel, J.M., Bongiorno, G., Zwetsloot, M.J. 2022. The life of soils: Integrating the who and how of multifunctionality. *Soil Biology and Biochemistry* 166:108561. https://doi.org/10.1016/j.soilbio.2022.108561

Davison, J., Öpik, M., Daniell, T.J., Moora, M., Zobel, M. 2011. Arbuscular mycorrhizal fungal communities in plant roots are not random assemblages. *FEMS Microbiology Ecology* 78:103-115. https://doi.org/10.1111/j.1574-6941.2011.01103.x

Derelle, D., Courty, P.E., Dajoz, I., Declerck, S., van Aarle, I.M., Carmignac, D., et al. 2015. Plant identity and density can influence arbuscular mycorrhizal fungi colonization, plant growth, and reproduction investment in coculture. *Botany* 93:405–412. https://doi.org/10.1139/cjb-2014-018

Dickie, I.A., Martínez-García, L.B., Koele, N., Grelet, G.A., Tylianakis, J.M., Peltzer, D.A., Richardson, S.J. 2013. Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development. *Plant and Soil* 367(1):11–39. https://doi.org/10.1007/s11104-013-1609-0

Dodd, J.C., Boddington, C.L., Rodriguez, A., Gonzalez-Chavez, C., Mansur, I. 2000. Mycelium of arbuscular mycorrhizal fungi (AMF) from different genera: form, function and detection. *Plant and soil* 226:131-151.

Drew, E.A., Murray, R.S., Smith, S.E., Jakobsen, I. 2003. Beyond the rhizosphere: growth and function of arbuscular mycorrhizal external hyphae in sands of varying pore sizes. *Plant and Soil* 251:105-114.

Drigo, B., Pijl, A.S., Duyts, H., Kielak, A.M., Gamper, H.A., Houtekamer, M.J., Kowalchuk, G.A. 2010. Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. *Proceedings of the National Academy of Sciences*, 107:10938–10942. https://doi.org/10.1073/pnas.0912421107

Fahey, T.J., Sherman, R.E., Tanner, E.V. 2015. Tropical montane cloud forest: environmental drivers of vegetation structure and ecosystem function. *Journal of Tropical Ecology* 32:355–367. https://doi.org/10.1017/S0266467415000176

Fall, A.F., Nakabonge, G., Ssekandi, J., Founoune-Mboup, H., Apori, S.O., Ndiaye, A., Ngom, K. 2022. Roles of arbuscular mycorrhizal fungi on soil fertility: Contribution in the improvement of physical, chemical, and biological properties of the soil. *Frontiers in Fungal Biology 3*. https://doi.org/10.3389/ffunb.2022.723892

Gai, J.P., Tian, H., Yang, F.Y., Christie, P., Li, X.L., Klironomos, J.N. 2012. Arbuscular mycorrhizal fungal diversity along a Tibetan elevation gradient. *Pedobiologia* 55:145–151. https://doi.org/10.1016/j.pedobi.2011.12.004

García, D., Davison, J., Moora, M., Öpik, M., Feng, H., Hiiesalu, I., Zobel, M. 2018. Anthropogenic disturbance equalizes diversity levels in arbuscular mycorrhizal fungal communities. *Global Change Biology* 24(6):2649–2659. https://doi.org/10.1111/gcb.14131

Garrido, J.L., Alcántara, J.M., López-García, Á., Ozuna, C.V., Perea, A.J., Prieto, J., Azcón-Aguilar, C. 2023. The structure and ecological function of the interactions between plants and arbuscular mycorrhizal fungi through multilayer networks. *Functional Ecology* 37(8):2217-2230. https://doi.org/10.1111/1365-2435.14378

Gavito, M.E., Olsson, P.A. 2003. Allocation of plant carbon to foraging and storage in arbuscular mycorrhizal fungi. *FEMS Microbiology Ecology* 45:181–187. https://doi.org/10.1016/S0168-6496(03)00150-8

Gerdemann, J.W., Trappe, J.M. 1974. The Endogonaceae in the Pacific Northwest. Memoir No. 5. The New York Botanical Garden, New York.

González-Vargas, T., Gutiérrez-Castorena, M.D.C. 2022. Brightness Values-Based Discriminant Functions for Classification of Degrees of Organic Matter Decomposition in Soil Thin Sections. *Spanish Journal of Soil Science* 12:10348. https://doi.org/10.3389/sjss.2022.10348

Graham, E.B., Wieder, W.R., Leff, J.W., Weintraub, S.R., Townsend, A.R., Cleveland, C.C., et al. 2014. Do we need to understand microbial communities to predict ecosystem function? A comparison of statistical models of nitrogen cycling processes. *Soil Biology and Biochemistry* 68:279–282. https://doi.org/10.1016/j.soilbio.2013.08.023

Guo, Y., Ren, C., Yi, J., Doughty, R., Zhao, F. 2020. Contrasting responses of rhizosphere bacteria, fungi and arbuscular mycorrhizal fungi along an elevational gradient in a temperate montane forest of China. *Frontiers in Microbiology* 11:514865. https://doi.org/10.3389/fmicb.2020.02042

Gutiérrez-Castorena, M.C., Gutiérrez-Castorena, E.V., González-Vargas, T., Ortiz-Solorio, C.A., Suástegui-Méndez, E., Cajuste-Bontemps, L., Rodríguez-Mendoza, M.N. 2018. Thematic micro-maps of soil components using high-resolution spatially referenced mosaics from whole soil thin sections and image analysis. *European Journal of Soil Science* 69: 217-231. https://doi.org/10.1111/ejss.12506

Haggerty, B.P., Galloway, L.F. 2011. Response of individual components of reproductive phenology to growing season length in a monocarpic herb. *Journal of Ecology* 99:242–253. https://doi.org/10.1111/j.1365-2745.2010.01744.x

Hart, M.M., Reader, R.J. 2002. Does percent root length colonization and soil hyphal length reflect the extent of colonization for all AMF? *Mycorrhiza* 12:297–301. https://doi.org/10.1007/s00572-002-0186-5

Hart, M.M., Reader, R.J. 2005. The role of the external mycelium in early colonization for three arbuscular mycorrhizal fungal species with different colonization strategies. *Pedobiologia* 49: 269–279. https://doi.org/10.1016/j.pedobi.2004.12.001

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., Totland, Ø. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184–195. https://doi.org/10.1111/j.1461-0248.2008.01269.x

Hodge, A. 2014. Interactions between arbuscular mycorrhizal fungi and organic material substrates. *Advances in applied microbiology 89*:47–99. https://doi.org/10.1016/B978-0-12-800259-9.00002-0

Hodge, A., Fitter, A.H. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proceedings of the National Academy of Sciences of the United States of America* 107:13754–13759. https://doi.org/10.1073/pnas.1005874107

Hodge, A., Storer, K. 2015. Arbuscular mycorrhiza and nitrogen: Implications for individual plants through to ecosystems. *Plant Soil* 386:1–19. https://doi.org/10.1007/s11104-014-2162-1

Hodge, A., Campbell, C.D., Fitter, A.H. 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* 413:297–299.

Horsch, C.C.A., Antunes, P.M., Kallenbach, C.M. 2023. Arbuscular mycorrhizal fungal communities with contrasting life-history traits influence host nutrient acquisition. *Mycorrhiza* 33:1-14. https://doi.org/10.1007/s00572-022-01098-x

Hou, E., Chen, C., Luo, Y., Zhou, G., Kuang, Y., Zhang, Y., Wen, D. 2018. Effects of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. *Global Change Biology* 24(8): 3344–3356. https://doi.org/10.1111/gcb.14093

Jansa, J., Bukovská, P., Gryndler, M. 2013. Mycorrhizal hyphae as ecological niche for highly specialized hypersymbionts or just soil free-riders? *Frontiers in Plant Science* 4:1–8. https://doi.org/10.3389/fpls.2013.00134

Jeewani, P.H., Luo, Y., Yu, G., Fu, Y., He, X., Van Zwieten, L., Xu, J. 2021. Arbuscular mycorrhizal fungi and goethite promote carbon sequestration via hyphal-aggregate mineral interactions. *Soil Biology and Biochemistry* 162:108417. https://doi.org/10.1016/j.soilbio.2021.108417

Jiménez-Martínez, A., del Carmen Gutiérrez-Castorena, M., Montaño, N.M., Gutiérrez-Castorena, E.V., Alarcón, A., Gavito, M.E. 2024. Micromorphology and thematic micro-mapping reveal differences in the soil structuring traits of three arbuscular mycorrhizal fungi. *Pedobiologia* 104:150953. https://doi.org/10.1016/j.pedobi.2024.150953

Johnson, N.C. 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytologist* 185:631–647. https://doi.org/10.1111/j.1469-8137.2009.03110.x

Jurado, E., Flores, J. 2005. Is seed dormancy under environmental control or bound to plant traits? *Journal of vegetation Sciences* 16:559–564. https://doi.org/10.1111/j.1654-1103.2005.tb02396.x

Kemmelmeier, K., Dos Santos, D.A., Grittz, G.S., Stürmer, S.L. 2022. Composition and seasonal variation of the arbuscular mycorrhizal fungi spore community in litter, root mat, and soil from a subtropical rain forest. *Mycorrhiza* 1–15. https://doi.org/10.1007/s00572-022-01084-3

Kemper, W.D., Rosenau, R.C. 1986. Aggregate Stability and Size Distribution. Methods of soil analysis. Part 1. In: Arnold K. (Ed.) Methods of Soil Analysis: Part 1. Physical and Mineralogical Methods, 2nd Ed., American Society of Agronomy/Soil Science Society of America, Madison, WI, USA, pp. 425-444.

Klironomos, J.N., Hart, M.M. 2002 Colonization of roots by arbuscular mycorrhizal fungi using different sources of inoculum. *Mycorrhiza* 12:181–184. https://doi.org/10.1007/s00572-002-0169-6

Koide, R.T. 2000. Mycorrhizal symbiosis and plant reproduction. In: Kapulnik, Y., Douds, D.D.J. (eds.), *Arbuscular Mycorrhizas: physiology and function*, pp 19–46. Kluwer academic, Dordrecht. The Netherlands.

Koide, R.T., Kabir, Z. 2000. Extraradical hyphae of the mycorrhizal fungus *Glomus intrarradices* can hydrolyse organic phosphate. *New Phytologist* 148:511–517. https://doi.org/10.1046/j.1469-8137.2000.00776.x

Krüger, C., Kohout, P., Janoušková, M., Püschel, D., Frouz, J., Rydlová, J. 2017. Plant communities rather than soil properties structure arbuscular mycorrhizal fungal communities along primary succession on a mine spoil. *Frontiers in Microbiology* 8:719. https://doi.org/10.3389/fmicb.2017.00719

Laiolo, P., Illera, J.C., Meléndez, L., Segura, A., Obeso, J.R. 2015. Abiotic, biotic and evolutionary control of the distribution of C and N isotopes in food webs. *The American Naturalist* 185:169–182. http://dx.doi.org/10.5061/dryad.g4p92

Lehmann, A., Rillig, M.C. 2015. Understanding mechanisms of soil biota involvement in soil aggregation: A way forward with saprobic fungi?. *Soil Biology and Biochemistry* 88:298-302. https://doi.org/10.1016/j.soilbio.2015.06.006

Lehmann, A., Leifheit, E.F., Rillig, M.C. 2017. Mycorrhizas and soil aggregation. In: Collins Johnson, N., Gehring, C., Jansa, J. (eds.), *Mycorrhizal mediation of soil*, pp. 241-262. Elsevier.

Leigh, J., Fitter, A.H., Hodge, A. 2011. Growth and symbiotic effectiveness of an arbuscular mycorrhizal fungus in organic matter in competition with soil bacteria. *FEMS Microbiology Ecology* 76:428–438. https://doi.org/10.1111/j.1574-6941.2011.01066.x

Li, Y., Xie, Y., Liu, Z., Shi, L., Liu, X., Liang, M., Yu, S. 2023. Plant species identity and mycorrhizal type explain the root-associated fungal pathogen community assembly of seedlings based on functional traits in a subtropical forest. *Frontiers in Plant Science 14*:1251934. https://doi.org/10.3389/fpls.2023.1251934

Ludwig-Müller, J. 2010. Hormonal responses in host plants triggered by arbuscular mycorrhizal fungi. In: Kapulnik, Y., Douds, D.D.J. (eds.), *Arbuscular mycorrhizas: physiology and function*, pp. 169–190. Kluwer academic, Dordrecht. The Netherlands.

Lugo, M.A., Ferrero, M., Menoyo, E., Estévez, M.C., Siñeriz, F., Antón, A. 2008. Arbuscular mycorrhizal fungi and rhizospheric bacteria diversity along an altitudinal gradient in South American Puna grassland. *Microbial Ecology* 55:705–713. https://doi.org/10.1007/s00248-007-9313-3

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S., Vesk, P.A. 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography* 19:423–431. https://doi.org/10.1111/j.1466-8238.2010.00532.x

Morris, E.K., Buscot, F., Herbst, C., Meiners, T., Obermaier, E., Wäschke, N.W., et al. 2013. Land use and host neighbor identity effects on arbuscular mycorrhizal fungal community composition in focal plant rhizosphere. *Biodiversity and conservation 22*:2193-2205. https://doi.org/10.1007/s10531-013-0527-z

Nicolson, T.H. 1959. Mycorrhiza in the Gramineae. I. Vesicular-arbuscular endophytes with special reference to the external phase. *Transactions of the British Mycological Society* 42:421–438. https://doi.org/10.1016/S0007-1536(59)80043-7

Olivera-Morales, D., Castillo-Argüero, S., Guadarrama, P., Ramos-Zapata, J., Álvarez-Sánchez, J., Hernández-Cuevas, L. 2011. Establecimiento de plántulas de *Quercus rugosa* Née inoculadas con hongos micorrizógenos arbusculares en un bosque templado de México. *Boletín de la Sociedad Botánica de México* 89:115–121.

Paterson, E., Sim, A., Davidson, J., Daniell, T.J. 2016. Arbuscular mycorrhizal hyphae promote priming of native soil organic matter mineralization. *Plant and Soil* 408:243–254. https://doi.org/10.1007/s11104-016-2928-8

Perea-Rojas, Y.D.C., Arias, R.M., Medel Ortiz, R., Trejo Aguilar, D., Heredia, G., Rodríguez Yon, Y. 2019. Effects of native arbuscular mycorrhizal and phosphate-solubilizing fungi on coffee plants. *Agroforestry Systems* 93:961-972. https://doi.org/10.1007/s10457-018-0190-1

Piotrowski, J.S., Denich, T., Klironomos, J.N., Graham, J.M., Rillig, M.C. 2004. The effects of arbuscular mycorrhizas on soil aggregation depend on the interaction between plant and fungal species. *New Phytologist* 164:365-373. https://doi.org/10.1111/j.1469-8137.2004.01181.x

Powell, J.R., Parrent, J.L., Hart, M.M., Klironomos, J.N., Rillig, M.C., Maherali, H. 2009. Phylogenetic trait conservatism and the evolution of functional trade-offs in arbuscular mycorrhizal fungi. *Proceedings of the Royal Society Biological Sciences* 276(1676):4237–4245. https://doi.org/10.1098/rspb.2009.1015

Pozo, M.J., Azcón-Aguilar, C. 2007. Unraveling mycorrhiza-induced resistance. Current opinion in plant biology 10:393-398. https://doi.org/10.1016/j.pbi.2007.05.004

Pozo, M.J., Verhage, A., García-Andrade, J., García, J.M., Azcón-Aguilar, C. 2008. Priming plant defence against pathogens by arbuscular mycorrhizal fungi. In: Azcón-Aguilar, C., Barea, J.M., Gianinazzi, S., Gianinazzi-Pearson, V. (eds.), *Mycorrhizas-functional processes and ecological impact*, pp. 123-135. Springer Berlin Heidelberg. Berlin, Heidelberg.

Ramos-Zapata, J., Marrufo-Zapata, D., Guadarrama-Chávez, P., Solís-Rodríguez, U., Salinas-Peba, L. 2013. Ruderal plants: temporary hosts of arbuscular mycorrhizal fungi in traditional agricultural systems? *Tropical and Subtropical Agroecosystems* 16:399–406.

Rillig, M.C., Mummey, D.L. 2006. Mycorrhizas and soil structure. *New phytologist* 171:41-53. https://doi.org/10.1111/j.1469-8137.2006.01750.x

Roman-García, F., Yahuaca-Mendoza, M.P., Farias-Larios, J., López-Aguirre, J.G., Aguilar-Espinosa, S., del Rocío Flores-Bello, M. 2004. Hormonal Concentration and Growth in Chili Plants Inoculated with Several Mycorrhizal Fungus, Evaluated in Different Steps. *HortScience* 39:832–833. https://doi.org/10.21273/HORTSCI.39.4.832D

Sánchez-Fuente, G.J. 2019. Diversidad funcional y disturbio crónico en el bosque húmedo de montaña de San Luis Potosí, implicaciones para su conservación.

Schnoor, T.K., Lekberg, Y., Rosendahl, S., Olsson, P.A. 2011. Mechanical soil disturbance as a determinant of arbuscular mycorrhizal fungal communities in semi-natural grassland. *Mycorrhiza* 21:211–220. https://doi.org/10.1007/s00572-010-0325-3

Sepp, S.K., Davison, J., Jairus, T., Vasar, M., Moora, M., Zobel, M., Öpik, M. 2019. Non-random association patterns in a plant–mycorrhizal fungal network reveal host–symbiont specificity. *Molecular ecology* 28:365-378. https://doi.org/10.1111/mec.14924

Six, J., Elliott, E.T., Paustian, K. 2000. Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture. *Soil Biology and Biochemistry* 32:2099-2103. https://doi.org/10.1016/S0038-0717(00)00179-6

Smith, S.E., Read, D.J. 2008. Mycorrhizal Symbiosis. 3rd edition. San Diego, USA: Academic Press.

Smith, S.E., Smith, F.A. 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Annual Review of Plant Biology* 62:227–250. https://doi.org/10.1146/annurev-arplant-042110-103846

Solaiman, Z. 2024. Role of AMF in Organic Matter Decomposition, Carbon Sequestration and Climate Change Mitigation. In: Parihar, M., Rakshit, A., Adholeya, A., Chen, Y (eds.), *Arbuscular mycorrhizal fungi in sustainable agriculture: Nutrient and crop management*, pp. 131-141. Singapore: Springer Nature Singapore.

Teste, F.P., Dickie, I.A. 2017. Mycorrhizas across successional gradients. In: Collins Johnson, N., Gehring, C., Jansa, J. (eds.), *Mycorrhizal Mediation of Soil*, pp. 67–89. Elsevier.

Tisserant, E., Malbreil, M., Kuo, A., Kohler, A., Symeonidi, A., Balestrini, R., et al. 2013. Genome of an arbuscular mycorrhizal fungus provides insight into the oldest plant symbiosis. *Proceeding of the National Academy of Sciences* 110:20117–22. https://doi.org/10.1073/pnas.1313452110

Toljander, J.F., Lindahl, B.D., Paul, L.R., Elfstrand, M., Finlay, R.D. 2007. Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. *FEMS Microbiology Ecology* 61:295–304. https://doi.org/10.1111/j.1574-6941.2007.00337.x

van der Heyde, M., Ohsowski, B., Abbott, L.K., Hart, M. 2017. Arbuscular mycorrhizal fungus responses to disturbance are context dependent. *Mycorrhiza* 27:431–440. https://doi.org/10.1007/s00572-016-0759-3

Varela-Fregoso, L., Mora-Velázquez, A., Chávez-Hernández, C.G., Martínez-Bernal, A., García-Sánchez, R., Chimal-Sánchez, E., Montaño, N.M. 2017. *Acaulospora alpina* y *Ambispora fennica*, dos registros nuevos de hongos micorrizógenos arbusculares para México. *Revista mexicana de biodiversidad* 88:496-501. https://doi.org/10.1016/j.rmb.2017.06.005

Vázquez-Santos, Y. 2025. *La función de los hongos micorrizógenos arbusculares en especies de la vegetación secundaria en un bosque templado* (Doctoral dissertation). Facultad de Ciencias, Universidad Nacional Autónoma de Mexico, México. 185 pp.

Vázquez-Santos, Y., Castillo-Argüero, S., Martínez-Orea, Y., Sánchez-Gallen, I., Vega-Frutis, R., Camargo-Ricalde, S.L., Hernández-Cuevas, L.V. 2019. The reproductive phenology of *Acaena elongata* and its relation with arbuscular mycorrhizal fungi. *Symbiosis* 79:129–140. https://doi.org/10.1007/s13199-019-00629-z

Vázquez-Santos, Y., Castillo-Argüero, S., Montaño, N.M., Espinosa-García, F.J., Flores-Ortiz, C., Martínez-Orea, Y. 2024. Arbuscular mycorrhizal fungi affect early phenological stages of three secondary vegetation species in a temperate forest. *Plant Ecology* 225:983-996. https://doi.org/10.1007/s11258-024-01448-z

Vega-Frutis, R., Guevara, R. 2009. Different arbuscular mycorrhizal interactions in male and female plants of wild *Carica papaya* L. *Plant and Soil* 322:165-176. https//doi.org/10.1007/s11104-009-9903-6

Verbruggen, E., Kiers, E.T. 2010. Evolutionary ecology of mycorrhizal functional diversity in agricultural systems. *Evolutionary Applications* 3:547-560. https://doi.org/10.1111/j.1752-4571.2010.00145.x

Veresoglou, S. D., Rillig, M. C. 2012. Suppression of fungal and nematode plant pathogens through arbuscular mycorrhizal fungi. *Biology letters* 8:214-217. https://doi.org/10.1098/rsbl.2011.0874

Violi, H.A., Barrientos-Priego, A.F., Wright, S.F., Escamilla-Prado, E., Morton, J.B., Menge, J.A., Lovatt, C.J. 2008. Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico. *Forest Ecology and Management* 254:276–290. https://doi.org/10.1016/j.foreco.2007.08.016

Vosátka, M., Gryndler, M. 2000. Response of micropropagated potatoes to inoculation with arbuscular mycorrhizal fungi and soil bacteria. *Applied Soil Ecology* 15:145–152. https://doi.org/10.1016/S0929-1393(00)00090-1

Vosnjak, M., Likar, M., Osterc, G. 2021. The effect of mycorrhizal inoculum and phosphorus treatment on growth and flowering of Ajania (*Ajania pacifica* (Nakai) Bremer et Humphries) plant. *Horticulturae* 7:178. doi: https://doi.org/10.3390/horticulturae7070178

Wang, L., Tang, Z. 2022. How do arbuscular mycorrhizas affect reproductive functional fitness of host plants?. *Frontiers in Plant Science* 13:975488. https://doi.org/10.3389/fpls.2022.975488

Wang, F., Zhang, L., Zhou, J., Rengel, Z., George, T.S., Feng, G. 2022. Exploring the secrets of hyphosphere of arbuscular mycorrhizal fungi: processes and ecological functions. *Plant and Soil* 48:1-22. https://doi.org/10.1007/s11104-022-05621-z

Weber, S.E., Diez, J.M., Andrews, L.V., Goulden, M.L., Aronson, E.L., Allen, M.F. 2019. Responses of arbuscular mycorrhizal fungi to multiple coinciding global change drivers. *Fungal Ecology* 40:62-71. https://doi.org/10.1016/j.funeco.2018.11.008

Welc, M., Ravnskov, S., Kieliszewska-Rokicka, B., Larsen, J. 2010. Suppression of other soil microorganisms by mycelium of arbuscular mycorrhizal fungi in root-free soil. *Soil Biology & Biochemistry* 42:1534–1540. https://doi.org/10.1016/j.soilbio.2010.05.024

Went, F.W., Stark, N. 1968. The biological and mechanical role of soil fungi. *Proceeding of the National Academy of Sciences* 60:497–504. https://doi.org/10.1073/pnas.60.2.497

Xiao, D., Chen, M., He, X., Nie, Y., Jiang, N., Zhang, W., Wang, K. 2023. Soil nutrients and vegetation along a karst slope gradient affect arbuscular mycorrhizal fungi colonization of roots rather than bulk soil AMF diversity. *Plant and Soil 489*:139-154. https://doi.org/10.1007/s11104-023-06004-8

Zhang, J., Deng, L., Jiang, H., Peng, C., Huang, C., Zhang, M., Zhang, X. 2021. The effects of elevated CO 2, elevated O 3, elevated temperature, and drought on plant leaf gas exchanges: A global meta-analysis of experimental studies. *Environmental Science and Pollution Research 28*:15274-15289. https://doi.org/10.1007/s11356-020-11728-6

Zhang, M., Yang, M., Shi, Z., Gao, J., Wang, X. 2022. Biodiversity and variations of arbuscular mycorrhizal fungi associated with roots along elevations in Mt. Taibai of China. *Diversity* 14:626. https://doi.org/10.3390/d14080626

Zheng, Q., Hu, Y., Zhang, S., Noll, L., Böckle, T., Dietrich, M., Wanek, W. 2019. Soil multifunctionality is affected by the soil environment and by microbial community composition and diversity. *Soil Biology and Biochemistry* 136:107521. https://doi.org/10.1016/j.soilbio.2019.107521

Zhu, X., Song, F., Liu, F. 2017. Arbuscular mycorrhizal fungi and tolerance of temperature stress in plants. In: Wu, Q-S. (ed.) *Arbuscular mycorrhizas and stress tolerance of plants*, 163–194 pp. Springer, Singapore.

Zhu, Y. G., Smith, S.E., Barritt, A.R., Smith, F.A. 2001. Phosphorus (P) efficiencies and mycorrhizal responsiveness of old and modern wheat cultivars. *Plant and Soil* 237:249-255.

Zobel, M. 2016. The species pool concept as a framework for studying patterns of plant diversity. *Journal of Vegetation Science* 27:8-18. https://doi.org/10.1111/jvs.12333

Zobel, M., Öpik, M. 2014. Plant and arbuscular mycorrhizal fungal (AMF) communities–which drives which? *Journal of Vegetation Science* 25:1133–1140. https://doi.org/10.1111/jvs.12191