

RESEARCH ARTICLE

The potential of arbuscular mycorrhizal fungi to improve soil organic carbon agricultural ecosystems: A meta-analytical approach

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Abstract

1. Increasing soil organic carbon (SOC) in agroecosystems is a key objective for enhancing agricultural sustainability and mitigating climate change. Arbuscular mycorrhizal fungi (AMF) can increase yield and provide several other ecosystem services. Still, studies conducted in agricultural soils have shown that their effects on SOC can be either positive, neutral or negative. In this study, we conducted a quantitative review of the literature to evaluate the role of AMF in influencing SOC across various crop species and conditions.
2. Through a systematic search of publications, we compiled a dataset comprising 62 trials from 19 studies including field and pot experiments that directly manipulated the mycorrhizal status of plants. We conducted a meta-analysis to quantitatively evaluate the role of AMF on SOC across several crop species and conditions.
3. We found an overall positive effect of AMF on SOC, with an average increase of 21.5%. However, this positive effect was statistically significant only in pot experiments whereas in field experiments, the effect was mainly modulated by texture and organic matter content. The effect of AMF on SOC did not vary with crop species' functional type, AMF inoculation sources (single or mixed AMF species) or other soil variables considered.
4. Our results highlight the significant potential for AMF-mediated mechanisms to promote SOC accumulation in agricultural soils, although this effect is context-dependent. However, future research with different approaches and scales is needed to evaluate the impact of AMF on SOC dynamics in agricultural systems and elucidate the mechanisms behind their contribution to SOC accrual.

KEYWORDS

agroecosystems, AMF, mineral-associated organic carbon, particulate organic carbon, SOC, soil fertility, soil organic matter, symbiotic association

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1 | INTRODUCTION

Arbuscular mycorrhizal fungi (AMF), belonging to the phylum Glomeromycota, have existed for at least 460 million years and form mutualistic associations with nearly 80% of plant families species, including many major crop species (Brundrett & Tedersoo, 2018; Smith & Smith, 2011). These fungi can associate with plant roots facilitating nutrient exchange (Smith & Read, 2008). AMF form intricate networks of extraradical mycelium that extend into the bioactive zones of plants surrounding roots, scavenging for essential nutrients such as phosphorus, nitrogen, sulphur and trace elements. In return, these nutrients are transported to the plant roots in exchange for photosynthetically derived carbohydrates and lipids (Jiang et al., 2017; Luginbuehl et al., 2017; Smith & Read, 2008).

Globally, the soil carbon pool is estimated to contain approximately 1500 Gt of carbon (C) in the top meter of soil, surpassing the amount of C stored in the atmosphere (~800 Gt) and in all terrestrial vegetation combined (~450–650 Gt) (Batjes, 1996; Lal, 2004; Trumbore & Czimczik, 2008). Despite the critical role of AMF in transporting C from plants to soil, a quantitative understanding of the contribution of mycorrhizal associations to the global C cycle remains incomplete. Recent studies have reviewed the significance of mycorrhizal fungi in soils, emphasizing their crucial role in soil organic carbon (SOC) dynamics and storage (Frey, 2019; Hawkins et al., 2023; Parihar et al., 2020; Wei et al., 2019; Wu et al., 2024; Zhu & Miller, 2003). Hawkins et al. (2023) estimated the relative contribution of AMF to the global soil C pool, revealing that 6.2% of a host plant's net primary production (NPP) was directed to fungal mycelium globally, representing 1.07 Gt C per year.

AMF influence SOC dynamics through various mechanisms, including its formation, reprocessing, reorganization and stabilization (Fall et al., 2022; Frey, 2019; Hawkins et al., 2023; Parihar et al., 2020; Wei et al., 2019; Wu et al., 2024; Zhu & Miller, 2003). AMF can enhance total plant biomass through their active association with host plants (Zhang et al., 2019); however, the benefits of AMF symbiosis are context-dependent, and in certain cases, it may lead to reduced biomass or yield (Hoeksema et al., 2010). An expected increase in biomass results in a corresponding rise in decomposing plant litter and soil C inputs (Karlen & Cambardella, 2020). AMF also receive plant-derived C from an active symbiosis with the host plant, used to build and support the mycelial network (Smith & Read, 2008). This network channels plant-fixed C into the soil matrix. As mycorrhizal networks expand, they move C from the rhizosphere to areas with lower respiratory activity (Lehmann et al., 2017). The fungi produce multiple organic compounds, including exudates, small molecules such as sugars, monosaccharides, low-molecular-weight organic acids and decaying fungal hyphae, contributing to an AMF-associated 'chemodiversity' in the soil. These compounds, along with a specific hyphosphere microbial community induced by AMF activities, contribute to the reprocessing of soil organic matter (SOM), affecting its chemical persistence (Hooker et al., 2007; Toljander et al., 2007; Wu et al., 2024). Low-molecular-weight organic acids containing C and N are utilized and immobilized by other soil microbes, ultimately contributing to the formation of the most stable SOC pool—the mineral-associated organic C

(MAOC). Also, the decomposition of increased amounts of above- and belowground plant host residues can enhance the particulate organic C (POC) in the SOC pool (Klink et al., 2022). Simultaneously, the fine filamentous hyphae that forage for nutrients, also attach to soil particles through intertwining and close-binding mechanisms, as well as through the production of hyphal-binding exudates. These processes help create, stabilize and reorganize soil aggregates that protect SOM from decomposition (Godbold et al., 2006; Klink et al., 2022; Miller & Jastrow, 2000; Morris et al., 2019; Rillig et al., 2015; Rillig & Mummey, 2006; Tisdall & Oades, 1982).

Considering the complex SOC-related mechanisms mediated by AMF at different scales, the overall effect on SOC at the ecosystem level remains unclear. Some studies have reported that AMF can enhance C storage in soils (Godbold et al., 2006; Jeewani et al., 2021; Zhou et al., 2020), while others have indicated that AMF may increase C losses through mineralization (Cheng et al., 2012; Paterson et al., 2016). One potential mechanism underlying this effect involves the stimulation of SOM decomposition by saprotrophs, which is facilitated by the exudation of plant-derived labile C, thereby relieving their C limitation, a phenomenon known as 'priming effect' (Cheng et al., 2012; Chowdhury et al., 2022; Herman et al., 2012; Nottingham et al., 2013; Paterson et al., 2016). However, these SOC-related processes are highly context-dependent (Choreño-Parra & Treseder, 2024).

Particularly in agricultural systems, the intensification of soil management has historically reduced SOC, with direct consequences on crop yield (Oldfield et al., 2019; Sanderman et al., 2017). For instance, in the Corn Belt Region of the Midwestern United States, Thaler et al. (2021) estimated that 35% of the cultivated area lost the A horizon, which is rich in organic C, resulting in a 6% decrease in crop yields and causing annual economic losses of \$2.8 billion. In this context, rebuilding SOC through sustainable practices is considered one of the primary contemporary challenges. AMF-based sustainable practices, therefore, hold promise for improving soil fertility, reducing C emissions and enhancing stable crop yields while reducing dependence on external inputs such as mineral fertilizers and irrigation—critical components of sustainable intensification (Fageria, 2012; Foley et al., 2011).

The potential role of AMF as a complementary management strategy to increase SOC stocks has gained increasing attention (George & Ray, 2023; O'Callaghan et al., 2022; Verbruggen et al., 2012). However, the significance of AMF in SOC dynamics of agroecosystems can be obscured by common management practices (e.g. tillage, fertilization, non-host crops, pesticides) that negatively impact AMF, thereby diminishing their benefits (Bowles et al., 2017; de Graaff et al., 2019; Jeffries et al., 2003; Ryan & Graham, 2002). Moreover, selective breeding for fertilizer responsiveness, fungal resistance and intensive cultivation techniques often fail to promote the symbiosis establishment and colonization of plant roots by mycorrhizal fungi (Helgason et al., 1998).

Soil-related variables such as textural composition and chemistry could affect the overall effect of AMF on SOC dynamics and storage. For example, the AMF effect is expected to be more pronounced in coarsely textured and nutrient-poor soils, where any

change produced by AMF in SOC could have a great and profound effect by increasing the activity of C-limited microorganisms (Six et al., 2004). A recent meta-analysis including different crops and non-crop species found that AMF inoculation was more effective in soils with lower initial SOM levels (Tao & Liu, 2024). Several studies demonstrated that AM fungal colonization can be strongly affected by pH with a preference of AMF for a near neutral or alkaline soil pH, which is reflected in the development of a more extensive extraradical network (Helgason & Fitter, 2009; Marschner & Timonen, 2005; Tao & Liu, 2024), directly correlated with an increase in SOC accrual.

The functional identity of the host plant crop could also influence the effect of AMF on soil C since several root traits vary significantly among different functional plant groups such as grasses, shrubs or trees (e.g. root architecture, number of fine roots, root length and rooting depth) (Oades, 1993). Plant species with C_4 photosynthetic pathway generally have higher photosynthesis efficiency and are more responsive to mycorrhizal inoculation compared to C_3 plants, potentially due to their higher nutrient demands (Hoeksema et al., 2010; Tao & Liu, 2024).

The ultimate outcome of AMF on SOC may also depend on the experimental setting. Several studies have demonstrated that AMF exhibit different effects on plant performance and soil dynamics in pot versus field experiments, with more pronounced effects observed in the former (Delavaux et al., 2017; Leifheit et al., 2014; Zhang et al., 2019). All these suggest that while pot experiments provide valuable insights into the mechanisms and potential benefits of AMF inoculation under controlled conditions, field experiments are essential for understanding the practical implications and effectiveness of AMF in natural and agricultural ecosystems, where biotic and abiotic conditions interact in a complex manner. Additionally, it has been proposed that AMF species richness in the inoculum positively affects plant host growth rates (Guo et al., 2022; Hoeksema et al., 2010), thereby increasing the amount of decomposing plant material and so, the accrual of SOC. The more positive response to multiple AM fungal species in the inoculum could be due to complementary within the different fungal species in the benefits provided to the host plants (Hart & Reader, 2002; Maherali & Klironomos, 2007), or it may result from an increased likelihood of beneficial fungi being present in a mixed inoculum (Vogelsang et al., 2006).

Although it is assumed that AMF have the potential to increase SOC, no quantitative reviews have specifically assessed their overall effects in agricultural ecosystems. In this study, we synthesized available information on the effect of AM fungi on SOC in agroecosystems. We aimed to determine whether this effect is widespread and if so, to identify any environmental conditions that mediate it. We compiled data from 19 published studies containing 62 trials to test the effect of the presence of AM fungi on SOC. By performing a meta-analysis, we tested the hypothesis that AM fungi alter SOC and its fractions on agroecosystems and that this effect is context-dependent. Specifically, we expect that AM fungi would have a greater effect on SOC in nutrient-poor, coarsely textured soils with neutral or alkaline pH. This effect is expected to be more pronounced in pot experiments compared to field studies and boosted

by diverse inoculums. Differences in the functional characteristics of host plants will also influence the impact of AMF on SOC, with stronger effects usually observed in trees and C_4 grasses as compared to C_3 grasses.

2 | MATERIALS AND METHODS

2.1 | Literature search

This meta-analysis followed the PRISMA guidelines (Moher et al., 2009) (Figure S1). We focused on worldwide agriculture ecosystems including woody and non-woody dominant crop species. We searched on Scopus (last accessed in July 2021) to collect published articles according to our search criteria. Our search terms were: 'TITLE-ABS-KEY ("soil organic matter" OR "soil organic carbon" OR "particulate organic carbon" OR "mineral associated organic carbon" OR "particulate organic matter" OR "mineral associated organic matter" OR pom OR poc OR maom OR maoc) AND TITLE-ABS-KEY ("arbuscular mycorrh*" OR glomal* OR *grsp OR *brsp OR hma) AND TITLE-ABS-KEY (crop* OR *cultur* OR farm* OR cultiva* OR agro*) AND TITLE-ABS-KEY (pot OR greenhouse OR experiment* OR inoculat*)'. We found 118 articles that matched these criteria from 1993 to 2021, which were screened according to the selection criteria described below to be included in our compilation. The articles had to be original research articles performed in agricultural ecosystems; report SOC concentrations or stocks, POC and/or MAOC, and involve both an AMF inoculation treatment and a corresponding control without inoculation. We defined the AMF treatment (AMF+) and the control treatment (AMF-) including studies where the application of an AM fungal inoculum represented the AMF+ treatment while the treatment without the application of the inoculum was the corresponding control (AMF-). This type of intervention allows the highest level of attribution of causality of effects, particularly in the case of pot experiments. For field experiments, control treatments represent the local soil without inoculation, with an expected lower AMF abundance in comparison with the inoculated treatments. Inoculation treatments under pot experiments included inoculation of seeds or soil with AMF inoculum previously propagated under sterilized conditions, usually including spores, root fragments and/or mycelia. For pot experiments, depth was always considered as surface soil (<0–15 cm depth). In field experiments; however, we selected variables sampled <0–30 cm of soil, or soil samples from the rhizospheric soil (i.e. adhered to the roots). Since both treatments (AMF+ and AMF-) were performed on the same soil (i.e. same bulk density), both terms SOC stocks and SOC concentration could be used indistinctly given we calculated the net change, not the net value. To evaluate if AMF inoculation treatments increased the abundance of mycorrhizal mycelium relative to control treatments, we also registered root colonization values reported in the studies and performed an additional meta-analysis for this variable. A list of data sources used in the study is provided in the Data Sources section and Table S1.

For studies that presented different crop species or AMF strains, those treatments were included as different trials. In studies with repeated measurements over time, we only considered the response variables from the final harvest. Although our search terms were focused on agricultural ecosystems, we included some species that although they may not be necessarily considered crop species, have been domesticated for other purposes such as agroforestry (e.g. *Prunus discadenia*, *Prunus dictyneura* and *Xanthoceras sorbifolium*). We decided to keep this species to increase the analytical power of field experiments although their inclusion did not significantly change the final result of the meta-analytical model. After screening and filtering across a global database, a total of 19 studies were selected, including 62 comparisons (trials) for subsequent analyses (Table S1; Conti et al., 2021). From these, we extracted average values with their corresponding variance and sample size (N). Together with this information, auxiliary variables covering plants, microorganisms, soil properties and experiment-related factors of the studies were also registered. When data were only graphically available, we used free digitizing software for data extraction (Tummers, 2006).

2.2 | Effect size calculations

We performed our analysis using the natural log response ratio (RR) as effect size in order to evaluate the AM-mediated effect on SOC (RR_{SOC}) considering the mean and variance of the AMF+ and AMF- treatments according to the equation form

$$RR_{SOC} = \ln(\bar{X}_{AMF+} / \bar{X}_{AMF-})$$

with $\bar{X}_{AMF+}$ denoting the mean of the soil variable in the AMF+ treatment and $\bar{X}_{AMF-}$ indicating the mean of the soil variable in the corresponding control treatment (AMF-), according to Lajeunesse (2011).

The associated variance (v_{RR}) was calculated as proposed by Hedges et al. (1999).

$$v_{RR} = \frac{(SD_{AMF+}^2)}{n_{AMF+} \times \bar{X}_{AMF+}} + \frac{(SD_{AMF-}^2)}{n_{AMF-} \times \bar{X}_{AMF-}},$$

where SD and n are the standard deviation and sample size of the AMF+ and AMF- mean treatments, respectively. Standard errors (SE) were converted to SD following the function:

$$SD = SE \times \sqrt{N}.$$

We calculated the effect sizes in R v.4.0.2 (R Core Team, 2024) using the 'metafor' package (Viechtbauer, 2010).

2.3 | Moderators

In addition to the information about soil and AMF-related variables, we gathered information on six factors that could potentially affect

soil processes and included them as categorical and continuous explanatory variables. For categorical variables, and to maximize the statistical power of our tests, the number of levels of each categorical moderator was reduced to a minimum by merging information on related categories. We considered categorical moderators' levels that present a minimum number of trials to be included in the different subgroups analysis ($N \geq 3$). For continuous explanatory variables, we assessed possible causes of heterogeneity among study results by performing a meta-regression. A detailed description of the moderators included in the analysis is explained below.

2.3.1 | Experimental variables

The type of study included two levels: *pot experiments* and *field experiments*. *Pot experiments* represent experiments carried out under controlled conditions, while *field experiments* include inoculation management applied in the field. Pot experiments included sterilized seeds and soil, excepting one study where soil sterilization was not explicitly mentioned (Quintero-Ramos et al., 1993). Most of the studies conducted under controlled conditions used soil collected from agricultural systems as substrate, and only three included a mix of soil with sand and organic substrate.

Non-AMF treatments usually included the addition of a filtrate of the inoculum for similar microflora except the mycorrhizal fungus. Although pot experiments are useful to control confounded effects and assign causality to the manipulated variables (here, the AMF inoculation), any conclusions about the benefits of AMF require verification under real agricultural conditions across a range of environments and management practices (Ryan & Graham, 2018). The *experiment duration (days)* was also obtained from each study and considered as a continuous moderator variable.

2.3.2 | Soil-related variables

From each study, we extracted data regarding soil texture, soil pH and initial SOM content as continuous variables. When any of these data were not reported, we searched these values on a global grid-based soil information database (soilgrids.org) (Batjes et al., 2020) using the georeferenced location.

2.3.3 | Main crop-related variables

The dominant plant crop was initially categorized as C_4 grasses, C_3 grasses, herbs and woody plants according to differences in functional types and their photosynthetic metabolism. However, after filtering processes, we found that all the C_3 plants were *Triticum aestivum* and all the C_4 plants were *Zea mays*. Therefore, for full transparency, the category for ' C_3 ' was replaced with *Triticum aestivum* and the category for ' C_4 ' was replaced with *Zea mays*.

2.3.4 | AMF-related variables

We considered separately fungal inoculum obtained from a *single* AMF species or *mixed* AMF species. Reviewed studies usually used greenhouse-produced inoculum. A mix of different single-species inoculum was used to analyse the effect of mixed-species inoculum.

2.4 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Crops-soils systems colonized with AMF	Soils analysed under different cropland systems (studies)	62 trials from 19 studies

2.5 | Statistical analysis

We applied a random mixed effect meta-analytical model to deal with the non-independence of multiple within-study observations (Koricheva et al., 2013), using the `rma.mv` function from the 'metafor' package (Viechtbauer, 2010) in R statistical software (R Core Team, 2024). A model was first run without any moderator variables to assess the overall heterogeneity, testing each considered moderator one by one as a sole covariate since not all moderator categories were represented in other moderators' levels. Since POC and

MAOC fractions had only two trials from only one study, the meta-analytical model was applied only to SOC, testing the effect of the considered moderators. Moderators were considered statistically significant if the significance level of the random probability value of the Q statistics was $p < 0.05$.

Finally, to verify the presence of publication bias we used (i) funnel plots and radial plots (Philibert et al., 2012) together with the Egger's Regression Test (Egger et al., 1997). We also used the 'trim and fill' procedure (Duval & Tweedie, 2000) to estimate if funnel asymmetry is due to publication bias (Figure S4). All models were fitted using restricted maximum likelihood estimation. To facilitate the interpretation, mean log response ratios and upper and lower bounds of 95% confidence intervals around the mean were back-transformed and expressed as a per cent change relative to the control.

3 | RESULTS

Our quantitative synthesis showed an overall positive and significant effect of AMF on SOC of 21.5% (CI = 10.4%–33.7%) (Figure 1). None of the evaluated studies reported statistically significant negative results of AMF on SOC, but the effects of AMF on SOC were higher in pot studies than under field conditions, with overall effects under field conditions remaining not significant ($p = 0.1651$). Within the trials with positive effects, pot experiments showed increases in SOC of around 40%. For field experiments, average increases were around 11%, with maximum values around 27%. We found only one study (two reported trials per variable) including POM and MAOM as response variables after inoculating with AMF, showing that AMF increases POC but decreases MAOC (Figure S3).

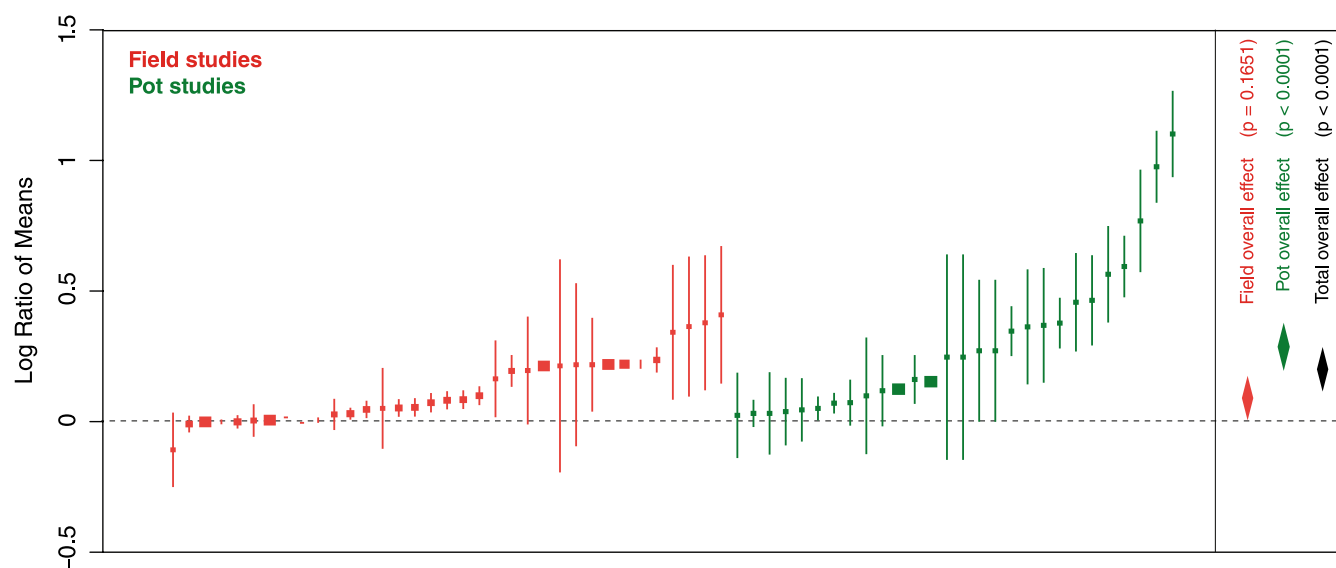


FIGURE 1 The effect of AMF on SOC across field and pot studies. Effect sizes (mean and 95% confidence interval) derived from individual trials ordered from the lowest to the highest, comparing SOC in AMF inoculation treatments (AMF+) relative to control without inoculation (AMF-). Log ratio of means = $\ln(\text{AMF+}/\text{AMF-})$. Effect sizes < 0 represent negative effects while effect sizes > 0 represent positive effects. Red points represent effect sizes from field trials and green points effect sizes from pot trials, no negative effect sizes were registered. The red diamond represents the average field effect size while the green diamond represents the average pot effect size.

When considering different moderators in the analysis of the effects of AMF on SOC, soil-related variables showed different results for pot and field studies (Figure 2). Only soil clay content appeared as a significant moderator when considering the overall dataset ($p=0.0270$), as also in the pot and field datasets separately ($p=0.0242$ and $p<0.0001$, respectively), showing a reduction in the effect size with higher clay content (Figure 2a). Soil sand content and initial SOM content appeared as significant moderators only for field studies ($p<0.0001$) (Figure 2b,c). A higher amount of sand content increased the effect size of AMF on SOC, while the opposite was true when considering the initial SOM (increasing initial SOM reduces the effect of AMF on SOC). Silt content and pH did not show significant effects as continuous moderator variables. On the other side, the experimental duration appeared as a significant moderator only when considering the overall dataset ($p=0.0176$), showing a lower effect of AMF on SOC under long-term experiments (Figure 2d).

Neither the AMF inoculum source (single or mixed species) nor the functional type categorization of the host crop species, as considered in the present study, seemed to be important factors explaining the effect of AMF on SOC (Figure 3). Finally, AMF inoculation showed a trend toward higher increases in SOC when associated with woody crop species, however, differences between host functional types were not statistically significant ($p=0.3443$) (Figure 3). The statistical descriptors for models including the complete dataset are detailed in Table S2. In addition, when performing a meta-analysis to evaluate if AMF inoculation treatments increased the abundance of mycorrhizal mycelium relative to control treatments, we found a clear significant positive effect on root colonization in inoculation treatment compared to control ones ($p<0.0001$) (Figure S2). In Figure S4 (Supplementary Material) we showed the result for possible publication bias using statistical and graphical tools.

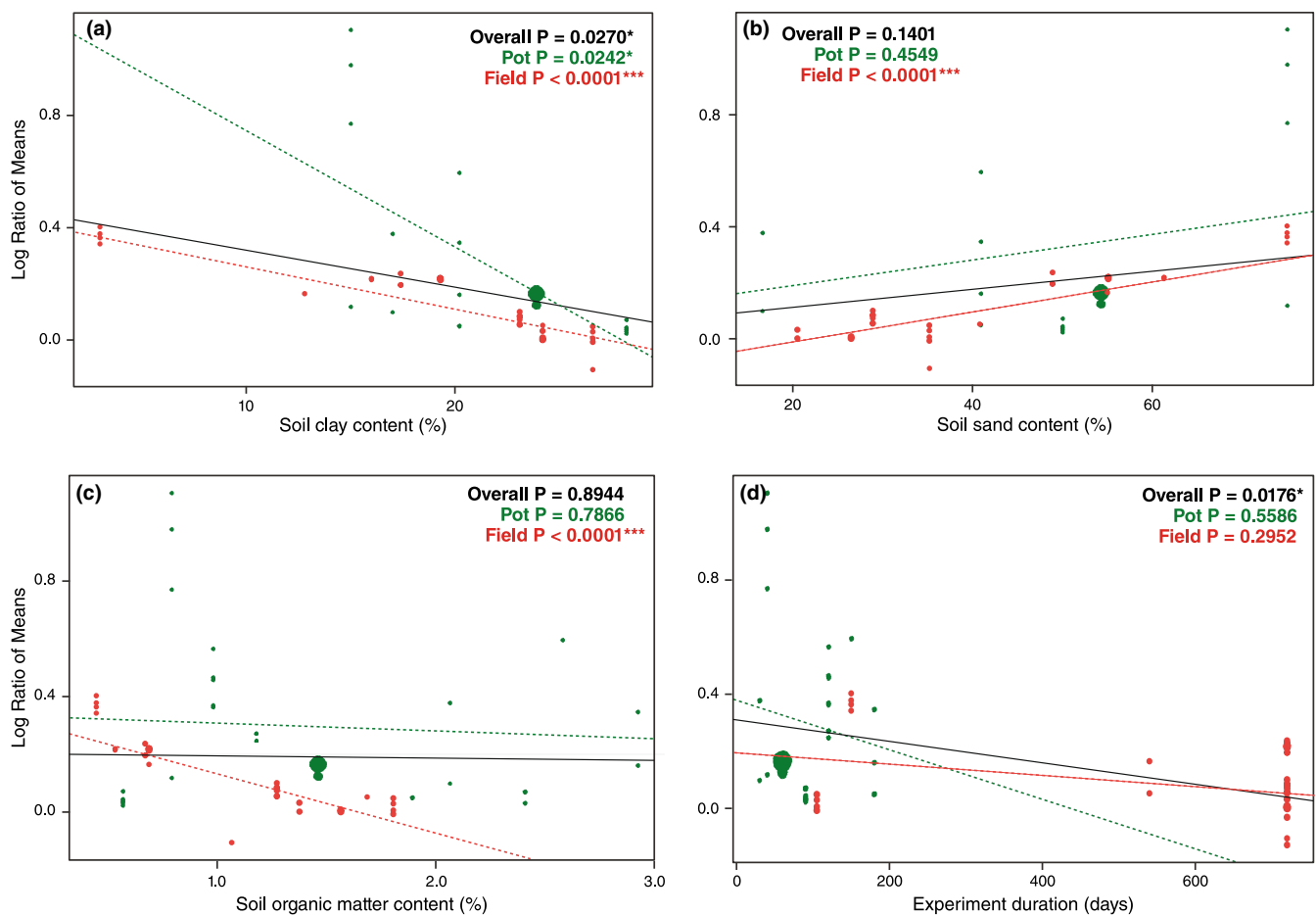


FIGURE 2 Meta-regression on the effect of AMF on SOC considering soil texture (a, b), initial SOM content (c) and experiment duration (d) as continuous moderators. (a) Meta-regression of soil clay content (%) on the effect of AMF on SOC. (b) Meta-regression of soil sand content (%) on the effect of AMF on SOC. (c) Meta-regression of SOM content (%) on the effect of AMF on SOC. Log ratio of means = $\ln(\text{AMF+}/\text{AMF-})$. (d) Meta-regression of experiment duration (days) on the effect of AMF on SOC. Log ratio of means = $\ln(\text{AMF+}/\text{AMF-})$. The black line represents the adjusted meta-regression when considering the overall dataset. The green line represents the adjusted meta-regression when considering only pot studies, while the red line represents the adjusted meta-regression when considering only field studies. Only soil clay content showed a significant effect as a moderator on the effect of AMF on SOC for overall, pot and field datasets. Soil sand content and SOM content showed significant effects only when considering field studies while experiment duration showed a significant effect only for the overall dataset. Significance levels: $^{ns}p > 0.05$, $^*p < 0.05$, and $^{***}p < 0.0001$.

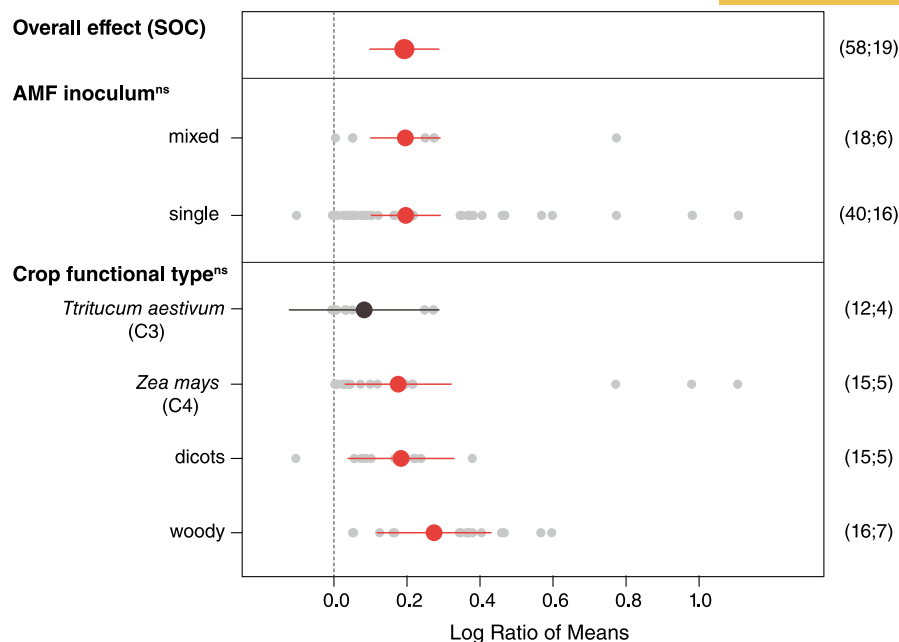


FIGURE 3 The effect of AMF on SOC as affected by crop functional type and the AMF inoculum (mean effect size $\pm$ 95% confidence intervals). Log ratio of means = $\ln(\text{AMF+}/\text{AMF-})$. Effect sizes <0 represent negative effects while effect sizes >0 represent positive effects. Statistically significant effect sizes are shown in red, while no statistically significant effect sizes are shown in dark grey. Numbers in parentheses represent the number of trials and the number of studies for each soil variable (trials; studies). Light grey data points represent the original data distribution of all the corresponding trials. Moderators did not explain a significant amount of variance for the selected variables. AMF inoculum source, $p=0.8632$; Crop functional type, $p=0.3443$.

4 | DISCUSSION

Based on our dataset comprising 62 comparisons from 19 scientific studies to test the effect of AMF on SOC, we found evidence for an overall positive effect (average increase of 21.5%), supporting our hypothesis that AMF alter SOC in agroecosystems and that this effect is, in general, positive but context-dependent. Our analyses revealed a significant influence of various ecological factors, both biotic and abiotic, as well as experimental conditions on the observed results, as discussed below.

4.1 | Soil properties

Our results support the idea that the AMF effect on agricultural soils is context-dependent, and the variation in soil properties, such as texture, nutrient levels and pH, directly affects the success of AMF in increasing SOC (Fu-Sheng et al., 2006; Kumar et al., 2006; Zhou et al., 2008). Specifically, we showed that soil texture and initial SOM are an important modulator of the effect of AMF on SOC in field conditions. This pattern seems to follow the expectation that AMF effects are more pronounced in coarsely textured and nutrient-poor soils, where small changes in SOC dynamics due to AMF could increase the activity of C-limited microorganisms, as compared with fine-textured organic matter-rich soils (Six et al., 2004). This relates to the idea that sandy soils typically have lower SOC levels, so absolute increases in SOC result in larger relative increases, making them statistically identifiable. Additionally, finer soil texture could

hinder root growth and AMF colonization (Carrenho et al., 2007), reducing their effect on SOC in these soils. Our results showed similar patterns to those presented by Tao and Liu (2024) which found that AMF inoculation increased SOC when the initial SOM content was lower than 3.2% (1.88% SOC content). In our work, most studies had initial SOM content lower than 2%, as typically reported in agricultural soils (Oldfield et al., 2019). Although previous results found higher AMF colonization and have associated higher SOC in soils with pH ranging from 4.5 to 9.1 (Carrino-Kyker et al., 2016; Tao & Liu, 2024), we did not find any clear trend for a pH-dependent AMF influence on SOC in a similar pH range (4.7–8.7), indicating that other soil variables may be more relevant moderating this effect.

4.2 | Functional identity of host plant

The functional identity of the host plant, as analysed here, did not significantly explain the effect of AMF in SOC. We hypothesized that woody species exert a more pronounced influence as moderators of the AMF effect on SOC compared to non-woody species. The latter typically have finer and more abundant roots enabling greater nutrient absorption and reducing their reliance on AMF colonization and extraradical hyphae development (Yang et al., 2015), essential for the expected changes in the soil. Although trees seem to have a higher effect size than the remaining functional types, these differences were not statistically significant. On the other side, the effect of AMF was not significant for wheat (*Triticum* spp., a C₃ plant) compared with the remaining plant functional types. It is expected that C₃ plants are less

responsive to mycorrhizal inoculation than C_4 plants due to the higher nutrient demand of the latter (Frew, 2019; Hoeksema et al., 2010; Wilson & Hartnett, 1998). However, since in our database the C_4 and C_3 grasses are represented by only one species each (*Zea mays* and *Triticum aestivum*, respectively), our results are limited to the response of these particular species. These results partially support our hypothesis that the functional differences among host plants mediate the effect of AMF on soils. However, they also highlight the importance of edaphic conditions as primary determinants in regulating this effect. This is different from what was found for the AMF effects on plant responses, where the plant functional characteristics of host plants were the main determining factor (Hoeksema et al., 2010; Zhang et al., 2019).

4.3 | Inoculum type

Unexpectedly, the type of AMF inoculum (single vs. multiple species) did not regulate the effect of AMF in SOC in our database. This pattern is similar to that found in other studies (Leifheit et al., 2014; Tao & Liu, 2024), where inoculum diversity does not appear to significantly affect the impact of AMF on plant and soil variables. One potential explanation is the competition between AMF species in the mixed inoculum in comparison with single-species inoculum which could ameliorate their effectiveness (Maherali & Klironomos, 2007). However, our results showed a huge variability within the category 'single species' indicating that it would be important to individually evaluate the effects of the most commonly used species to compare the effects between species and identify AMF species or groups that specifically impact soil properties. In this sense, most of the used bioinoculants include few genotypes (Hart et al., 2018), either isolated or in combination, which are not necessarily selected for their ability to improve soil conditions. Additionally, assessing the effect of applying inoculants derived from native fungi would be crucial to achieving truly sustainable management of agroecosystems.

4.4 | Experimental setting

Our results provide evidence that AMF can potentially stimulate SOC accrual under controlled environments with sterile soils. However, the same clear evidence was not observed under field conditions, suggesting that while managing AMF can be a potential tool to improve SOC in agricultural systems lacking an active AMF community, replicating these results under real conditions requires a greater understanding of the variables that moderate this effect.

The most obvious explanation for the disparity between experimental settings is that controlled greenhouse experiments compare treatments with and without AMF, while in field experiments, treatments without inoculation do not imply the absence of AMF because these fungi are present in most agricultural soils (Smith & Read, 2008). In other words, field settings compare the addition versus the non-addition of inoculum, but AMF were present

in the soil in both cases. This opens up two perspectives for the observed results: On the one hand, controlled greenhouse experiments that include comparisons between inoculated and sterile soils, which also lack the environmental heterogeneity found in field settings, allow for clearer quantification of patterns and causality (Madawala, 2021; O'Callaghan et al., 2022). In this regard, the evidence supports a clear positive effect of AMF on SOC in soils. On the other hand, while more realistic, field experiments only provide evidence on the effects of AMF inoculation but not on the effect of AMF themselves. In these cases, results are conditioned by the multiple factors that influence soil responses to AMF colonization in the field, including soil properties such as texture, water holding capacity, nutrient levels, soil temperature or pH (Fu-Sheng et al., 2006; Kumar et al., 2006; Zhou et al., 2008) but mostly refer to commercial AMF inoculum that must compete with native AMF species and other root endophytes (Verbruggen et al., 2013). It is important to highlight that although the effect size on AMF colonization in roots was lower under field conditions compared to controlled conditions (Figure S2), it was significantly positive in both scenarios. This suggests that the effect of AMF on soil SOC in the field is also influenced by environmental conditions and not solely attributable to the mycorrhizal colonization of the host species, as shown in several studies (Carrino-Kyker et al., 2016; Clark & Zeto, 1996; Medeiros et al., 1994; Van Aarle et al., 2002).

It is also important to note that most pot experiments, where the effect of AMF on SOC is more evident, typically have shorter durations and do not extend beyond the host plant's vegetative stage. Consequently, our understanding of their effect on SOC through AMF-related processes is relatively limited in time under these conditions (Smith & Smith, 2011). Although experimental duration appeared to modulate the impact of AMF on SOC in the short-term experiments analysed here, we cannot draw conclusive results over longer periods, as the effects of AMF may vary (Qin et al., 2022). In our analyses, all pot experiments were short-term (<200 days), while field experiments generally had longer durations. There were no intermediate durations available to test for a non-monotonic relationship between experimental duration and the AMF effect on SOC, similar to what was observed for soil aggregation, which showed a maximum timespan of about 5 months after which the positive effects of AMF on soil became less likely to occur (Leifheit et al., 2014). Therefore, in addition to the noted differences in experimental settings, our dataset does not allow for effective testing of the relationship between experimental duration as a moderator of the AMF effect on SOC.

5 | FUTURE RESEARCH DIRECTIONS

Despite the growing attention to AMF in agricultural soil management, our research highlights a limited number of studies exploring their relative impact on SOC and the mechanisms underlying this relationship. To bridge this gap, we propose three high-priority research areas to advance our understanding of AMF's role in agricultural soils, as described in Figure 4:

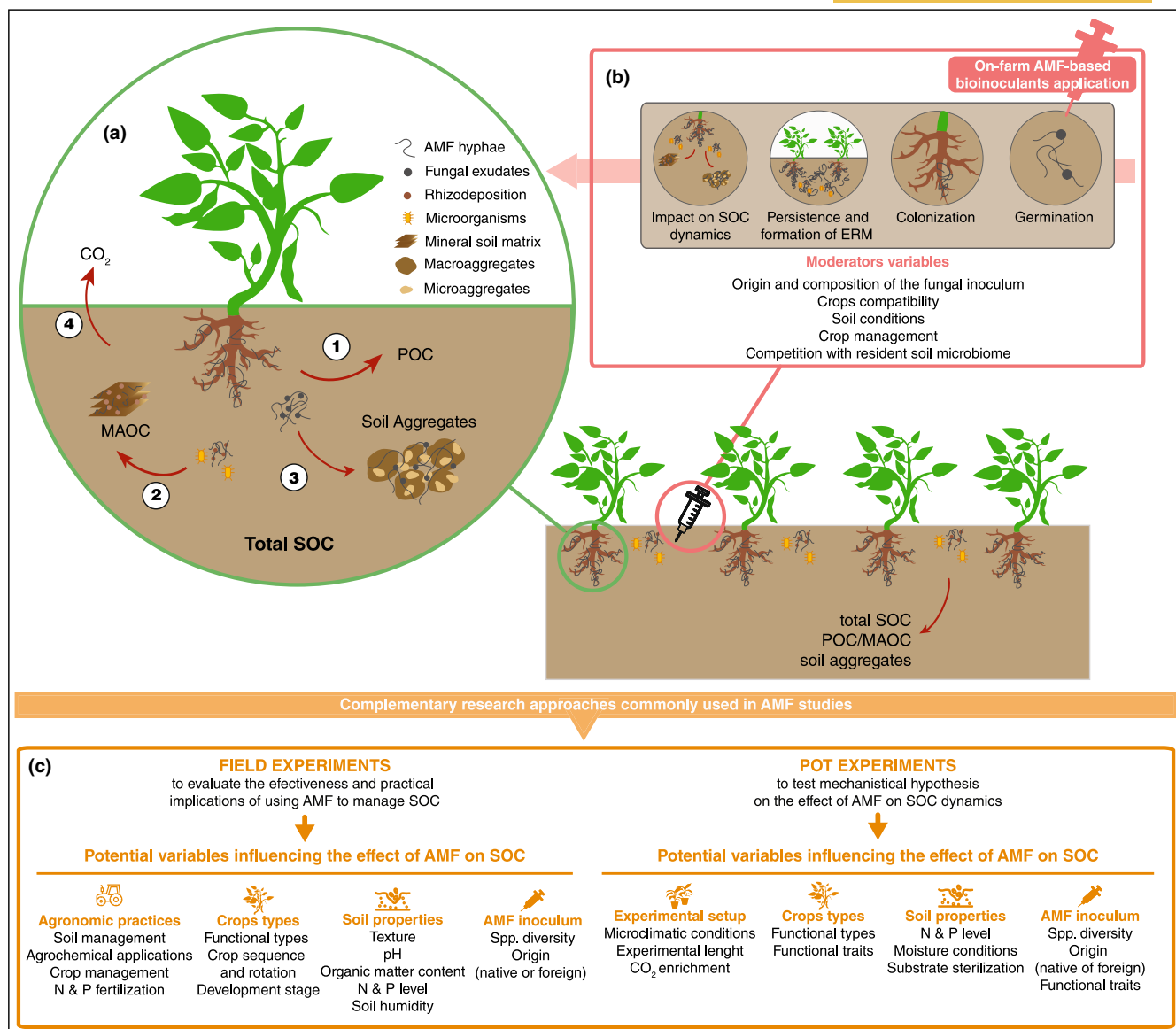


FIGURE 4 Schematic representation of key research areas for addressing the effects of AMF on SOC dynamics. (a) Potential mechanisms to be tested through which AMF may affect SOC dynamics and its fractions: AMF colonization enhances nutrient uptake, boosting plant productivity and the decomposition of aboveground and belowground structural residues. This primarily supplies the faster-cycling particulate organic carbon (POC) fraction (1). Additionally, AMF stimulates root exudation, and together with the turnover of fine roots and hyphal mycelia (rhizodeposition) by soil biota, this process promotes the formation of mineral-associated organic carbon (MAOC) through occlusion within mineral surfaces (2). External hyphae facilitate macroaggregate formation and stability through intertwining and binding mechanisms, as well as glycoprotein exudation, thereby enhancing the stabilization and magnitude of the POC fraction (3). Finally, an increased supply of fresh plant-derived biomass may stimulate microbial activity and accelerate SOC decomposition via a priming effect, primarily affecting the MAOC fraction (4). All these potential pathways and their relative importance require further analysis and exploration integrating mycorrhizal and soil ecology approaches. (b) Successful application and use of AMF-based bioinoculants needs increasing research efforts on unravelling specific mechanisms through which bioinoculants exert their effects under various field conditions. ERM, extraradical mycelium. (c) Research approaches at different spatial and temporal scales, and key variables for testing mechanistic hypotheses and identifying significant effect moderators: Pot experiments provide a controlled environment for testing short-term mechanistic hypotheses on the influence of AMF on SOC dynamics. In contrast, field experiments are crucial for evaluating the medium- and long-term effectiveness of AMF inoculum additions in managing SOC, by identifying meaningful relationships between key moderators and effect sizes. Both approaches should rely on standardized response and effect variables to ensure comparability across studies and facilitate the development of comprehensive global databases for future analysis.

5.1 | Mycorrhizal and soil ecological research focused on the mechanisms by which AMF affect SOC fractions and their relative contribution to SOC formation and stabilization

The differentiation of SOC into POC and MAOC fractions is a useful framework for understanding SOC dynamics in the context of cultivated systems (Cambardella & Elliott, 1992; Lavalley et al., 2020). Our meta-analysis found a large research gap in studies including SOC fractionation, such as POC and MAOC. Results from the sole study including soil fractions in our review (Ren et al., 2021) suggest that AMF may increase POC but decrease MAOC, indicating contrasting effects on these commonly evaluated fractions. Several studies have demonstrated that the decomposition of aboveground and belowground C-rich structural residues primarily contribute to POC formation (Figure 4a, arrow 1) (Cotrufo et al., 2015; Villarino et al., 2021), while MAOC is mainly derived from low-molecular-weight C substrates derived from rhizodeposition, foliar litter leachates and hyphal exudates (Figure 4a, arrow 2) (Cotrufo et al., 2015; Haddix et al., 2016; Sokol et al., 2019; Villarino et al., 2021). An increase in POC as a result of higher amounts of decomposing plant C-rich tissues together with the effect of the physical action of extraradical hyphae, will increase soil aggregation and POC stabilization (Figure 4a, arrow 3). On the other side, microbes receiving higher amounts of C-rich substrates through hyphae rhizodeposition could trigger the priming of the MAOC fraction (Figure 4a, arrow 4) (Meier et al., 2017; Phillips et al., 2011). However, more research under controlled conditions is needed to quantify the relative importance of these mechanisms by which AMF affect SOC storage and its fractions. Studies incorporating isotopic tracing analysis can significantly enhance our understanding of the fundamental mechanisms underlying organic matter dynamics mediated by AMF.

5.2 | Agronomic research on AMF-based bioinoculants for improving soil conditions

An increasingly global industry is now focused on producing and marketing microbial-based inoculants, including AMF. This development is driven by the growing need to make agroecosystems more sustainable by reducing the use of external inputs such as agrochemicals and synthetic fertilizers. Therefore, appropriate and effective management of these symbiotic fungi could potentially not only improve crops' nutrient supply and yield, but also related ecosystem properties like soil fertility, including soil aggregation (Leifheit et al., 2014; Rillig & Mummey, 2006), soil N and P (Qiu et al., 2022) and SOC, as shown in this study. However, their direct use for improving these soil properties remains uncommon (O'Callaghan et al., 2022). Moreover, only a few AMF genotypes currently produced are globally distributed as bioinoculants, with limited evidence of their efficacy and a huge risk in terms of replacement of resident fungi (Hart et al., 2018). Many AMF species remain unstudied, and among those that have been studied, the most efficient species, in terms of their benefits to plant nutrition, are not present in the

commercial inoculum (Marro et al., 2022). The bioinoculant industry faces numerous challenges mainly related to the scalability of inoculation production and propagation, the lack of simple and easily trackable methods to assess actual root mycorrhizal colonization, and the presence of extraradical mycelium in the soil, as well as deficient quality control methodologies (Berruti et al., 2016; Madawala, 2021). The key research gaps that must be addressed to enable the widespread on-farm application of AMF include improving germination, colonization and persistence by the formation of extraradical mycelium (ERM) in conventional cropping systems (Figure 4b), where common agricultural practices (i.e. tillage, fertilization, pesticide use, presence of non-host crops and monoculture practices) can adversely affect AMF communities and their direct benefits to crops (Bowles et al., 2017; Cofré et al., 2020; de Graaff et al., 2019; Jeffries et al., 2003; Marro et al., 2020; Ryan & Graham, 2002). Research questions should be addressed collaboratively with farmers, technicians and ecologists to obtain more applicable, efficient and scalable results.

Although the use of bioinoculants is undergoing increasing development, the potential to restore conditions to enhance the native mycorrhizal community is an alternative to large-scale inoculation. The restoration of low-productivity areas with local perennial plant biodiversity could serve as 'fertility islands' where mycelial networks from native AMF spp. would gradually be reestablished with reduced costs, serving as a diverse and native source of local inoculum production for farmers (Berruti et al., 2016). Many more studies are needed to facilitate their effective design, application and management to move toward agroecosystem sustainability.

5.3 | Standardized global databases from agroecosystems to investigate the impact of AMF on SOC dynamics

Global databases can be invaluable tools for understanding how AMF influence SOC dynamics across different ecosystems (i.e. Chaudhary et al., 2016; Soudzilovskaia et al., 2020; Větrovský et al., 2023). These databases can serve for unravelling key moderators for studying the impact of AMF on SOC dynamics considering different spatial scales and study approaches to have more comparable studies on agricultural settings (Figure 4c). By providing extensive and standardized data on soils, crops, agronomic management, climate and AMF biodiversity across various agricultural contexts, they would enable more comprehensive and comparative analyses, identifying patterns, generating hypotheses and facilitating the integration of mycorrhizal pathways into global biogeochemical models. This enables the development of specific management recommendations and the design of agricultural practices that enhance the role of AMF in C cycling, thereby improving sustainability in agricultural systems.

Tackling these aspects would benefit from diverse but complementary methodological approaches such as pot or field experiments (Figure 4c). Controlled pot experiments offer valuable insights into causal and univariate factors influencing SOC dynamics mediated by AMF. These studies help identify key mechanisms and drivers in the

short term. In contrast, field experiments are essential for examining broader, multivariate relationships that influence the effect of AMF on SOC. They provide an opportunity to evaluate the effectiveness and practical implications of AMF inoculation for SOC management, shedding light on the magnitude of effects and the relative contributions of moderating factors over medium and long-term timescales. Both methodological approaches need to inform and complement each other to develop efficient, science-based recommendations for effectively managing SOC in agroecosystems.

6 | CONCLUSIONS

Our results demonstrate the potential of AMF to increase SOC under controlled conditions. However, under real field conditions, this effect is influenced by resident AMF communities and primarily determined by edaphic factors rather than by the type of AMF inoculum or plant species. Therefore, we emphasize the need for more comparable studies, particularly in agricultural settings, to further explore other potential pathways by which AMF may influence SOC. While our results are based on the best available evidence, they remain geographically biased and should be interpreted cautiously. Nevertheless, our findings contribute to the ongoing discussion on this critical topic, providing preliminary evidence that effective AMF inoculation may enhance soil processes, leading to SOC accrual rather than SOC losses. To improve the scientific foundations for an effective, soil-targeted bioinoculant application, more research is needed to quantify the relative importance of different moderators under real on-farm conditions by which AMF affects SOC storage and its fractions (Figure 4). We conclude that AMF, together with other soil biota, can significantly contribute to soil fertility, a crucial ecosystem service tightly linked to sustainable management. However, more field-based research is essential to develop integrated mycorrhizal technologies, including agronomic practices that promote the abundance and diversity of native AMF communities in soils (Gianinazzi et al., 2010; Guzman et al., 2021; Rillig et al., 2016), such as no-till farming and the reduced use of synthetic agrochemicals. Adopting practices aimed at increasing AMF on agricultural soils would foster an integrated perspective of agroecosystems, paving the way toward sustainable agricultural development.

AUTHOR CONTRIBUTIONS

Georgina Conti and Gervasio Piñeiro planned and designed the research. Georgina Conti conducted literature search, data collection, data analysis and led the writing of the manuscript. Georgina Conti, Gervasio Piñeiro, Carlos Urcelay and Pedro E. Gundel contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

Data available from the FigShare Repository: <https://doi.org/10.6084/m9.figshare.17153441.v2> (Conti et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: PRISMA flow diagram showing the identification, screening, and eligibility process.

Figure S2: The effect of AMF inoculation on root colonization across studies.

Figure S3: The effect of AMF on soil fractions and total SOC.

Figure S4: Publication bias.

Table S1: List of published studies included in the meta-analysis.

Table S2: Summary of statistical descriptors from the meta-analysis considering the complete dataset.

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