CODEX PLANETARIUS

Mycorrhizal Fungi as Indicators of Soil Health

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About *Codex Planetarius*

Codex Planetarius is a proposed system of minimum environmental performance standards for producing globally traded food. It is modeled on the *Codex Alimentarius*, a set of minimum mandatory health and safety standards for globally traded food. The goal of Codex Planetarius is to measure and manage the key environmental impacts of food production, acknowledging that while some resources may be renewable, they may be consumed at a faster rate than the planet can renew them.

The global production of food has had the largest impact of any human activity on the planet. Continuing increases in population and per capita income, accompanied by dietary shifts, are putting even more pressure on the planet and its ability to regenerate renewable resources. We need to reduce food production's key impacts.

The impacts of food production are not spread evenly among producers. Data across commodities suggest that the bottom 10-20% of producers account for 60-80% of the impacts associated globally with producing any commodity, even though they produce only 5-10% of the product. We need to focus on the bottom.

Once approved, *Codex Planetarius* will provide governments and trade authorities with a baseline for environmental performance in the global trade of food and soft commodities. It won't replace what governments already do. Rather, it will help build consensus about key impacts, how to measure them, and what minimum acceptable performance should be for global trade. We need a common escalator of continuous improvement.

These papers are part of a multiyear proof of concept to answer questions and explore issues, launch an informed discussion, and help create a pathway to assess the overall viability of *Codex Planetarius*. We believe *Codex Planetarius* would improve food production and reduce its environmental impact on the planet.

This proof-of-concept research and analysis is funded by the Gordon and Betty Moore Foundation and led by World Wildlife Fund in collaboration with a number of global organizations and experts. For more information, visit www.codexplanetarius.org

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Summary

Soil health in agroecosystems has become a major focus for sustainability efforts and developing nature-based solutions to the climate crisis. However, it has been difficult to define a soil health indicator that intersects across multiple axes of important soil variables. Here we explore whether arbuscular mycorrhizal (AM) fungi can be suitable as bioindicators in agroecosystems as studies show that AM fungi are sensitive to many agricultural management interventions, including tillage regime, fertilization intensity and pesticide use. By reviewing and focusing on how AM fungi respond to conventional agricultural management practices, we discuss whether this group of organisms could be a broadly relevant indicator of soil health based on their functional impacts on soil systems and sensitivity to multiple types of land intensification stressors. We present current challenges of deploying traditional AM fungal quantification techniques at large scale, as well as the potential of using new spectral imaging technologies to remotely monitor the state of these symbioses.

Soil Health Indicators

Soil health is a controversial concept: it is embraced by practitioners, policy makers and various interested parties because of its evocative nature and its immediately apparent parallel with human health. However, the term is often met with skepticism by soil scientists because it is difficult to define operationally. The main challenges are: (i) translating this broad concept into a specific set of parameters to measure, and (ii) choosing baselines for comparisons.

While soil quality and soil health are sometimes used as mostly equivalent terms (Doran & Zeiss, 2000; Bünemann et al., 2018), others have argued that soil quality and soil health represent distinct concepts (Lehmann et al., 2020). Here, we adopt the distinct concept perspective in which soil quality is more focused on agricultural yield and abiotic factors, while soil health is a broader concept focused on the "capacity of soil to function as a vital living ecosystem that sustains plants, animals and humans" (as in Lehmann et al., 2020). Soil quality, in turn, occupies an intermediate position in terms of scope, scale, functions and relevance to Sustainable Development Goals (Lehmann et al., 2020). We advocate for the term "soil health" to function as an overarching concept, which acts as a catalyst to contribute knowledge — rather than just as a trait to quantify — and which is also useful in terms of communicating with parties outside of science.

Metrics of soil health have changed with scientific progress. The most notable difference has been between historical definitions dominated by physical and chemical measurements, such as pH, water holding capacity and soil organic carbon content, which only partially capture the status of a soil. In contrast, there is an increasing focus now on soil biotic components. As a result, the conceptual focus in soil health is shifting from a metric used to quantify aboveground productivity towards soil itself, and toward its ability to foster soil biodiversity, food webs and soil carbon draw down potential (Lehmann et al., 2020).

Soil biodiversity summarizes the collection of underground animals, invertebrates, and microorganisms that make up the most diverse ecosystem type on the planet containing 59% of all Earth's species (Anthony et al., 2023). On the whole, these organisms are responsible for intricate soil functions at the foundation of global terrestrial ecosystems (Orgiazzi et al., 2016; Geisen et al., 2019). As a metric, species richness (the total number of different species per sample) is becoming a prime target of soil health assessments. This type of measure is appealing in its simplicity, and it can help capture the large variety of functions performed by soil communities — particularly microbial groups — from nutrient cycling and waste decomposition to regulating climate and plant growth (Guerra et al., 2021). The problem is that microbial communities are highly variable, and the contributions of many different species to soil health are often unknown. As a result, more total microbial diversity is not always better since healthy soils are unlikely to have a consistent, "optimal" microbiome (Fierer et al., 2021). In agricultural settings, there is a strong argument for focusing on specific organismal groups that both are: (i) strongly affected by agricultural management practices and/or (ii) strongly influence soil processes themselves.

Of the possible 2-3 million fungal species estimated on Earth (Niskanen et al., 2023), arbuscular mycorrhizal (AM) fungi are a group of soil fungi that warrant attention based on their ability to both: (i) drive soil health, and (ii) act as indicators of soil health (Gupta, 2020). AM fungi (Glomeromycota) are defined by their intimate relationships with plant roots, forming nutrient trade associations with an estimated 70% of all plant species (Brundrett & Tedersoo,

2018), including most food and fiber crops. These fungi penetrate root cells, where carbon (sugars and lipids) is delivered by their plant partners. In turn, AM fungi form complex mycelia networks in soils to collect large amounts of inorganic nutrients (mainly phosphorus and nitrogen) that are delivered to plants. As the most common plant root-fungus mutualistic symbiosis in agroecosystems, this partnership serves as a bridge between roots and the soil. In some cases, up to 80% of phosphorus and 20% of nitrogen are provided to plants by fungal partners. In addition to nutrition, these fungi also form a key entry point for carbon into soil systems, with plants allocating roughly ~3.93 Gt CO_2e to AM fungi every year (Hawkins et al., 2023).

AM Fungi as Key Drivers of Soil Health?

The productivity of agriculture systems is tied to soil health. For instance, a recent study across European croplands found a positive relationship between primary productivity and soil health using a composite index that combined information from soil properties, soil biodiversity, and plant disease control (Romero et al., 2024). To effectively assess the role of AM fungi as a driver of soil health in agroecosystems, we need to consider their contributions beyond just promoting primary productivity (Powell & Rillig, 2018). These roles include soil aggregation and structure, generation of organic compounds, biological weathering, and protection against leaching **(Figure 1, page 9)**.

Soil Aggregation and Structure

First, AM fungi, along with other soil biota, have major and well-documented effects on soil structure, the spatial arrangement of particles, aggregates and pore spaces in the soil matrix (Lehmann et al., 2017). Soil structure is a key parameter influencing soil physical and chemical processes and biological communities (Philippot et al., 2024). AM fungi form complex physical scaffolds in soils. They primarily influence soil structure through the formation and stabilization of soil aggregates, which are defined as complexes of particles adhering more strongly to each other than to surrounding particles (Kemper & Rosenau, 1986). Soils with greater aggregate stability have reduced erosion and better water capture, storage, and availability to plants (Rieke et al., 2022).

AM fungal extraradical mycelial networks are of particular importance for the stabilization of macroaggregates (>250 μm). Along with plant root hairs, AM fungal hyphae grow into pore spaces between microaggregates (<250 μm) and entangle the smaller structures in nets of mycelium (Tisdall & Oades, 1982; Tisdall, 1994). This process physically enmeshes soil particles, pushing and holding pieces of clay, silt, sand, and organic matter together. Although individual hyphae are easily broken, the combined strength of AM fungal hyphae acting as a mycelial net helps to stabilize macroaggregates in three dimensions, minimalizing their disruption upon mechanical stress such as irrigation or tillage. The degree to which AM fungi affect soil aggregation varies across AM fungal species and community composition (Piotrowski et al., 2004), a topic which requires further research (Rillig & Mummey, 2006). AM fungi further shape soil properties by regulating soil water flow (Prove et al., 1990), physically protecting soil organic matter (SOM) (Tisdall & Oades, 1982), likely releasing substances that serve as binding agents (Rillig, 2004a), absorbing nutrients and reducing leaching (see below, Linquist et al., 1997; Barthés & Roose, 2002) and structuring microbial communities (Hattori, 1988).

New research is also revealing that AM fungi play an important role in carbon processing in the soil (Rillig, 2004b; Frey, 2019). Beyond their effects on plant productivity (and thus the generation of more plant-based carbon), there are several pathways via which AM fungi can contribute to soil carbon stabilization (Wu et al., 2024). This includes their more recently explored effects on molecular chemodiversity and mineral weathering. AM fungi are major contributors to SOM dynamics and carbon stabilization in soils. They help protect stabilized aggregates, and influence biogeochemical processes driving SOM generation, reprocessing, reorganization and stabilization (Wu et al., 2024). Thoroughly characterizing AM fungal-mediated carbon fluxes and stability in soils requires not only models of AM fungal promotion of plant productivity (Braghiere et al., 2021) and transfer of carbon from plants to extraradical hyphae of their fungal partners (Hawkins et al., 2023), but also models of the subsequent biological processing of the transferred carbon. Large proportions of carbon received from plant partners are stabilized in soils as SOM in the form of hyphal necromass, which is predominantly composed of proteins, polysaccharides, lipids, aromatic and phenolic compounds (Horsch et al., 2023). AM fungi also produce a diversity of exudates, including proteinaceous compounds, monosaccharides and low molecular weight organic acids (Hooker et al., 2007; Toljander et al., 2007).

Mycorrhizal fungi form a physical infrastructure upon which other organisms depend. The often highly abundant extraradical hyphae of AM fungi in the soil (Hawkins et al., 2023) can act as an organizing hub for the soil microbiome. In particular the hyphosphere microbiome which can be defined as taxa coating and moving along the exterior of AM hyphae include bacteria that help solubilize phosphorus (Johnson & Marín 2023; Wang et al., 2024). As a result, AM fungi contribute to the soil food web by virtue of their biomass alone.

Generation of Organic Compounds

The molecular diversity of organic compounds derived from AM fungi likely determines their overall rates of decomposition. Molecular properties such as structure, elemental composition and chemical bond types determine the energetic requirements for decomposition via the production of enzymes and the net energy gained by saprotrophic microbes (the cost-benefit ratio) (Lehmann et al., 2020). Additionally, these properties may influence molecular association with soil minerals, modulating their persistence (Coward et al., 2018). The molecular diversity of AM fungal organic compounds remains poorly understood. This is especially true because the reprocessing of these compounds by saprotrophic microorganisms may further expand the diversity of organic compounds in soils originating from the AM symbiosis, in the form of decomposition products and/or anabolic metabolites (Liang et al., 2017). Developments in analytical technologies such as ultrahigh-resolution mass spectrometry (Perry et al., 2008) offer promise for greater elucidation of AM fungi-derived molecular diversity, which would enable greater insight into the dynamics and fluxes of carbon sequestered in soils via the AM symbiosis.

Biological Weathering

AM fungi influence SOM dynamics via the biological weathering of soil minerals. While foraging for limiting nutrients such

as P, N, and K (Smith & Read, 2008), AM fungi can break apart mineral particles and release nutrient elements via their secretion of organic acids and by exerting mechanical pressure with hyphal growth. AM extraradical hyphae are also widely associated with P-solubilizing bacteria, which can secrete phosphatase enzymes that liberate phosphate ions from minerals (Johnson & Marin, 2023). Weathered nutrient elements can form secondary minerals, which generally have higher specific surface area and covalent reactivity (Kleber et al., 2015). These properties likely enhance adsorption of SOM and increase aggregate formation and stability. Additionally, these mineralogical changes resulting from AM fungi mediated weathering may increase mineral catalysis of SOM processes, such as macromolecule degradation and oxidation (Kleber et al., 2021). Although AM fungi have been demonstrated to stimulate mineral weathering and formation of secondary minerals which further stabilized N-rich SOM compounds in young Fe-rich soils (Li et al., 2022), links between AM fungal mineral weathering and SOM dynamics remain mostly theoretical and require experimental studies in diverse soils to elucidate (Smits & Wallander, 2017). Nonetheless, mineral weathering constitutes a further example of the complex influences of AM fungi on soil physical and chemical composition, key parameters influencing ecosystem processes and community composition.

Nutrient Flux and Leaching

AM fungi are important regulators of nutrient fluxes in soils and can reduce leaching and nutrient loss, particularly for nitrogen (Cavagnaro et al., 2015). Nitrate (NO_{3}-) and sulfate (SO_4^{2-}) are highly mobile in soils, and large proportions of fertilizer inputs are lost annually from agroecosystems due to leaching and surface runoff (Herzog et al., 2008), which can be exacerbated by agricultural practices such as intensive tillage regimes (García-Díaz et al., 2017). Additionally, nitrogen is also lost from soils in gaseous forms, including as the greenhouse gas nitrous oxide (N_2O) (Bender et al., 2015).

Other, less mobile nutrients such as phosphorus can also be lost via leaching when bound to SOM or organomineral complexes (Adesemoye & Kloepper, 2009). Loss of excess nutrients not only impacts agricultural economy and outputs, but can contaminate water systems, leading to eutrophication, loss of biodiversity and ecosystem services (Withers & Haygarth, 2007). The main factor reducing nutrient loss from soils is uptake by plants, but for most crops and land plants in general, major proportions of nutrient uptake are mediated by AM fungi (Smith & Smith, 2011). AM fungal extraradical mycelia form extensive absorbing networks that extend beyond nutrient depletion zones around plant root hairs and significantly enlarge the area in which nutrients can be intercepted and sequestered within biomass (Li et al., 1991; Marschner & Dell, 1994).

Through increasing biological nutrient immobilization in soils, AM symbioses can reduce the overall amount lost through runoff and leaching (Cavgnaro et al., 2015). Evidence for AM symbioses reducing N loss via leaching is extensive, but underlying mechanisms, modulating factors and forms of N involved are less clear and may be complex, involving interactions with different kinds of microorganisms, including nitrifying and denitrifying bacteria, preferential uptake of different forms of N, and the influence of factors such as soil type and temperature (Carvagno et al., 2015). One important modulating parameter may be soil phosphorus content. While AM symbioses can also reduce inorganic phosphorus loss as leachate from soils through reducing soil pools via increased uptake by plants (Asghari et al., 2005; Corkidi et al., 2011), at relatively high concentrations of soil phosphorus (common in fertilized agroecosystems) AM fungal colonization of roots is reduced, likely leading to increased leaching of nitrogen and phosphorus due to reduced plant uptake (Bruce et al., 1994; van der Heijden, 2010).

While extensive further research is required to accurately model the influences of AM fungi and other soil biota on nutrient stabilization, AM fungi are clearly of major importance in the provision of these essential ecosystem services, and both the service provision and the fungi themselves are threatened by modern industrial agricultural practices.

AM Fungi as Key Indicators of Soil Health?

In terms of being sensitive indicators of soil health, AM fungi are probably an excellent choice. AM fungal community composition has been shown to be very sensitive to change in agricultural settings. Many management practices in agroecosystems known to impair soil health also harm AM fungi (Rillig et al., 2019). Chiefly among these are the use of pesticides (Dodd & Jeffries, 1989; Riedo et al., 2021; Edlinger et al., 2022), especially fungicides.

Several recent studies indicate that pesticides negatively impact AM fungi. For instance, by comparing 60 agricultural cereal fields in Switzerland, Riedo et al., (2021) demonstrated that the abundance of AM fungi in plant roots was negatively linked to the number of pesticides detected in the soil **(Figure 2, page 9)**. Pesticides, together with soil pH, were identified as the main factor driving AM fungal abundance. It has been long known that soil pH is a controlling factor on AM fungi (Peat & Fitter, 1993; Van Aarle et al., 2002). However, new work is revealing that pesticides regulate AM fungal abundance, but this has received far less attention. A study using soils from 150 croplands demonstrated that the application of fungicides by farmers reduced AM fungal diversity across a large European network (Edlinger et al., 2022). Moreover, P-uptake by AM fungi hyphal networks and supply to their host plants was reduced in soils where farmers applied fungicides compared to soils where no fungicides were applied (Edlinger et al., 2022). This aligns with research showing that pesticide application alters AM fungal community composition and abundance (Rivera-Becerill et al., 2017), although results are variable, depending on agricultural context and soil type, and some pesticides have no or small effects (Buysens et al., 2015; Hage-Ahmed et al., 2019). Though initially considered to present low risks to non-target biodiversity, the widely used herbicide glyphosate (Roundup®) has been demonstrated to decrease AM fungal spore viability and plant root colonization (Druille et al., 2013 a,b)**(Box 1, page 4)**. Further research is necessary to make robust conclusions and provide clear guidelines. For instance, pesticide risk assessments have been performed for earthworms and mites, but to date AM fungi have not been considered, despite growing evidence that AM fungal can be highly sensitive to pesticide application.

Fertilization, especially with P, is known to reduce the abundance of AM fungi (Smith & Read, 2008). A range of studies have shown a clear negative relationship between AM fungal abundance (e.g., root colonization) and the amount of P applied.

This is not surprising as AM fungi supply P to plants and if P-availability is high, plants tend to reduce carbon supply to AM fungi (Kiers et al., 2011). Nitrogen fertilization can also negatively impact AM fungi. A recent meta-analysis found that croplands recorded the strongest overall declines in AM fungal richness (-27.6%) compared to grasslands and forests, with more significant declines occurring with more intense and longer N fertilization use (Han et al., 2020). Baseline levels of soil available N/P ratio was the best explanatory factor for these effects, indicating that the mechanisms behind negative N fertilization effects on AM fungi were linked to the relative availability of soil phosphorus. Broadly, the balance between nitrogen and phosphorus likely shapes the severity of AM fungal response to fertilization.

Use of highly-bred, non-responsive host plant genotypes may also change AM fungal community dynamics belowground (Bennett et al., 2013). Generally, modern crop breeding programs are designed to select genotypes with high productivity under conventional fertilization regimes. These conditions may be producing some crop varieties with diminished AM dependency and abundance (Tawaraya, 2003). For example, older wheat landraces had about twice as much AM fungal abundance as modern cultivars (Zhu et al., 2001). Breeding for fungal disease resistance in maize also reduced AM colonization compared to susceptible genotypes (Toth et al., 1990). These crop breeding impacts on AM fungal symbioses might also have ecosystem function consequences, as a recent meta-analysis found that crop plants allocate nearly half the amount of carbon to AM fungal symbionts compared to wild plants (Hawkins et al., 2023).

What is most worrying is that the combined action of several of these factors simultaneously has serious potential to affect the ability of AM fungal communities to survive in agricultural systems. For instance, high fertilizer and high pesticide use are very often interlinked in intensively managed agricultural fields. This leads to the observation that in some production agroecosystems AM fungi play no role, at least in terms of crop yield (Ryan & Graham, 2002, 2018). This is most likely because fungal populations have been depleted and because many of the functions they provide have been replaced by intensive management practices (Rillig et al., 2019).

Box 1. Does glyphosate affect AM fungi?

Glyphosate (N-phosphonomethylglycine) is the most widely used herbicide in the world, applied in agricultural and domestic environments and in restoration interventions to control the spread of invasive species (Barnes, 2007). Glyphosate works by inhibiting the enzyme 5-enolpyruvylshikimate-3-phosphate synthase (ESPS), a component of the Shikimate pathway in which plants synthesize the essential aromatic amino acids phenylalanine, tryptophan and tyrosine (Steinrucken & Amrhein, 1980). The Shikimate pathway is not a component of animal metabolism, but it is present in diverse soil microorganisms, such as bacteria, archaea, algae, protists and fungi (Kepler et al., 2020). Though previously considered to present low risks to non-target biodiversity due to rapid adsorption onto soil particles and degradation (Giesy et al., 2000), the fate of applied glyphosate is now known to vary with soil type and management practices. Notably, co-application of phosphate fertilizers is known to result in extended persistence and mobility of glyphosate in soils, as phosphate ions compete for adsorption sites (Bott et al., 2011). Additionally, the glyphosate degradation product aminomethylphosphonic acid retains mobility in soils for long timescales (>4 weeks) and is an equally potent inhibitor of ESPS and the Shikimate pathway (Kjaer et al., 2005; Giesy et al., 2000).

Mounting evidence suggests that glyphosate application may detrimentally impact AM fungi. Druille et al., (2013 a,b) experimentally applied glyphosate at industrially recommended and fractional dosages to soil and associated living plant samples collected from the Flooding Pampa grassland region of Argentina, and observed major decreases in AM fungal spore viability and root colonization at all glyphosate dosages compared to control samples. Studies exploring the effects of glyphosate application on AM fungal and wider microbial communities over time are lacking, but changes in community structure would likely influence plant communities and wider ecosystems above and below ground, since plant-AM fungal relationships vary in specificity and dynamics (Habte & Manjunath, 1991). Loss of AM fungal diversity could not only impact plant diversity and ecosystem processes in agricultural landscapes, but also potentially limit the ability of native plants to reestablish following glyphosate-mediated removal of invasive species in restoration interventions (de Mesquita et al., 2023).

The absence of AM fungal effects on crop yield is thus not an argument against using AM fungi as a tool for assessing soil health; quite the contrary. It shows AM fungi might be a valuable indicator of soil health by being strongly affected by management practices. As one example, the molecular diversity of AM fungi decreased with years since soil has been under agricultural management along a 52-year chronosequence (Roy et al., 2017); potentially, phylotypes being lost from agroecosystem are among the more beneficial ones for plant growth promotion (Verbruggen et al., 2015). Finally, agricultural management can be adjusted to be more favorable for AM fungi (Oviatt & Rillig, 2021). This is important because these fungi might also serve to indicate recovery of systems, not just degradation. For example, inoculation with AM fungi can help to restore crop yield, especially in soils with poor soil quality or where plant pathogens are abundant (Lutz et al., 2023).

Beneficial Management Practices for AM Fungi

Sustainable management practices are increasingly being embraced to promote soil health goals (Lal et al., 2021). This includes specific quantitative European Union targets of 75% healthy soils by 2030. These recommendations include practices like minimum tillage, crop diversification and rotation, and cover cropping **(Table 1, page 11)**. The benefits of such practices have largely focused on building soil organic matter, increasing water and nutrient retention, reducing pathogen loads, and limiting soil erosion. However, these practices have also been shown to positively affect AM fungi (Verbruggen et al., 2010), and there is immense space to explore management combinations that are beneficial to AM fungi and soil health (Rillig and Lehmann, 2019).

Tilling soil physically disrupts fungal hyphal networks. These frequent, repeated disturbances lead to conditions where only highly disturbance-tolerant fungal species

can persist, species that have less mutualistic traits (Chagnon et al., 2013). For example, some taxa (e.g., Gigaspora) decline or disappear in regularly tilled soils (Jansa et al., 2003). Reducing tillage has been shown to improve AM fungal species diversity, spore densities, and functional benefits across a variety of field trials (Brito et al., 2012; Säle et al., 2015; Higo et al., 2020; Lin et al., 2023). For instance, data from a 20-year row crop experiment comparing no-till against conventionally managed row crops showed higher soil glomalin, an exudate of AM fungal networks that increases soil aggregation and water retention, and more diverse and stable AM fungal communities, in no-till treatments (Gottshall et al., 2017). Additionally, AM fungal root colonization of winter wheat increased when tillage was removed as a land management practice in a 5-year field experiment, which resulted in the same nutrient acquisition rates and crop biomass yield as the conventionally tilled and fertilized control fields (Verzeaux et al., 2016). Minimizing soil disruption from tillage is one option for managing native AM fungal biodiversity towards their greatest soil health benefits and sustainably intensify crop systems (Brito et al., 2021).

Diverse crop systems are cited as a remedy for the instability and environmental harm of intensive monoculture cropping (Altieri et al., 2015; Brooker et al., 2015). Diversifying the range of plant hosts with which AM fungi can form symbioses may open more ecological niches for different species and functional types of AM fungi to thrive. Crop rotations are one method of increasing plant diversity through time, often by incorporating legumes with N-fixing symbionts to boost soil nitrogen availability. One recent study found AM fungal biomass was roughly 35% higher in rotating wheat-soybean systems than wheat monocultures in the central US Great Plains (Lin et al., 2023). Polyculture (or intercropping) increases crop diversity in space by planting multiple species in combination and has been shown to build soil environments with 50% more AM fungal species than monocultures (Guzman et al., 2021).

Cover crops grown in agriculture fields eliminate periods of bare fallow when AM fungi have no host partner. Because AM fungi depend on plant hosts for most of their carbon resources, fallow periods can significantly lower AM fungal populations, which can lead to poor crop growth and plant nutrient deficiencies over time (Thompson et al., 2013). Supporting AM fungal communities during the non-cash crop producing months has effects that carry over into the primary cash crop growing season. Specifically, a meta-analysis found that winter cover-cropping increased AM fungal root colonization in the following summer cash crop plants (Bowles et al., 2017), possibly due to increased spore production in soils. Moreover, cover crop benefits may translate into higher mycorrhizal tolerance for other management practices, such as how the negative effects of tillage on AM fungal abundance were less severe in combination with cover cropping (Bowles et al., 2017). However, not all cover crops benefit AM fungi, particularly if they are non-AM hosts or if plants produce AM-inhibiting compounds, or both (e.g., isothiocyanates by Brassicaceae), and the results to date on cover crop benefits for enhancing AM fungal diversity are mixed (e.g., Ramos-Zapata et al., 2012; Njeru et al., 2015).

Building AM Fungal Communities Via Inoculation

Directly adding AM fungi via soil inoculation is a growing area of agriculture research, and a major emerging market. The vast majority of inoculum research focuses on how introduced AM fungi affect crop productivity and nutrition. There are relatively few examples of effects on soil features. Many greenhouse studies conducted under controlled conditions show clear plant growth benefits of AM fungal inoculum on a range of crop species. However, under field conditions, the results are more inconsistent. For instance, recent field tests of commercial inoculants on soybeans in South Dakota, USA, showed no difference in AM fungal root colonization levels compared to uninoculated controls, and variable plant yield responses (Salomon et al., 2022). Developing microbial inoculants for consistent, widespread benefits under field conditions also faces many major challenges from production to establishment to downstream impacts (Kaminsky et al., 2019). Complicating these studies is an immense and growing commercial market of biofertilizer products, many of which may be ineffective at best, or actively harmful in spreading invasive fungal species (Hart et al., 2018; Jack et al., 2021). As a result, it might be best to consider inoculation as a last resort, only to be used if the resident AM fungal community is depleted. To build productive, resilient underground microbial communities, it is crucial to avoid creating monocultures of fungal symbionts (Averill et al., 2022). However, there are significant challenges to cultivating local communities of AM fungi, and AM fungal species locally adapted to cropping systems are often unavailable (Middleton et al., 2015). Recent work has shown the importance of native fungi in promoting native grass and prairie restoration (e.g., Koziol et al., 2023). However, more research is needed to test the viability of AM fungal inoculum approaches at scale for sustainable agriculture goals, which includes evaluating their effects beyond plant productivity to include soil health measures.

New Technologies to Scale Mycorrhizal-Based Soil Health Monitoring

The United Nations recently warned that 90% of soil could be at risk of degradation by 2050, with intensive agriculture being a key culprit (Cherlet et al., 2018). Given the sheer scale of this problem, the most valuable soil health metrics are likely those which can be repeatably and cost-effectively deployed across considerable spatial scales to track our global progress in adopting more sustainable management practices. Unfortunately, we lack efficient methods to precisely monitor mycorrhizal fungal abundance, diversity, and function across large areas over time. As a result, there are enormous challenges in adopting any mycorrhizal-based metric of soil health. The issue is largely in scalability: mycorrhizal fungal communities are difficult to monitor because samples can be time-intensive to collect, typically require specific lab conditions to process, often represent a snapshot in time, tend to cover relatively small areas, and samples can take weeks to months for proper quality control and analysis, as this usually involves bioinformatics of large eDNA sequencing datasets **(Box 2, page 6)**. New technological innovations will be required to move beyond site-level assessments.

Hyperspectral imaging is a powerful tool that is increasingly being used to remotely measure and monitor aboveground features of plant vegetation (Jetz et al., 2016; Wang et al., 2020), including for agriculture applications (Lu et al., 2020). Spaceborne or airborne images are cap-

Box 2. Methods of measuring AM fungi in environmental samples

DNA amplicon sequencing – Extraction of DNA from sample (soil or root material), PCR amplification with fungal primers, sample barcoding and library multiplexing, molecular sequencing, and bioinformatic processing of amplicon reads (Tedersoo et al., 2022).

Fungal biomass – Concentration of fatty acid markers present in AM fungal cell membranes (e.g., neutral lipid fatty acid 16:1ω5) measured via lipid extraction from sample, purification with silicic acid chromatography, separation with gas chromatography, and quantification with a mass spectrometer (Frostegård & Bååth, 1996; Lekberg et al. 2022). Other fungal cell wall markers (e.g., chitin, ergosterol, and phospholipid fatty acid 16:1ω5) can also be quantified but are less specific to AM fungi.

Hyphal length – Aqueous extraction, membrane filtration, staining of fungal cell wall material (e.g., trypan blue or non-toxic ink stains), and quantifying hyphal length via gridline intersection method (Brudrett, 1994).

Root colonization – Root material isolation and washing to remove attached soil particles, staining of fungal cell wall material (e.g., trypan blue or non-toxic ink stains), quantify proportion of root length colonized via gridline intersection method (Giovannetti & Mosse, 1980), and identify AM fungal structures (e.g., hyphae, vesicles, arbuscules) (McGonigle et al., 1990).

Spore density – Wet sieving of soil sample through fine mesh (45 µm), centrifugation in a sucrose solution, and counting via microscopy or Hemocytometer (Gerdemann & Nicolson, 1963).

tured over a specific area using a sensor that measures a wide range of wavelengths. Imaging spectrometers capture information across the electromagnetic spectrum based on refracted wavelengths from the Earth's surface. The images can contain a wealth of information about plant reflectance properties (e.g., color, texture, geometry, and chemical composition). These properties are then connected to key ecological processes. Specifically, light reflectance signatures from vegetation, parsed into visible and non-visible wavelength bands, are processed into estimates of ecosystem function (e.g., Net Primary Productivity and Normalized Difference Vegetation Index), leaf functional traits (e.g., leaf area and mass, nutrient profiles, and water content), and species designations. Because remote sensing data are often calibrated with extensive field datasets, these tools show immense promise for monitoring key ecosystem health at finer spatial and temporal resolutions than on-the-ground surveys alone (Anderson, 2018). It is anticipated that new fleets of hyperspectral sensors will soon deliver higher resolution images (30m or less), complete with hundreds of spectral bands on a submonthly basis (Cawse-Nicholson et al., 2021). So far, spectral remote sensing technology has proven capable of creating highly detailed spatial models of biodiversity and ecosystem functioning (Cavender-Bares et al., 2022a), as well as estimating crop biochemical features, evaluating crop stress, and detecting weeds and foliar diseases (Lu et al., 2020). However, this work has almost exclusively focused on aboveground vegetative dynamics. The application of spectral imaging for underground ecosystems remains a significant frontier.

To date, the applications of remote sensing tools to detect soil microbial changes have used plant traits as an intermediary. In two experimental prairie systems, airborne imagery quantifying ecosystem productivity and plant functional traits were compared with soil microbial measurements (Cavender-Bares et al., 2022b). While there was success in predicting microbial biomass, bacterial and fungal diversity, soil respiration rates, and extracellular enzyme activity levels, some of the correlations between the image-derived variables and microbial variables were inconsistent between sites. In forest ecosystems, remotely sensed spectral data of tree canopies show consistent divergence between types of tree mycorrhizal associations (Fisher et al., 2016; Sousa et al., 2021), which might be helpful mapping soil carbon and nutrient dynamics due to predictable differences in mycorrhizal resource gathering strategies (Phillips et al., 2013). However, recent work has called into question whether mycorrhizal differences or plant evolutionary history are driving these unique forest spectral signatures (Jantzen et al., 2023). Results from natural forest ecosystems may also be inapplicable in agroecosystems for a variety of reasons (e.g., crop plants overwhelming form only the AM symbiosis type, and some are non-mycorrhizal), emphasizing the need to apply remote sensing tools specifically for plant-mycorrhizal symbioses in crop systems.

These studies are the first exploration of how high-dimensional spectral imagery may be used to characterize underground ecosystems. However, to date there have been no studies utilizing hyperspectral data to extract unique soil biodiversity patterns directly. It is possible that this may be unfeasible – plant spectral signals could be too convoluted to parse into AM fungal components against competing effects of soil fertility, symbiont and pathogen abundance, plant genotype, and varying climatic and soil conditions. Given this, we define three key research areas for evaluating the potential of remote sensing tools for linking aboveground imagery to AM fungal abundance, diversity, and soil health.

1. Develop mycorrhizal reference datasets

First, mycorrhizal datasets are needed in which soils are collected directly in-sync with airborne observations. This will involve sampling specific agricultural fields and grasslands during known or routine flyovers by satellites or aircraft. These datasets are essential for calibrating the first generation of models using remote sensing data to make underground spatial predictions **(Figure 3, page 10)**. Ideally, these reference datasets would include various measurements, including mycorrhizal abundance and diversity (root colonization, richness estimates, endemic species, community composition), functional traits (spore densities, hyphal length), and even genomic information (gene clusters associated with carbohydrate metabolism and other carbon or nutrient dynamics) (Chaudhary et al., 2022). Once acquired, models can undergo similar testing, training, and validation steps established for other types of remotely sensed variables, such as individual tree species mapping in Panama (Baldeck et al., 2015) and plant functional trait mapping across the Peruvian Amazon (Asner et al., 2016).

These ground-truthed reference datasets are critical for developing base models to expand remote sensing measurement capabilities for mycorrhizal variables.

Specifically, there is a need to establish clear connections between remotely sensed mycorrhizal metrics and other soil health indicators, such as soil organic carbon, carbon mineralization, or aggregate stability. Repeated measurements over the same locations undergoing aboveground land-use or management changes will also be critical. This is because specific analyses are needed to test whether changes in land management aimed at improving soil health goals are linked to detectable changes in remotely sensed mycorrhizal measurement. For instance, algorithms are already being developed to detect whether regenerative agriculture practices (e.g., no-till, cover cropping) are adopted in specific fields over specific time periods (Melaas et al., 2024), and it may be possible to incorporate mycorrhizal metrics into these workflows. Space-for-time surveys may also be useful here, such as imaging transects over different farm management types in the same area to set comparative baselines. Ultimately, these reference datasets will help determine whether any fungal-based spectral measures are useful for remotely quantifying and tracking soil health.

2. Define mycorrhizal mechanisms in spectral biology

A second key step to better utilize remote sensing tools to track mycorrhizal symbioses and abundance is to define the ways in which spectral data are influenced by mycorrhizal specific changes. It is well established that mycorrhizal fungi impact the chemical and physical structure of plants. As a result, there are multiple pathways by which these fungal symbionts could be influencing the hyperspectral reflectance data of terrestrial vegetation. Some reflectance patterns may be attributable to certain mycorrhizal variables over others. For example, changes could depend on which specific fungal species are present or simply on the total abundance of the whole fungal community. It will be necessary to test which mycorrhizal variable (e.g., root colonization, community diversity, spore or hyphal biomass, or individual species distributions) has the strongest correlation/signal to foliar reflectance data and with what level of certitude. It will also be important to determine how these mycorrhizal variables interact with abiotic factors, such as soil resources, nutrient availability and/or the surrounding vegetation context. This effort will require a combination of controlled experiments and strategic field measurements. Controlled experiments are needed to manipulate the abundance and diversity of AM fungi, vary soil resource conditions, and hold all other variables constant. These study designs will provide the clearest evidence for if and how AM fungi belowground mediate leaf spectral signatures aboveground through nutrient symbiosis mechanisms. Strategic field measurements are also needed to collect foliar reflectance images across different agriculture practices aimed at enriching AM fungi. For instance, if cover cropping in certain areas is known to improve AM fungal colonization in cash crops, comparing spectral data from cash crop fields following cover crop vs. bare fallow treatments could help determine how positive AM fungal management shapes remotely sensed leaf traits. Additional field studies could focus on phylogenetically similar crop species that are known to vary between AM symbioses vs. non-mycorrhizal states, which may help disentangle mycorrhizal-specific drivers of leaf spectral properties. A clearer understanding of the mechanisms by which mycorrhizal fungi are physiologically linked to plant trait profiles measured via leaf reflectance imagery will accelerate the usefulness and confidence in using satellite data to extend remote sensing applications underground.

3. Design mycorrhizal-specific sensors

The third step is to innovate towards mycorrhizal-specific spectral sensors. This is likely the hardest, but arguably most important step. Ideally, new types of earth observation sensors could be uncovered to pinpoint mycorrhizal-specific biomarkers from plant tissue. For example, bluemenols are a new group of apocarotenoid signal molecules that may be a chemical indicator for mycorrhizal symbioses (You et al., 2023). A recent experiment found greater concentrations of bluemenol metabolite compounds in leaf tissues of plants with higher arbuscular mycorrhizal root colonization rates (Wang et al., 2018). Although the mechanism of this fungal-mediated metabolite transport into leaf tissues is unknown, bluemenols could be a promising target for developing new types of imaging sensors to remotely detect mycorrhizal colonization rates.

Ergothioneine is an amino acid synthesized by fungi (and some bacteria) that ultimately ends up in plant tissues as a beneficial dietary component, possibly through mycorrhizal symbioses (Carrara et al., 2023). Because this compound is not synthesized by plants, this could be a potential leaf chemical target to measure the intensity of mycorrhizal resource exchange. If this (or similar) foliar compounds can be isolated in hyperspectral data, this would open the door to measure spectral signatures of mycorrhizal-specific information at scale.

There may also be other types of mycorrhizal-specific metabolites that appear in plant tissue, or individual slices of electromagnetic bands isolatable from the next generation of spectral technologies that can specifically target fungal symbiosis effects. For instance, NASA's Landsat NeXt program, scheduled to launch May 2031, aims to collect superspectral information with more than double the number of spectral bands (26 total) at 3x finer spatial resolution (10m) and 10-days quicker temporal revisiting (https://landsat.gsfc.nasa.gov/satellites/landsat-next/). We are still at the beginning stages of using these tools for aboveground earth observations. However, the continued improvement of these technologies may unlock a greater potential for remotely observing the diversity and functioning of mycorrhizal networks underground.

Conclusions

AM fungi are likely to be strong bioindicators of soil health in agriculture ecosystems. We present an overview of how AM fungi significantly contribute to soil structure, nutrient cycling, carbon sequestration, and resilience against environmental stressors. This, in combination with their sensitivity to various agriculture practices, including tillage, fertilization, and pesticide application, makes them an excellent metric to assess and monitor soil health. We highlight that sustainable management practices aimed at improving soil also tend to promote AM fungal abundance and diversity, with massive space to explore different combinations of soil management approaches. Rapid developments and technological breakthroughs in earth observation via remote sensing could soon be applicable for underground biodiversity, with these tools significantly expanding the speed and scale of mycorrhizal fungal and soil health data collection. ■

Peer Reviewers

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Figures

Figure 1. The mechanisms by which AM fungi potentially influence soil health. Benefits of a thriving AM fungal community can include: enhanced soil physical structure, production of organic compounds that impact carbon processing and soil microbiome composition, biological weather of soil minerals, and regulation of nutrient fluxes and leaching. Management practices that are detrimental to the abundance and diversity of AM fungi may therefore suffer worse soil health outcomes, such as increased nutrient loss and soil erosion.

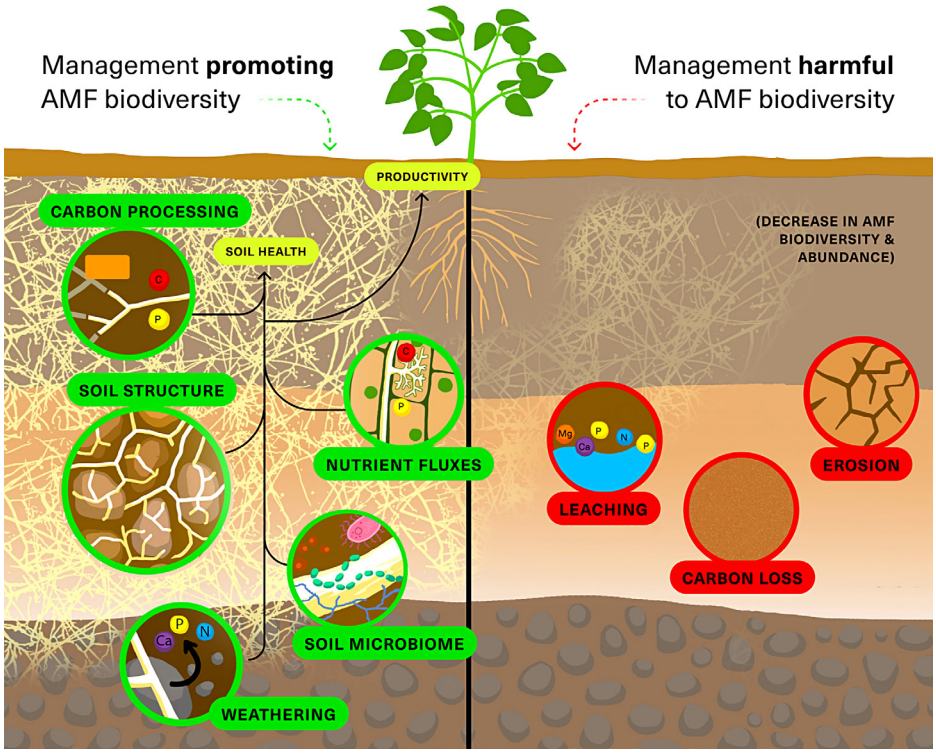


Figure 2. Pesticides reduce AM fungi. AM fungal abundance, measured by percent root colonization, is lower in fields with higher pesticide usage. Points are colored by farm management type, including organic (no addition of synthetic fertilizers or pesticides and tillage up to 25cm), No-till (no soil tillage but added synthetic fertilizers and pesticides), and conventional (tillage up to 25cm depth with synthetic fertilizers and pesticides). Data and figure from Riedo et al., 2021.

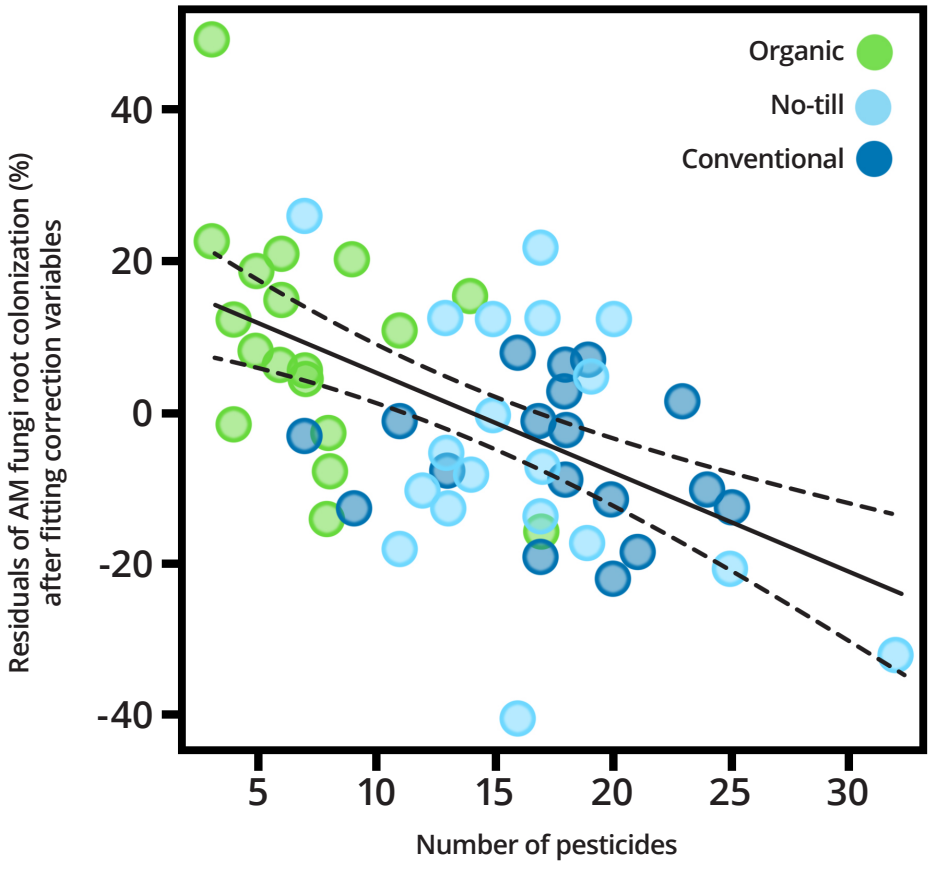
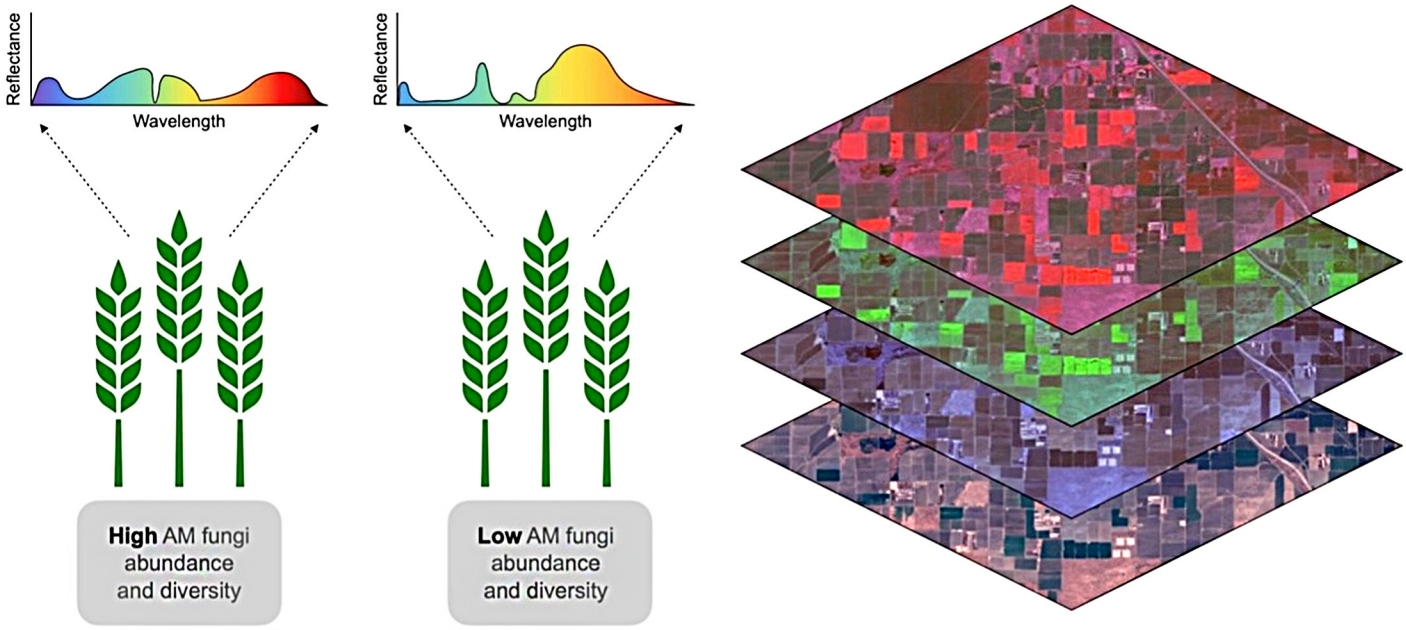


Figure 3. Overview of how remote sensing might be used to monitor belowground AM fungal indicators in agroecosystems. Management practices can result in different levels of AM fungal abundance and diversity, with consequences for soil health and plant nutrition. As a result, these AM fungal differences might appear in vegetative spectral signatures from airborne or spaceborne images (left). This is because different leaf structure, leaf morphology, plant water balance, and leaf nutrient concentrations are all likely to be affected by AM fungal links to plant and soil functioning. With sufficient data, machine-learning models can be trained to detect relationships between leaf spectra and AM fungi datasets, followed by ground-truthing and model validation across un-sampled regions. Assuming these steps are viable and successful, remote sensing tools could drastically increase underground monitoring abilities via changes in spectral signatures of crop systems (right), delivering critical information at significantly larger spatial and temporal scales than current field methods.



Tables

Table 1. Agricultural management practices and their effects on AM fungi

Management practice	AM fungal response	Soil health effect
Tillage	Reduces community diversity and stability (Gotshall et al., 2017). Disturbance-tolerant taxa increase in prevalence and often have less mutualistic traits (Chagnon et al., 2013).	Likely reduces AM fungal contributions towards crop growth, health and yields. Reduced AM fungal exudates contribute to soil structural degradation (Gotshall et al., 2017).
Cover crops	Increase AM fungal populations by eliminating periods of bare soil with no plant partners. Effects on AM fungi vary, and some crops can be detrimental, e.g., Brassicaceae (Bowles et al., 2017; Njeru et al., 2015).	AM fungal populations support soil structural integrity (Lehmann et al., 2017) and crop growth, productivity and disease resistance (Smith & Read, 2008).
Crop rotation	Facilitates an increased presence of AM fungi, possibly more species and functional types in soils. Including N-fixing plants can increase biomass of other rotation crops and AM fungi (Bowles et al., 2017).	Soils may better support a greater diversity of plant species. Increased soil organic matter and C storage (Tisdall & Oades, 1982).
Fertilization	Fertilization, especially with P, using natural or synthetic fertilizers reduces AM fungal abundance and diversity (Smith & Read, 2008).	Structural degradation from loss of AM fungi could limit the sustainability of productivity and reduce soil carbon storage and water retention.
Pesticides	Reduce AM fungal colonization of roots and can alter community composition, (Riedo et al., 2021). Fungicides reduce AM fungal diversity, abundance, and activity (Edlinger et al., 2022).	Reduced mutualistic symbioses with AM fungi are likely detrimental to crop growth, health and yields.
Herbicides	Glyphosate (Roundup®) can reduce AM fungal root colonization and spore viability, but effects may be context dependent (Druille et al., 2013b).	In restoration, herbicides may limit the ability of native plants to reestablish through loss of AM fungal partners (de Mesquita et al., 2023).
AM fungal inoculants	Inoculant persistence and symbiosis establishment are limited and likely highly context dependent. Can reduce prevalence and diversity of indigenous AM fungi (Islam et al., 2021).	Crop productivity benefits are likely highly taxon dependent (Kaminsky et al., 2019). Displacing indigenous AM fungi could limit reestablishment of native plants or success of traditional crops.

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