Revista de
CIENCIAS AGRÍCOLAS

e-ISSN Online 2256-2273

Received: June 21 2024 Accepted: October 22 2025 Published: December 28 2025

Research article: Soil science

Effects of soil properties on mycorrhizal fungi responses: A meta-analysis

Efectos de las propiedades del suelo en las respuestas de los hongos micorrízicos: un meta-análisis

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Cite : Aranguren, R. A.; Cañón, J.E. (2025). Effect of sol properties on mycorrhizal fungi responses: A Meta-Analysis. *Revista de Ciencias Agrícolas*. 42(3): e3282. https://doi.org/10.22267/rcia.20254203.282

ABSTRACT

Recent studies have tested the sensitivity of Microbial-Based Indicators (MBIs), such as Arbuscular Mycorrhizal Fungi (AMF), for monitoring changes in soil properties across a wide range of environments. However, the direction and magnitude of AMF responses depend on contextual factors such as land use, vegetation type, geography, and environmental variables. Thus, there is still no consensus about whether AMF show a consistent response to changes in certain soil properties. Likewise, a better understanding of how interactions among different aspects of the microbial community can modify the influence of soil properties on AMF responses is needed. Based on data compiled across a wide geographic range, this study analyzes the responses observed in several aspects of AMF to soil properties across different land uses. A Dependency Network Analysis (DEPNA) was performed within a correlation network constructed using average correlation coefficients to evaluate the strength of relationships between soil properties and different MBIs while controlling the effect of another MBI. Average correlation coefficients were estimated via meta-analysis to account for experimental heterogeneity. The total Influence Degree (TID), computed from partial correlations, suggests strong dependencies between MBIs (related to AMF diversity, mycorrhizal colonization rate, and Glomalin Soil Proteins) and soil properties (Pb concentrations, soil structural features, and nutrient stocks). The results suggest that AMF emerge as robust microbial indicators of soil condition, reflecting both fertility enhancement and degradation. Partial correlation and dependency network analyses show that soil effects on AMF and GRSP are largely mediated by microbial biomass, respiration, and diversity, explaining responses across land uses and stress gradients.

Keywords: glomalin related to soil proteins; microbiological indicators; nutrients; partial correlations; soil quality; total influence degree

RESUMEN

Estudios recientes han evaluado la sensibilidad de indicadores microbiológicos (MBI) como los Hongos Micorrícicos Arbusculares (AMF), para monitorear alteraciones en las propiedades del suelo en una amplia variedad de entornos. Sin embargo, la dirección y la intensidad de las respuestas de los AMF dependen de factores contextuales como el uso del suelo, el tipo de vegetación, la geografía y las variables ambientales. Por lo tanto, aún no existe un consenso acerca de si los AMF tienen una tendencia de respuesta a cambios en determinadas propiedades del suelo. Asimismo, aún no se ha dilucidado cómo las interacciones entre diferentes aspectos de la comunidad microbiana pueden modificar la influencia de las propiedades del suelo en las respuestas de los AMF. Considerando datos recopilados a lo largo de diferentes entornos geográficos, en este estudio se analizan las respuestas de los AMF ante variaciones en las propiedades del suelo. Se realizó un Análisis de Red de Dependencia (DEPNA) dentro de una red de correlaciones construida a partir de coeficientes de correlación promedio para evaluar la fuerza de las interacciones entre las

propiedades del suelo y diferentes MBI. Los coeficientes de correlación promedio se estimaron mediante un meta-análisis para tener en cuenta la heterogeneidad experimental. El Grado de Influencia Total (TID), calculado a partir de correlaciones parciales, sugiere fuertes dependencias entre los MBI (relacionados con la diversidad de AMF, la tasa de colonización micorrícica y las Proteínas Relacionadas con la Glomalina del Suelo) y las propiedades del suelo (concentraciones de Pb, características estructurales del suelo y reservas de nutrientes). Los resultados indican que estas fuertes influencias pueden deberse a los efectos de correlaciones parciales con la diversidad microbiana, el carbono de la biomasa microbiana y la respiración microbiana del suelo.

Palabras clave: calidad del suelo; correlaciones parciales; grado de influencia total; indicadores microbiológicos; nutrientes; proteínas del suelo relacionadas con la glomalina

INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) and their glomalin-related soil proteins (GRSP) are widely recognized as microbial-based indicators for assessing soil alterations and associated shifts in microbial lineages (Lutz *et al.,* 2023; Miranda *et al.,* 2025). For example, AMF diversity reflects variation in plant diversity (Van Galen *et al.,* 2025), losses of soil organic carbon (SOC) (Ao *et al.,* 2025), and differences in mineral fertilization (Wang *et al.,* 2023). Moreover, AMF are associated with phosphate mobilization, plant pathogen resistance, and improved soil structure (Bi *et al.,* 2019; Chen *et al.,* 2018). Additionally, due to their cementing properties, glomalin-related soil proteins (GRSP) are regarded as indicators of soil structural stability, contributing to the formation of water-stable aggregates and acting as binding agents for heavy metals (Wang *et al.,* 2020). Their allocation in various fractions has also been linked to mechanisms of soil organic contents dynamics, especially with soil organic carbon pools (Xiao *et al.,* 2019). Nevertheless, AMF responses are highly context-dependent, as with most MBIs, and therefore there is no consensus on how AMF respond to alterations in soil properties (Fierer *et al.,* 2021; Soucémarianadin *et al.,* 2018; Van Der Heyde *et al.,* 2017). For example, large variability in AMF diversity patterns caused by contextual factors such as habitat type, plant diversity, and land use intensity, have been documented in experimental designs across a wide spectrum of ecosystems (Albornoz *et al.,* 2022; Faggioli *et al.,* 2019; Sepp *et al.,* 2018). Furthermore, several studies report that the drivers shaping AMF communities differ across ecosystems and land-use types. For instance, plant diversity strongly structures AMF composition in grasslands but shows no significant effect in desert ecosystems (Adenan *et al.,* 2021). Also, multiple reports indicate that different variations in soil pH, organic carbon and nitrogen content, and moisture alter AMF communities across spatial scales (Albornoz *et al.,* 2022; Yang *et al.,* 2021).

Similarly, environmental factors like forest composition or land use can significantly affect GRSP allocation (Wang *et al.,* 2019; Zhao *et al.,* 2022). Although MBIs vary with context, unifying principles guiding microbial responses have been studied employing cross-biome data compilations to find pooled effects (Pathak *et al.,* 2020). Cross-biome compilations, for example, have shown that N fertilization has affected AMF symbiosis rates (Hoeksema *et al.,* 2010). Likewise, analyses of such cross-biome compilations have suggested a positive relationship between microbial enzyme activity and SOC (Nunes *et al.,* 2020). Moreover, they have identified associations of microbial biomass and fungal diversity with C:N inputs and cover cropping (Muhammad *et al.,* 2021).

However, understanding the MBI interactions in depth may require post-hoc analysis of the interdependencies observed among physical, biological, and biochemical attributes of the soil on MBI (Dahal *et al.,* 2021; Raiesi & Kabiri, 2016). Additionally, co-regulation processes should be considered, as multiple studies have demonstrated that soil microbial attributes are interrelated. In particular, microbial enzyme activity, microbial biomass carbon (MBC), and AMF diversity jointly modulate how changes in soil features, such as nutrient inputs, influence microbial community structure and their functions (Bai *et al.,* 2021; Bi *et al.,* 2019). Given the influence of contextual factors and microbial interdependencies on MBI responses to changes in soil properties, the following question was investigated: How can response tendencies of AMF-related MBIs to variations in soil properties be identified?

Peer-reviewed studies published over the last decade were compiled to synthesize divergent responses of AMF and commonly used MBIs in soil quality assessments. From these data, correlations were estimated and the strength of interactions between soil microbial attributes and variations in soil properties was quantified. Then, local correlations computed from contrasting land uses (forests, mining sites, croplands, pastures, wastelands) were averaged to produce overall correlation coefficients. To assess how related microbial attributes influenced AMF responses, partial correlation coefficients were computed from triads of linked variables identified within correlation-based network. Each triad comprised a soil property that was simultaneously correlated with two microbial-based indicators. Finally, the Total Node Influence was estimated by considering the total influence of node *j* on node *i*, as the average influence of node *j* on the correlations over all nodes linked with node *i* (Wang, Xie, *et al.,* 2018). Using this method, partial correlations within a given set of node-node correlations were measured. The metrics derived from this approach enabled identification of multiple AMF responses. These measures explicitly accounted for interactions among MBI that may mediate the effects of soil properties on AMF.

MATERIAL AND METHODS

Study selection and data compilation

The literature review was conducted in the SCOPUS ELSEVIER database using as keywords “soil properties” combined with the following relevant MBIs: “microbial respiration”, “catalase activity”, “urease activity”, “bacterial diversity”, “fungal diversity”, “actinobacteria diversity”, “glomalin-related soil proteins”, “mycorrhizal colonization rate” and “mycorrhizal fungi spores”. The selected studies included only those published from 2010 to 2020. With this review, a set of 564 documents were found and the lists of soil properties (Table 1) and MBIs (Table 2) were delimited with relevant measures recorded within this first set of studies. Afterward, 77 papers were selected from that first set of studies according to the following criteria: 1) The paper showed raw values of at least one MBI and one soil property listed in Table 1 and Table 2; 2) The soils analyzed were retrieved from mining or agricultural areas; 3) The study assessed at least one control treatment within an area with a different manage system. The information related to land uses, treatments assessed, and raw values of measured indicators was compiled from every study selected. The list of selected papers is presented in Supplementary Table 1.

Table 1. *Physical and chemical parameters commonly measured in soils from mining and agricultural areas*

Parameter	Definition
Bulk Density	Relation between soil weight and its volume.
Total Porosity	Gap, holes, or pores between soil particles, which contain water and air in a specific soil portion.
Soil Penetration Resistance	Relation between the force applied to an object against a soil matrix and the range of distance that this element can travel through the soil matrix.
Electrical Conductivity	Measurement of electrical resistance or ability of a soil to carry an electric current.
Cationic Exchange Capacity	Total capacity of soil to hold exchangeable positively charged ions on the fine earth fraction.
Soil Moisture	Weight of water stored in the soil.
Soil Water-Stable Aggregates	The mean weight of different soil stable aggregate sizes is exposed to humidity.
Water Holding Capacity	The soil moisture that will remain in the soil after the water drains off the large pores against a specific force.
Total Potassium	The recoverable amount of the element K.
Total Phosphorus	The recoverable amount of the element P.
Arsenic concentration	The recoverable amount of the element As.
Cadmium concentration	The recoverable amount of the element Cd.
Chromium concentration	The recoverable amount of the element Cr.
Copper concentration	The recoverable amount of the element Cu.
Total Iron recoverable	The recoverable amount of the element Fe.
Nickel concentration	The recoverable amount of the element Ni.
Lead concentration	The recoverable amount of the element Pb.
Zinc concentration	The recoverable amount of the element Zn.
Total nitrogen concentration	Soil total nitrogen concentration.
Nitrates	Nitrate nitrogen recoverable in soil (NO_3^-).
Ammonium nitrogen	Ammonium nitrogen recoverable in soil (NH_4^+).
Total Organic Carbon	Total C stored on soil organic matter.

Table 2. *Definitions of soil quality indicators based on microbiological parameters*

Parameter	Definition
Acid Phosphatase Activity	Amount of enzyme required to release 1 µmol of p-nitrophenol/ml/min from di-Na p-nitrophenyl phosphate in pH 6.5.
Alkaline Phosphatase Activity	Amount of enzyme required to release 1 µmol of p-nitrophenol/ml/min from di-Na p-nitrophenyl phosphate in pH 11.
Beta-Glucosidase Activity	Formation of p-nitrophenol from a substrate (p-nitrophenyl-β-glucopyranoside) by an enzyme present in a specific weight of soil.

Parameter	Definition
Catalase Activity	Formation of H_2O_2 from a substrate by enzymes stored in a specific weight of soil.
Dehydrogenase Activity	Formation of triphenyl formazan-TPF from a substrate by enzymes stored in a specific weight of soil.
Invertase Activity	Reduction of glucose by microbial enzymes present in a specific soil weight.
Urease Activity	Formation of N-NH4 from a substrate by an enzyme present in a specific weight of soil.
Microbial Metabolic C Quotient	Relation of microbial respiration per unit of microbial biomass carbon.
Soil Microbial Basal Respiration	CO_2 released by microbial population in a specific weight of soil.
Microbial Biomass Carbon	Carbon mass released from lysed microbial cells.
Mycorrhizal Colonization Rate	The ratio of the AMF body to the plant root area.
Easily Extractable Glomalin-Related Soil Proteins	Glomalin-Related Soil Proteins extracted in an initial round of autoclaving for only 30 min with 20 mmol l–1 sodium citrate, pH 7.0.
Total Glomalin-Related Soil Proteins	Glomalin-Related Soil Proteins extracted in an initial round of autoclaving for only 60 min with 50 mmol l–1 sodium citrate, pH 8.0.
Abundance of AMF	Measure to quantify AMF spore abundance from a specific soil sample.
Enumeration of Actinomycetes	CFU enumerated by serial dilution method count in a selective culture medium.
Enumeration of Mesophilic Bacteria	CFU enumerated by serial dilution method count in a selective culture medium.
Enumeration of Molds and Yeasts	CFU enumerated by serial dilution method count in a selective culture medium.
Diversity of Actinomycetes	Measurement of microbial taxa diversity present in a soil sample (diversity indexes).
Diversity of Bacteria	Measurement of microbial taxa diversity present in a soil sample (diversity indexes).
Diversity of Fungi	Measurement of microbial taxa diversity present in a soil sample (diversity indexes).
Diversity of AMF	Measurement of microbial taxa diversity present in a soil sample (diversity indexes).

Weighted average correlation coefficients

First, the average values of MBIs and soil parameters measured in a treatment within a study were categorized using ranges. Then, Spearman's rank correlation coefficients "r_s1" were estimated between pairwise variables. After that, Zr_s1 values were obtained by transforming r_s1 coefficients with Fisher's Z function. Confidence intervals for Zr_s1(C.I1) were estimated by permutation method, using the *perm.CI* function from the R package RI2by2 (Rigdon & Hudgens, 2015).

The meta-analysis was performed to weigh r_s1 and estimate average correlation coefficients to pairwise of variables (r_s2) (Kontopantelis & Reeves, 2010). The variance within a study for r_s1 was estimated from an empirical null distribution. For each study and pairwise comparison, two uncorrelated variables were permuted 2000 times. For every permutation, the Spearman's

correlation coefficient $r_{su}1$ was computed. Then, Fisher's Z-transformation were applied to these coefficients. Next, we took the variance of those z-values as the study-level variance of Zr_s1 (S^2 Zr_s1). The inverses of S^2 Zr_s1 were assigned as the weight of each study. Later, to compute Zr_s2 coefficients and their C.I2, a weighted average of Zr_s1 and C.I1 was performed (Follmann & Proschan, 1999). The null distributions were simulated with R package *infer* (Couch *et al.,* 2021). Finally, a Fisher's Z inverse transformation was applied to the Zr_s2 coefficients to obtain average Spearman's rank correlation coefficients (r_s2) to each pairwise of variables (German *et al.,* 2017).

Dependency Network Analysis (DEPNA)

To construct the correlation-based network, each MBI and soil parameter was considered as a node. The model linked only nodes such as soil property-MBI and MBI-MBI . The threshold to define a significant edge between a node *i* and node *j* were average correlation coefficients $r_s2_{i,j}$ >0.5 or <-0.5 (Batushansky *et al.,* 2016; Kojaku & Masuda, 2019). The weighted and undirected graphical model was drawn using the R package *Igraph* version 1.3.4 (Singh & Garg, 2020). To quantify the influence of a soil property on an MBI, the effect of a third variable, namely a second MBI, was incorporated into the pairwise correlation. The *all_simple_paths* function from the R package *igraph* (cutoff = 2) was used to enumerate triplets in which a soil property node was connected to two mutually correlated MBI nodes.

The partial correlation coefficient of first-order (PC(*i, k|j*)) between a node *i* (soil property) and a node *k* (MBI) considering the influence of a node *j* (MBI) was computed using the equation (1) (Wu *et al.,* 2020):

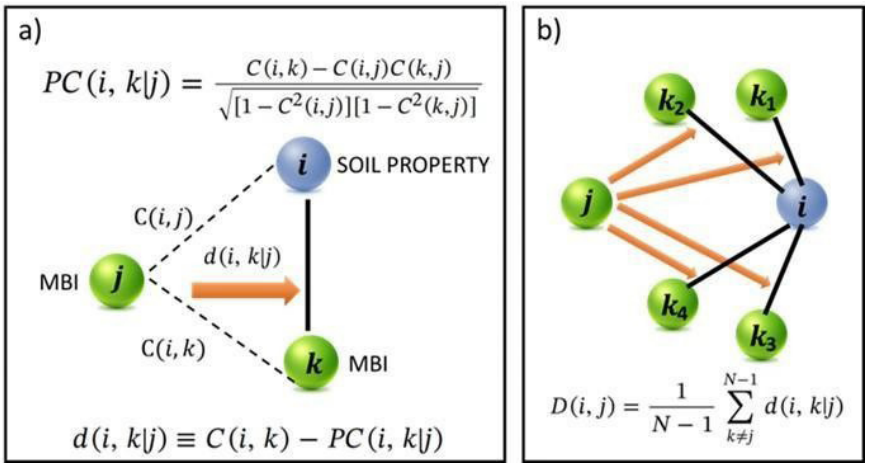
$$PC(i,k|j) = \frac{C(i,j) - C(i,k)C(j,k)}{\sqrt{\left(1 - C^2(i,k)\right)\left(1 - C^2(j,k)\right)}} \quad (1)$$

Where *C(i, j), C(i, k), and C(j, k)* are the correlations (measured by the average rank correlation coefficient r_s2) between variables *i - j*, *i - k* and *j – k,* respectively (Figure 1a). The difference between C(*i, j*) and PC(*i, k|j*) was denoted as the dependency effect of variable k on the correlation C(*i, j*), which is expressed by equation (2) (Wu *et al.,* 2020):

$$d(j) \equiv C(i,j) - PC(j) \quad (2)$$

When $d(i,j \mid k)$ equals zero, means that variable *k* has no impact on the correlation between *i* and *j*. On the contrary, higher values of $d(i, j \mid k)$, reflect a dependency effect of variable *k* on the correlation between *i* and *j*. The Total Influence Degree (TID) of node *j* on node *i*, D(*i, j*) was defined as the average of the dependency effects of variable *k* on C(*i, j*), over all nodes *k* (Figure 1b). In order to avoid cases with a sum over positive and negative influences, the TID was computed as the average of absolute values of the influences $d(i, j \mid k)$ (3) (Junior *et al.,* 2015):

$$D(i,j) = \frac{1}{N-1} \sum_{k \neq j}^{N-1} \left| d(j) \right| \quad (3)$$



Source Jacob *et al.,* (2020)

Figure 1. *Steps to quantify total influence between a pairwise of nodes within a correlation-based network using Dependency Network Analysis (DEPNA). (a) Estimation of the partial correlation of first-order. (b) Estimation of the total influence degree.*

RESULTS

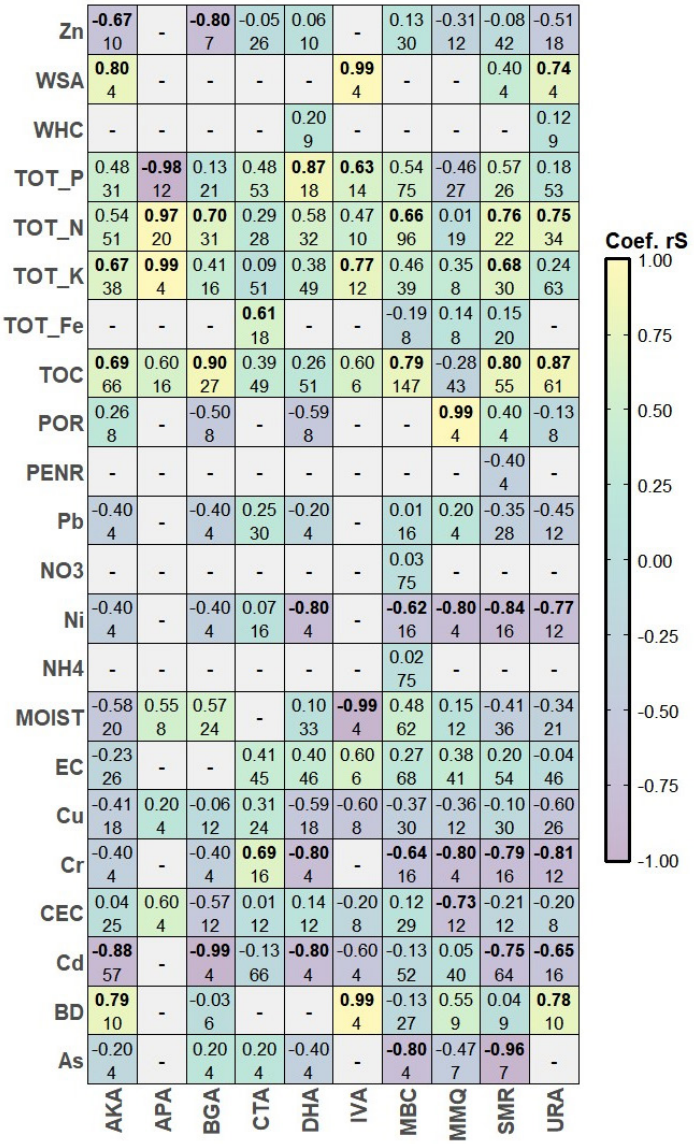
Average correlations

Selected studies encompassed a review of MBI relationships observed across a large range of environmental contexts represented by results documented in 5 continents, 19 countries, and 92 geographic regions. Despite wide variability in estimated correlations, many MBI showed strong positive or negative correlations with soil properties (r_s2) across land uses and management.

Regarding AMF responses, the Easily Extractable Glomalin Related Soil Proteins (EEGRSP) and Total Glomalin Related Soil Proteins (TGRSP) were positively correlated with water-stable aggregates (r_s2=0.67; 0.87), total organic carbon (r_s2=0.98; 0.98) and total N concentrations (r_s2=0.98; 0.95) although negatively correlated with bulk density (r_s2=-0.96; -0.99). Similarly, the correlations observed to mycorrhizal abundance were positive with soil nutrients as total organic carbon (r_s2=0.99), total N (r_s2=0.89), and P concentration (r_s2=0.70) but negative with bulk density (r_s2=-0.90). Moreover, mycorrhizal colonization rate was positively correlated with NO_3 (r_s2=0.99) and K concentrations (r_s2=0.74) as well as mycorrhizal diversity was positively correlated with NH_4 (r_s2=0.86). In contrast, both mycorrhizal colonization rate and mycorrhizal diversity show negative correlations with Pb concentrations (r_s2=-0.99; -0.99). Figures 2 and 3 reports cross-study mean correlation coefficients between microbial-based indicators and soil properties.

Simultaneously, interrelationships among MBI were observed. In particular, mycorrhizal colonization rate, mycorrhizal abundance, EEGRSP and TGRSP were strongly intercorrelated and showed positive associations with actinomycete diversity, MBC and soil microbial respiration (SMR) (Figure 4). In addition, mycorrhizal diversity was positively correlated with mycorrhizal colonization rate (r_s2=0.87) and bacterial diversity (r_s2=0.99). Finally, the high between-study variation contributed to the wide confidence intervals computed for cross-study average correlation values (Figure 5, 6 and 7). Mycorrhizal diversity and indicators based on undifferentiated

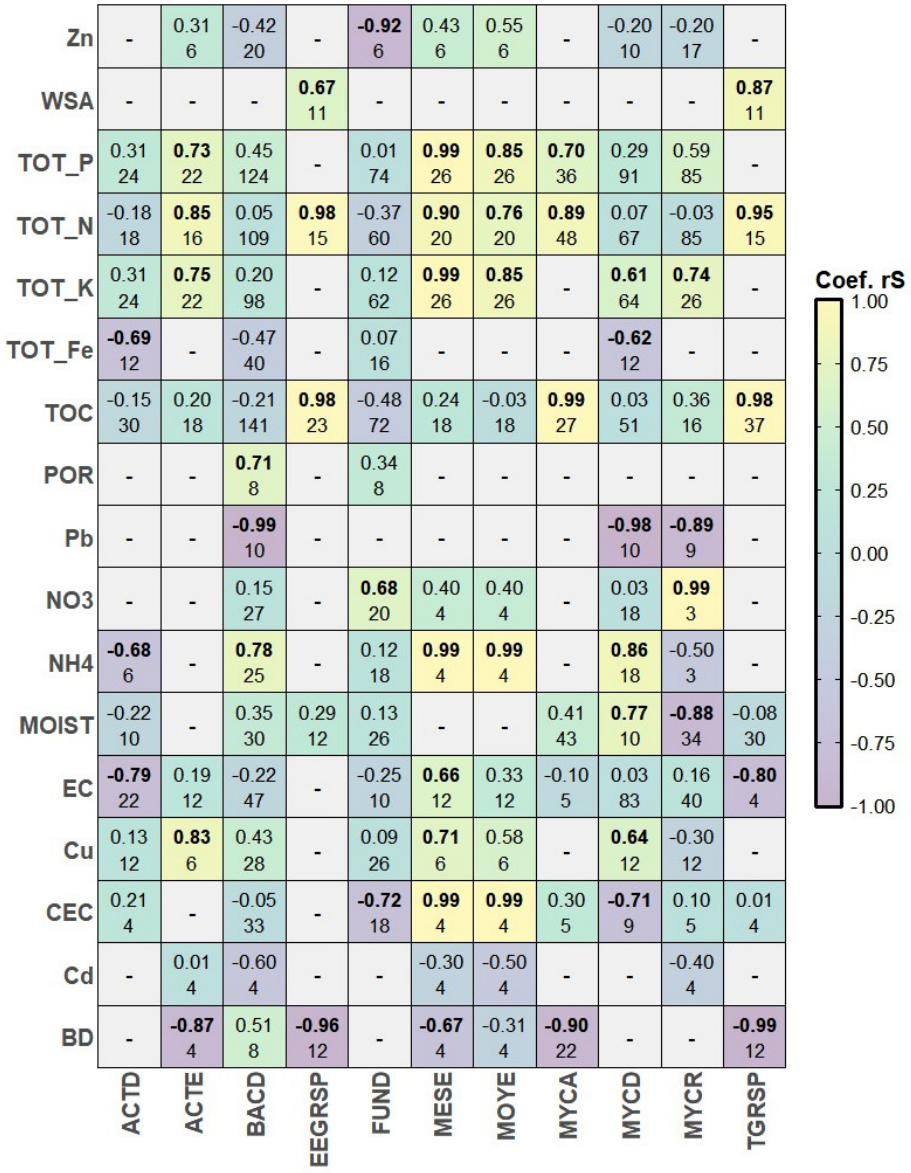
microbial activity (alkaline phosphatase, β-glucosidase, catalase, dehydrogenase, invertase, microbial metabolic C quotient) showed very broad C.I2 distributions. In many cases the correlations approached the full theoretical range from −1 to 1.



Note. NH4 (Inorganic ammonium, N form); NO3 (Inorganic nitrate, N form); TOT_N (Total N); TOT_K (Total K); TOT_P (Total P); TOC (Total organic carbon); MOIST (Soil moisture); CEC (Cation exchange capacity); EC (Electrical conductivity); PENR (Penetration resistance); POR (Porosity); WHC (Water holding capacity); WSA (Water-stable aggregates); BD (Bulk density); As (Arsenic); Cd (Cadmium); Cr (Chromium); Cu (Copper); Ni (Nickel); Pb (Lead); Zn (Zinc); TOT_Fe (Total iron); APA (Acid phosphatase activity); AKA (Alkaline phosphatase activity); BGA (Beta-glucosidase activity); CTA (Catalase activity); DHA (Dehydrogenase activity); IVA (Invertase activity); URA (Urease activity); MBC (Microbial biomass carbon); SMR (Soil microbial respiration); MMQ (Microbial metabolic quotient).

* The values located on the bottom of cells correspond to the number of studies contributing to the pooled estimate.

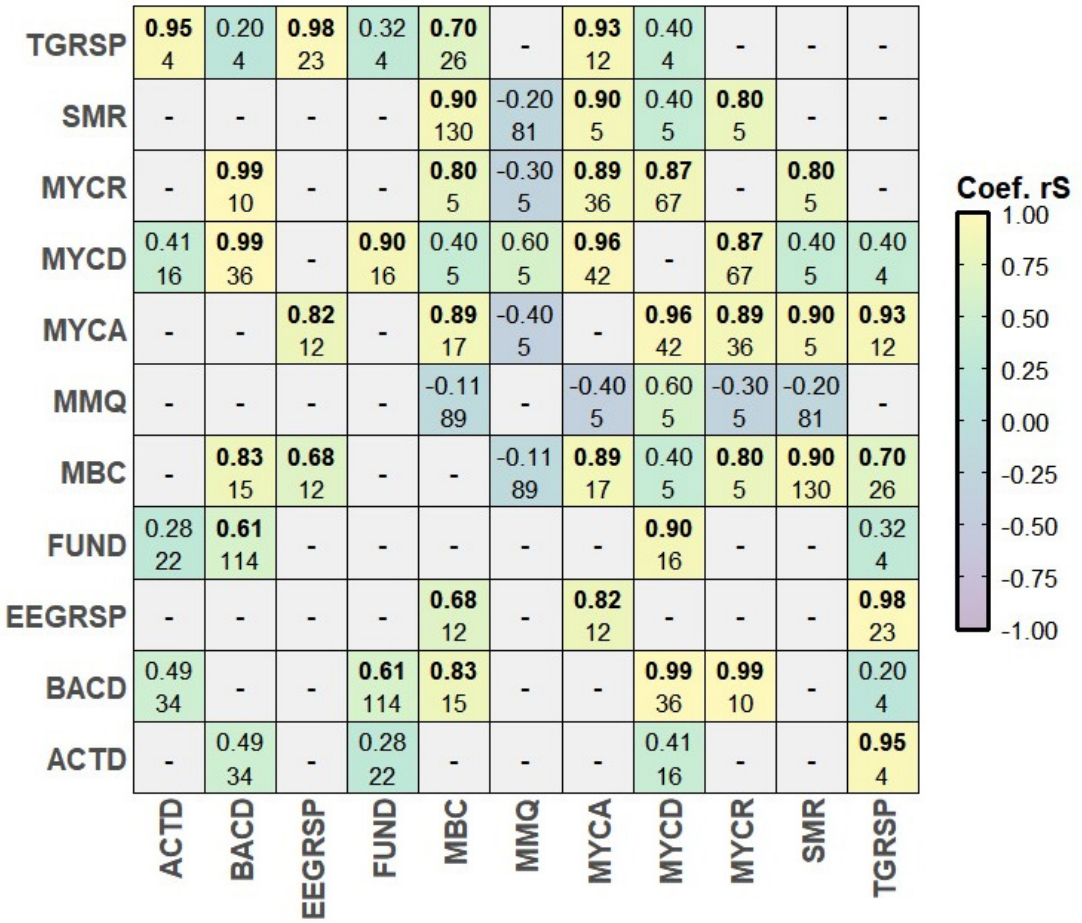
Figure 2. *Cross-study averages of the between-treatment Spearman's rank correlation (r_S2) for pairs of MBI which measures the activity of undifferentiated microbial consortia and soil properties.*



Note. BD (Bulk density); CEC (Cation exchange capacity); Cd (Cadmium); MOIST (Soil moisture); EC (Electrical conductivity); Cu (Copper); NH4 (Inorganic ammonium, N form); NO3 (Inorganic nitrate, N form); Pb (Lead); TOC (Total organic carbon); POR (Porosity); TOT_Fe (Total iron); TOT_N (Total N); TOT_K (Total K); TOT_P (Total P); WSA (Water stable aggregates); Zn (Zinc); ACTE (Actinomycetes enumeration); ACTD (Actinomycetes diversity); MESE (Mesophilic bacteria enumeration); BACD (Bacteria diversity); MOYE (Molds and yeast enumeration); FUND (Fungal diversity); MYCA (Mycorrhizal fungi abundance); MYCD (Mycorrhizal fungi diversity); MYCR (Mycorrhizal colonization rate); EEGRSP (Easily extractable glomalin related proteins); TGRSP (Total glomalin related proteins).

* The values located on the bottom of cells correspond to the number of studies contributing to the pooled estimate.

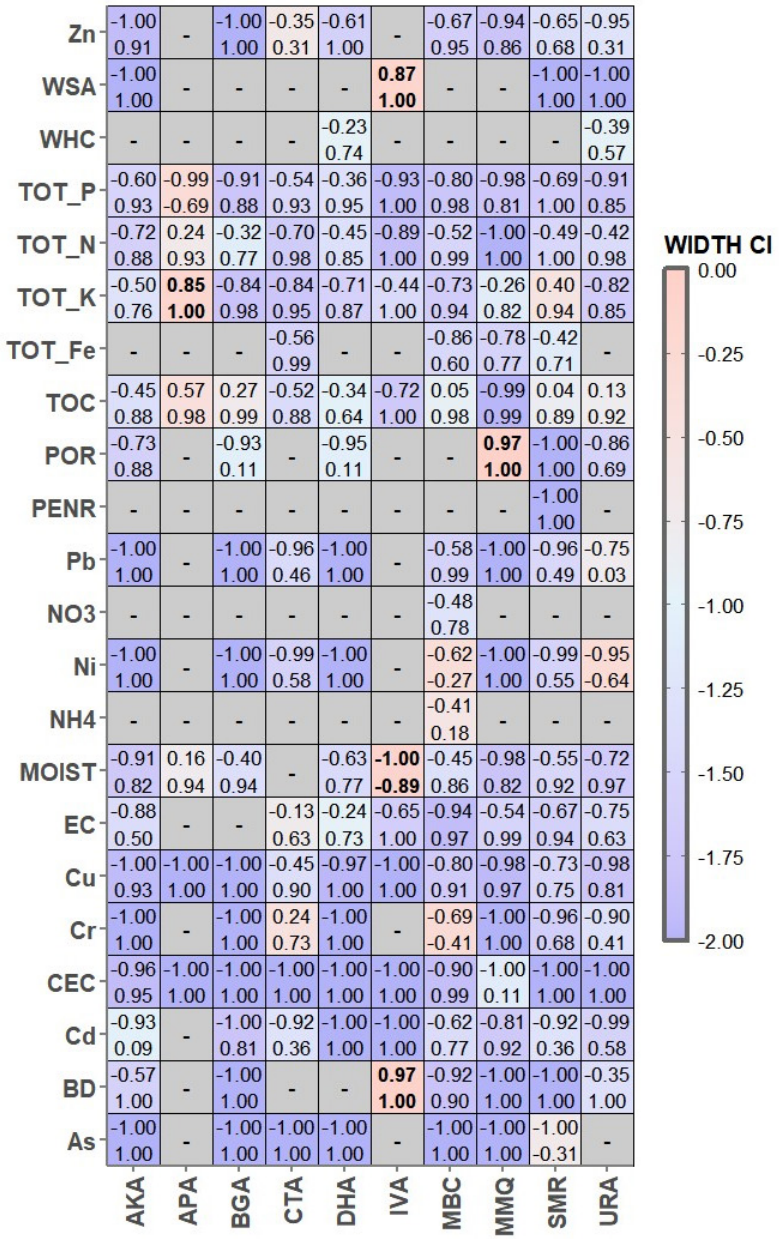
Figure 3. *Cross-study averages of the between-treatment Spearman's rank correlation (r_S2) for pairs of MBI which measures particular microbial phylogenies responses and soil properties.*



Note. APA (Acid phosphatase activity); AKA (Alkaline phosphatase activity); BGA (Beta-glucosidase activity); CTA (Catalase activity); DHA (Dehydrogenase activity); IVA (Invertase activity); URA (Urease activity); MBC (Microbial biomass carbon); SMR (Soil microbial respiration); MMQ (Microbial metabolic quotient); ACTE (Actinomycetes enumeration); ACTD (Actinomycetes diversity); MESE (Mesophilic bacteria enumeration); BACD (Bacteria diversity); MOYE (Molds and yeast enumeration); FUND (Fungal diversity); MYCA (Mycorrhizal fungi abundance); MYCD (Mycorrhizal fungi diversity); MYCR (Mycorrhizal colonization rate); EEGRSP (Easily extractable glomalin-related proteins); TGRSP (Total glomalin-related proteins).

* The values located on the bottom of cells correspond to the number of studies contributing to the pooled estimate.

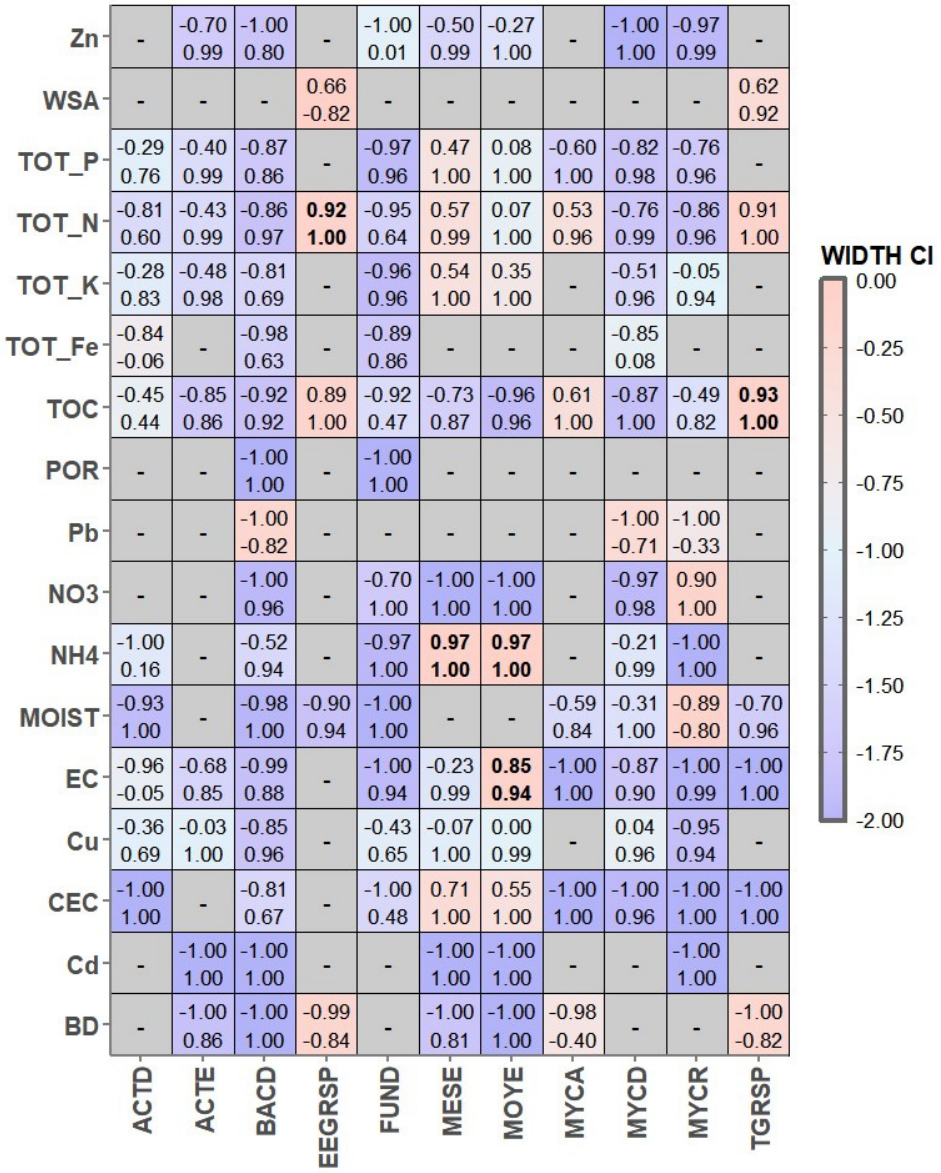
Figure 4. *Cross-study averages of the between-treatment Spearman's rank correlation (r_S2) for pairs of MBI related to AMF and several MBIs commonly implemented on soil quality assessments.*



Note. NH4 (Inorganic ammonium, N form); NO3 (Inorganic nitrate, N form); TOT_N (Total N); TOT_K (Total K); TOT_P (Total P); TOC (Total organic carbon); MOIST (Soil moisture); CEC (Cation exchange capacity); EC (Electrical conductivity); PENR (Penetration resistance); POR (Porosity); WHC (Water holding capacity); WSA (Water-stable aggregates); BD (Bulk density); As (Arsenic); Cd (Cadmium); Cr (Chromium); Cu (Copper); Ni (Nickel); Pb (Lead); Zn (Zinc); TOT_Fe (Total iron); APA (Acid phosphatase activity); AKA (Alkaline phosphatase activity); BGA (Beta-glucosidase activity); CTA (Catalase activity); DHA (Dehydrogenase activity); IVA (Invertase activity); URA (Urease activity); MBC (Microbial biomass carbon); SMR (Soil microbial respiration); MMQ (Microbial metabolic quotient).

* The values report the 2.5% (top of cell) and 97.5% (bottom of cell) confidence limits.

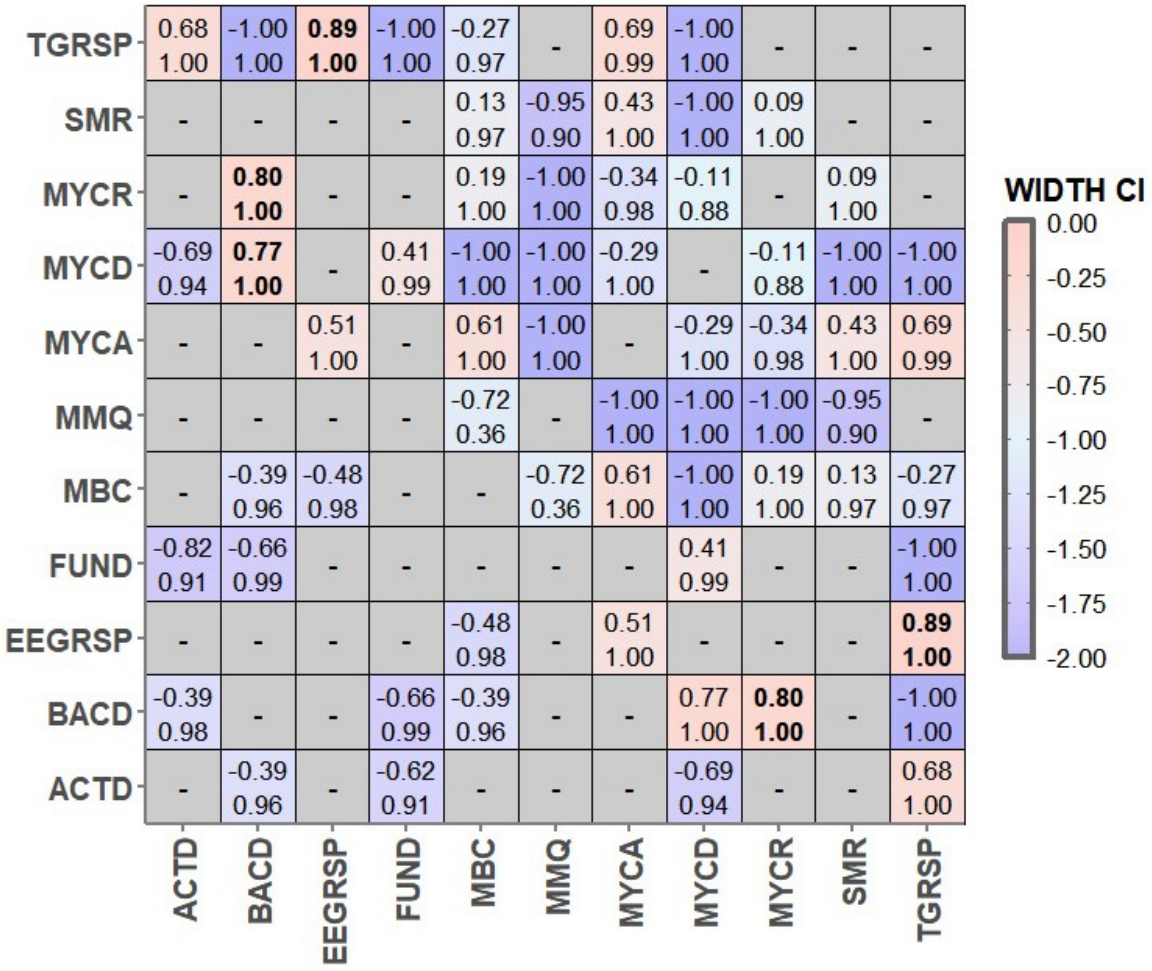
Figure 5. *Confidence Intervals (C.I 2) for the weighted average correlation coefficients (r_s2) for pairs of MBI which measures the activity of undifferentiated microbial consortia and soil properties.*



Note. BD (Bulk density); CEC (Cation exchange capacity); Cd (Cadmium); MOIST (Soil moisture); EC (Electrical conductivity); Cu (Copper); NH_4 (Inorganic ammonium, N form); NO_3 (Inorganic nitrate, N form); Pb (Lead); TOC (Total organic carbon); POR (Porosity); TOT_Fe (Total iron); TOT_N (Total N); TOT_K (Total K); TOT_P (Total P); WSA (Water stable aggregates); Zn (Zinc); ACTE (Actinomycetes enumeration); ACTD (Actinomycetes diversity); MESE (Mesophilic bacteria enumeration); BACD (Bacteria diversity); MOYE (Molds and yeast enumeration); FUND (Fungal diversity); MYCA (Mycorrhizal fungi abundance); MYCD (Mycorrhizal fungi diversity); MYCR (Mycorrhizal colonization rate); EEGRSP (Easily extractable glomalin related proteins); TGRSP (Total glomalin related proteins).

* The values report the 2.5% (top of cell) and 97.5% (bottom of cell) confidence limits.

Figure 6. *Confidence Intervals (C.I 2) for the weighted average correlation coefficients (r_s2) for pairs of MBI which measures particular microbial phylogenies responses and soil properties.*



Note. APA (Acid phosphatase activity); AKA (Alkaline phosphatase activity); BGA (Beta-glucosidase activity); CTA (Catalase activity); DHA (Dehydrogenase activity); IVA (Invertase activity); URA (Urease activity); MBC (Microbial biomass carbon); SMR (Soil microbial respiration); MMQ (Microbial metabolic quotient); ACTE (Actinomycetes enumeration); ACTD (Actinomycetes diversity); MESE (Mesophilic bacteria enumeration); BACD (Bacteria diversity); MOYE (Molds and yeast enumeration); FUND (Fungal diversity); MYCA (Mycorrhizal fungi abundance); MYCD (Mycorrhizal fungi diversity); MYCR (Mycorrhizal colonization rate); EEGRSP (Easily extractable glomalin related proteins); TGRSP (Total glomalin related proteins).

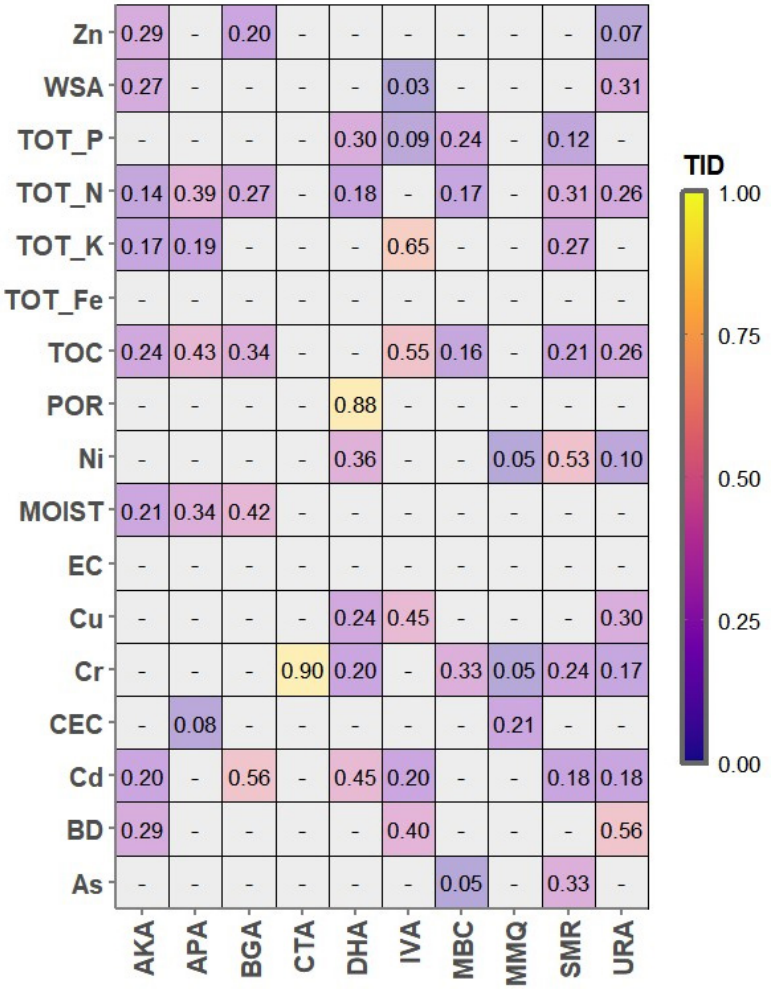
* The values report the 2.5% (top of cell) and 97.5% (bottom of cell) confidence limits.

Figure 7. *Confidence Intervals (CI2) for the weighted average correlation coefficient (r_s2) for pairs of AMF responses and several MBI commonly implemented on soil quality assessments.*

Total Influence Degree

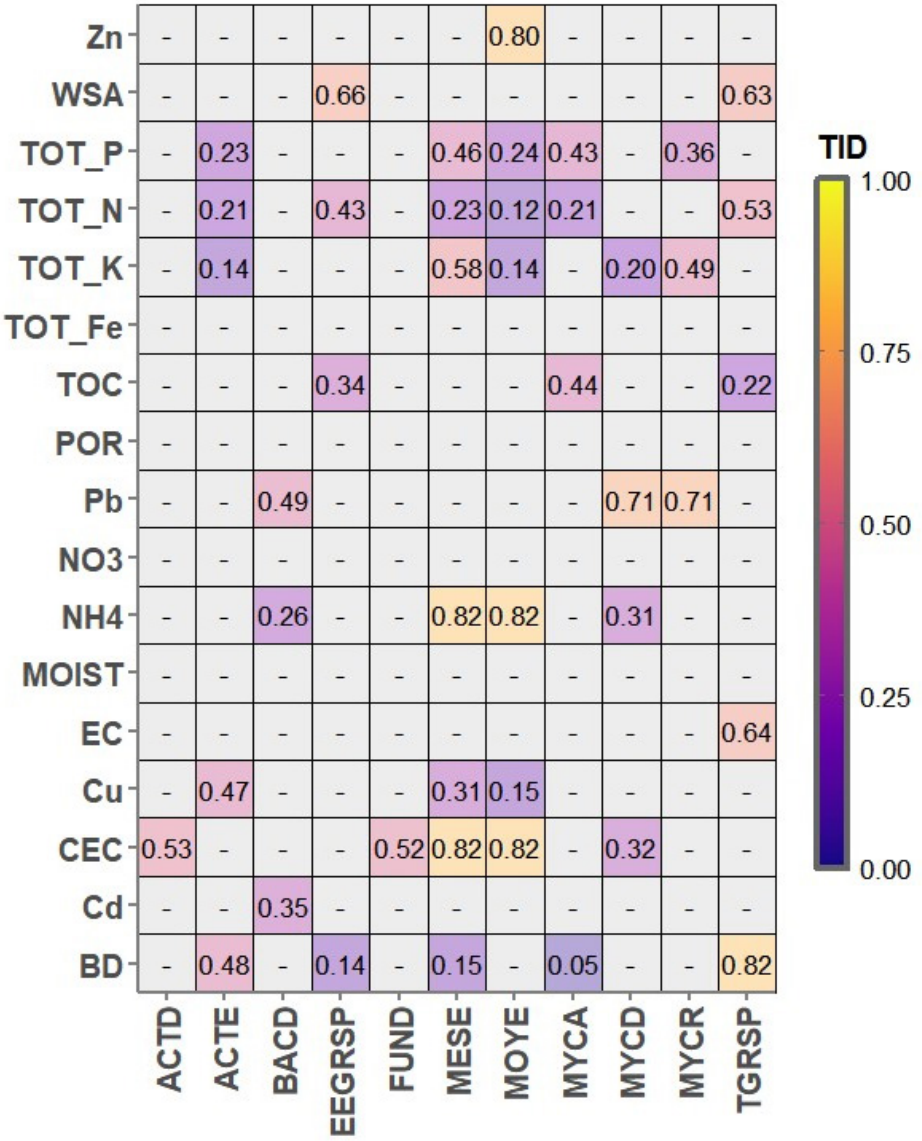
The topological analysis of the correlation-based network constructed from average correlation coefficients showed that chemical properties related to soil fertility (such as TOC, total N and K concentration) exerted strong influences on mycorrhizal abundance, mycorrhizal diversity, EEGRSP, and TGRSP (Figure 8 and 9). The total organic carbon has the strongest influence on mycorrhizal abundance (TID=0.44). This influence was driven by dependency effects on MBC (0.51) and SMR (0.67). Similarly, influences from K concentration on mycorrhizal colonization rate (TID=0.49) were attributed to their dependency

effects with mycorrhizal diversity (0.52) and soil microbial respiration (0.45). Total N has a high influence on EEGRSP and TGRSP (TID=0.53; 0.43) which were guided by dependency effects on MBC and mycorrhizal abundance. Furthermore, the highest influences were exerted by soil bulk density on TGRSP (TID=0.82) followed by Pb concentrations on mycorrhizal diversity (TID=0.71) and mycorrhizal colonization rate (TID=0.71). Likewise, TGRSP and EEGRSP were strongly influenced by water-stable aggregates (TID=0.63; 0.66), and TGRSP was affected largely by electrical conductivity (TID=0.64).



Note. TOT_N (Total N); TOT_K (Total K); TOT_P (Total P); TOC (Total organic carbon); MOISTs (Soil moisture); CEC (Cation exchange capacity); EC (Electrical conductivity); POR (Porosity); WSA (Water-stable aggregates); BD (Bulk density); As (Arsenic); Cd (Cadmium); Cr (Chromium); Cu (Copper); Ni (Nickel); Zn (Zinc); APA (Acid phosphatase activity); AKA (Alkaline phosphatase activity); BGA (Beta-glucosidase activity); CTA (Catalase activity); DHA (Dehydrogenase activity); IVA (Invertase activity); URA (Urease activity); MBC (Microbial biomass carbon); SMR (Soil microbial respiration); MMQ (Microbial metabolic quotient).

Figure 8. *Influence between nodes of soil properties and MBI which measures the activity of undifferentiated microbial consortia expressed as Total Degree Influence (TID).*



Note. BD (Bulk density); CEC (Cation exchange capacity); Cd (Cadmium); MOIST (Soil moisture); EC (Electrical conductivity); Cu (Copper); NH4 (Inorganic ammonium, N form); NO3 (Inorganic nitrate, N form); Pb (Lead); TOC (Total organic carbon); POR (Porosity); TOT_Fe (Total iron); TOT_N (Total N); TOT_K (Total K); TOT_P (Total P); WSA (Water stable aggregates); Zn (Zinc); ACTE (Actinomycetes enumeration); ACTD (Actinomycetes diversity); MESE (Mesophilic bacteria enumeration); BACD (Bacteria diversity); MOYE (Molds and yeast enumeration); FUND (Fungal diversity); MYCA (Mycorrhizal fungi abundance); MYCD (Mycorrhizal fungi diversity); MYCR (Mycorrhizal colonization rate); EEGRSP (Easily extractable glomalin related proteins); TGRSP (Total glomalin related proteins).

Figure 9. *Influence between nodes of soil properties and MBI which measures particular microbial phylogenies responses expressed as Total Degree Influence (TID).*

DISCUSSION

After weighting every observation in the cross-biome compilation, many indicators showed strong correlations, although their confidence intervals remained extremely wide. However, studies at large spatial scales that incorporate variables of soil quality are characterized by wide confidence intervals around the cross-study average of Spearman's rank correlation (German *et al.,* 2017). This pattern arises because the width of confidence intervals depends on study variance and sampling effort. Consequently, greater between-study variance produces wider intervals (Field, 2005; Welz *et al.,* 2022). For instance, mycorrhizal diversity response varies across studies under different regimes of NH_4 availability because AMF taxa may differ in their uptake of ammonium (Ma *et al.,* 2021; Yoshida & Allen, 2001). Likewise, previous large-scale studies have found inconsistent driver effects on soil microbial properties (e.g., MBC, SMR, abundance), which add considerable variance to estimates (Smith *et al.,* 2021).

The estimated correlations suggest microbial feedbacks to variations in soil features. These findings indicate that interrelations among MBI may be key to interpreting microbial co-regulation following changes in soil properties (Bai *et al.,* 2021; Deltedesco *et al.,* 2020). For example, the positive correlation observed between MBC and SMR show the indirect effect of soil temperature. In this scenario, higher temperatures increase microbial biomass and, consequently, drive larger CO_2 fluxes from the soil (Iqbal *et al.,* 2010). Similarly, correlations between MBC and bacterial diversity have been described as components of microbial networks that influence soil carbon mineralization. First, these interactions modify decomposition pathways and rates, thereby affecting mineralization. Second, they are themselves shaped by the availability and turnover of organic carbon (Wang, Liu, *et al.,* 2018; Yang *et al.,* 2018; Zhang *et al.,* 2020).

The DEPNA indicated that total organic carbon, and P and K concentrations exerted considerable influence on AMF. Specifically, these soil nutrients were strongly associated with AMF abundance, mycorrhizal diversity, and colonization rate. Consistent with these observations, multiple studies have shown that nutrient additions and higher soil fertility strongly affect AMF. For example, in fertilization trials, added P and N change AMF biomass and community composition and often decrease root colonization when inorganic P becomes readily available (Camenzind *et al.,* 2016; Stevens *et al.,* 2020).

The observed influences of soil nutrients on AMF may also be explained by partial correlations with SMR and MBC. Several studies report synergistic interactions between AMF and the bacterial communities associated with their spores and extraradical mycelium. In fact, these bacteria perform plant growth promoting functions, including N fixation, P solubilization and the production of phytohormones. For that reason, bacterial activities complement nutrient uptake mediated by AMF and together they improve plant growth and fitness (Giovannini *et al.,* 2020; Zhang *et al.,* 2024). Moreover, evidence indicates that intensive management and chemical fertilization alter cumulative soil respiration. Such alterations are associated with increased AMF abundance and concurrent shifts in bacterial communities. Combined changes in fungal and bacterial abundance can modify decomposition rates and microbial metabolic activity, thereby increasing soil CO_2 fluxes (Jin *et al.,* 2024; Kakouridis *et al.,* 2024). Likewise,

partial correlations estimated among mycorrhizal diversity, colonization rate, and AMF spore density with MBC and total organic carbon suggest that AMF communities may be global contributors to soil carbon dynamics (Kumar *et al.,* 2018; Zhang *et al.,* 2020).

The TID calculated for Pb concentrations showed a strong effect on AMF diversity and mycorrhizal colonization rate. Such a relationship may be linked to negative effects of Pb on soil microbiota (Sun *et al.,* 2023). The Pb increments in soils reduces AMF diversity and their abundances by disrupting key life-cycle stages. High Pb concentrations can delay or prevent spore germination, hinder pre-symbiotic hyphal growth, constrain extraradical mycelium expansion, and suppress sporulation (Jia *et al.,* 2024; Lv *et al.,* 2023). The Pb TID was estimated using partial correlations that incorporated bacterial diversity. Thus, the high TID likely indicates substantial alterations in the soil bacterial community under heavy-metal stress after AMF inoculation and may reinforce the signal attributed to mycorrhizal responses (Cao *et al.,* 2020). AMF presence can increase bacterial diversity because fungal spore walls and extraradical mycelium release fungal substances that modify beneficially the soil chemical composition and pH to bacterial community development (Kakouridis *et al.,* 2024; Meglouli *et al.,* 2018).

Similarly, partial correlations indicated strong associations of bulk density and total organic carbon with mycorrhizal abundance, EEGRSP, and TGRSP. The association of GRSP with bulk density is mechanistically plausible because of the limitations in air flow that an increase in soil bulk density implies (Cai *et al.,* 2023; Pulido *et al.,* 2024). Besides, a higher soil density increases soil electrical conductivity and promotes the dispersion of protein-disrupting monovalent cations (e.g., Na^+), thereby constraining GRSP (Wang *et al.,* 2015; Zhang *et al.,* 2017). Furthermore, increases in bulk density influence other drivers of GRSP release, including mycorrhizal abundance and organic carbon pools (Bonfim *et al.,* 2013; Nautiyal *et al.,* 2019; Šarapatka *et al.,* 2019).

Although electrical conductivity (EC) is usually weakly associated with GRSP (Zhang *et al.,* 2017), a negative mean correlation with a substantial EC effect on GRSP was found. In contrast, previous studies, for example, report a non-monotonic GRSP response to salinity, which is closely correlated with EC. In particular, GRSP increases to a threshold but then declines as salinity rises. This decline can be caused by reduced AMF abundance at high NaCl concentrations (Hammer & Rillig, 2011; Krishnamoorthy *et al.,* 2014).

Similarly, EC influenced TGRSP through its partial association with actinomycete diversity. An elevated EC, together with consequent pH shifts, suppresses microbial enzyme activity and reduces actinomycete diversity (Heng *et al.,* 2022; Kumar *et al.,* 2021). Consequently, biochemical processes mediated by actinomycetes, particularly C and N aggregation, decrease, and plant growth declines (Buyer *et al.,* 2011; Grover *et al.,* 2016). As a result, AMF colonization declines as well as its GRSP production (Ao *et al.,* 2025; Chen *et al.,* 2023). Other authors have described that vegetal growth depletion not only reduces the AMF spore densities and root colonization but also diminishes the AMF hyphae distributed in rhizosphere soil. Therefore, the AMF extrametrical hyphal growth was negatively impacted, leading to reduced GRSP secretion (Gong *et al.,* 2022).

Finally, a strong association was observed between water-stable aggregates with both EEGRSP and TGRSP. Soil aggregation arises from interactions among carbohydrates, microorganisms, and their secretions. In this context, GRSP

fractions act as major drivers of aggregate formation and stability (Zhu *et al.,* 2019). GRSP are hydrophobic, heat resistant, and insoluble binding agents. They promote soil particle adhesion and increase the abundance and stability of water stable aggregates. In addition, a positive association between GRSP content and water stable aggregates can indicate the presence of active AMF hyphal networks. These networks entangle soil particles, exude GRSP, and cross-link minerals with organic matter. As a result, microaggregates coalesce into much more stable aggregates (Liu *et al.,* 2021; Wilkes *et al.,* 2021; Yang *et al.,* 2022).

CONCLUSIONS

The study identifies arbuscular mycorrhizal fungi (AMF) and glomalin-related soil proteins (GRSP) as robust microbial indicators of soil condition, capable of reflecting both fertility improvements and stress impacts. Meta-analytic integration and dependency network analysis show that soil organic carbon (SOC), nitrogen (N), and potassium (K) strongly enhance AMF abundance, diversity, and GRSP production. In contrast, bulk density, electrical conductivity (EC), and increasing lead (Pb) concentrations exert significant negative effects. These results confirm the dual role of AMF and GRSP as both mediators of beneficial soil processes and sentinels of soil degradation.

AMF abundance is particularly suitable for monitoring SOC and phosphorus (P) availability, while colonization rates and AMF diversity are highly sensitive to heavy-metal stress, especially Pb. GRSP emerges as a strong indicator of soil structural stability, compaction, and salinity. Together, these microbial attributes form a cost-effective, biologically grounded toolkit for assessing soil quality across agricultural, mining, and restoration systems.

A major contribution of the study is the identification of microbial biomass carbon, soil microbial respiration, and overall microbial diversity as mediators transmitting soil property effects to AMF-related indicators. Fertility signals often operate indirectly through these microbial nodes, whereas stressors like Pb and compaction may act directly or via selective microbial shifts. Although strong correlations were detected, variability across land uses and wide confidence intervals caution against interpreting single microbial metrics in isolation. Methodologically, combining meta-analytic rank correlations with conditional dependency analysis offers a promising framework for improving causal inference and developing composite microbial indicators for soil monitoring and restoration.

ACKNOWLEDGMENTS

We would like to express our sincere gratitude to COLCIENCIAS and their program Doctorados Nacionales 727 for providing the financial support that made this study possible.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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