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OPINION

Sustainable and Resilient Agroecosystems Need Complexity of Soil Food Webs and Multivariate Soil Health Indicators

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ABSTRACT

WE need to adapt crop species and agricultural practices to produce high quantities of quality food for a growing world population, while also reducing the negative impact of agriculture on the environment to meet the targets of the Paris Agreement. It is increasingly recognised that healthy soils are at the heart of this endeavour, sustaining global geochemical cycles and the productivity of most terrestrial ecosystems. This ability of soils to support essential ecosystem services like nutrient cycling arises from diverse communities of soil organisms. Many ecosystem services are a function of how these soil organisms interact with each other, with the aboveground plant species and with the physio-chemical soil matrix. Here, we argue that multiple ecosystem processes and climate change resilience rely on diverse plant and soil communities with complex interactions among various actors carrying out complementary functions, rather than on individual indicator species on their own. We highlight areas of research which could be expanded to advance our understanding from single-species studies to the functional complexity of soil food webs and its integration into land management strategies with the aim to improve the resilience and sustainability of essential terrestrial ecosystems and the services they provide to the human population.

SUMMARY

- Healthy soils are central to achieving the Paris Agreement and sustainable food production goals.
- Multi- species interactions ensure ecosystem resilience, nutrient cycling, and stability.
- Understanding context dependency in biotic relationships requires linking taxonomy and function.
- Reliance on individual taxa as indicators risks incomplete insights to ecosystem functioning.

1. Resilience of Terrestrial Ecosystems Relies on Soil Biota Interactions

We need to adapt crop species and agricultural practices to produce sufficient quantities of high-quality food while reducing the impact of agriculture on the environment to meet the targets of the Paris agreement and feed a growing world population. It is increasingly recognised that healthy soils form the heart of this endeavour, which is why seven of the seventeen Sustainable Development Goals (SDGs) defined by the United Nations directly or indirectly address land and soil management (Lal et al. 2021), and why the European Commission launched the EU Mission: A Soil Deal for Europe to lead the transition towards healthy soils by 2030 (European Commission 2021). “Healthy Soil” is defined as a soil with the ability to sustain productivity, diversity, and ecosystem services of terrestrial environments (FAO 2020). Soil-based ecosystem services are an overarching concept referring to processes that sustain ecosystem functioning, such as water purification, carbon sequestration and cycling of nutrients (Schulte et al. 2014). Many of these processes that sustain crop growth and ecosystem functioning depend on the activity of soil organisms (Figure 1; De Vries et al. 2013). The level of biodiversity found in soils is comparable to that of tropical rainforests (Giller 1996). To unravel the complexity of soil biodiversity as a whole, we therefore highlight that the use of new technologies and advances in the analysis of multi-species interactions and microbial networks can provide new insights which will be useful for understanding processes that provide resilience and identify adaptation strategies that work in the face of climate change (Guseva et al. 2022; Awais et al. 2023; Hnini et al. 2024; Shen and Duan 2024). This goes beyond single-species studies because fostering soil biodiversity for the benefit of the whole ecosystem requires functional diversity and redundancy, and niche complementarity, in a diverse network of co-occurring organisms. More complex food webs with many species and trophic and non-trophic interactions may also allow more flexible adaptation to different climatic conditions and plant species, potentially conferring ecosystem resilience and adaptability (Moore et al. 1993; Rønn et al. 2012; Bascompte 2009). Accordingly, a long-standing complexity-stability debate in ecology has been addressed with stability analyses of 116 quantitative food webs, concluding that none of the common metrics of food web complexity, that is species richness, connectance and interaction strength, were associated with stability (McCann 2000; Jacquet et al. 2016). Instead, the effect of prey on predators and the effects of predators on prey, together with many weak interactions, which can only occur in sufficiently diverse ecosystems, stabilise food webs. Thus, understanding how different trophic levels interact to maintain biodiversity and measuring the strength of their interactions is key to understanding agroecosystem stability.

2. Diverse Soil Organisms and Their Intricate Interactions Drive Biogeochemical Cycles

Across temporal and spatial scales, ants, archaea, bacteria, earthworms, fungi, nematodes, protists, rotifers, springtails, termites, and many other organisms interact to sustain ecosystem services and together constitute the networks that directly drive biogeochemical cycles and disease dynamics (Table 1). Soil organisms drive biogeochemical cycles by catalysing redox reactions, which are essential for nutrient cycling and energy flows in ecosystems. These reactions include nitrogen fixation, nitrification, and denitrification, which regulate the availability of nitrogen, a critical nutrient for plant growth (Ma et al. 2021). The nitrogen cycle is closely linked to the carbon cycle and the phosphorus cycle; for example, methane oxidation and carbon utilisation rates vary with phosphorus bioavailability (Luo et al. 2022). These couplings are essential for maintaining ecosystem balance and nutrient availability and depend on a diverse range of soil organisms carrying out complementary processes across time.

FIGURE 1 *- Soil biodiversity underpins ecosystem services critical for agriculture such as nutrient cycling, soil structure, water retention, and plant growth. However, interactions among soil organisms, crops, and the physical soil matrix vary spatially and temporally. Therefore, translating soil biodiversity research into agricultural practices and policies requires data that captures these dynamics. Only multivariate data can guide the development of soil health indicators that take local and seasonal variability into account and thus can provide tailored recommendations.*

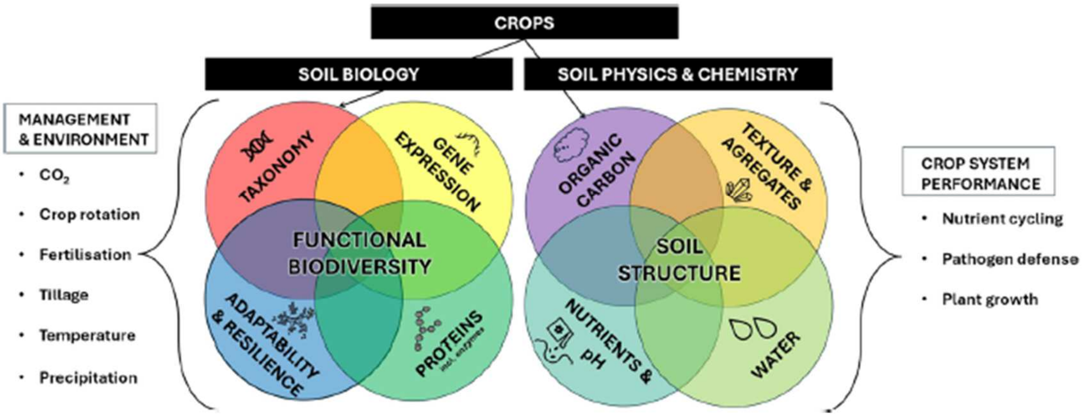
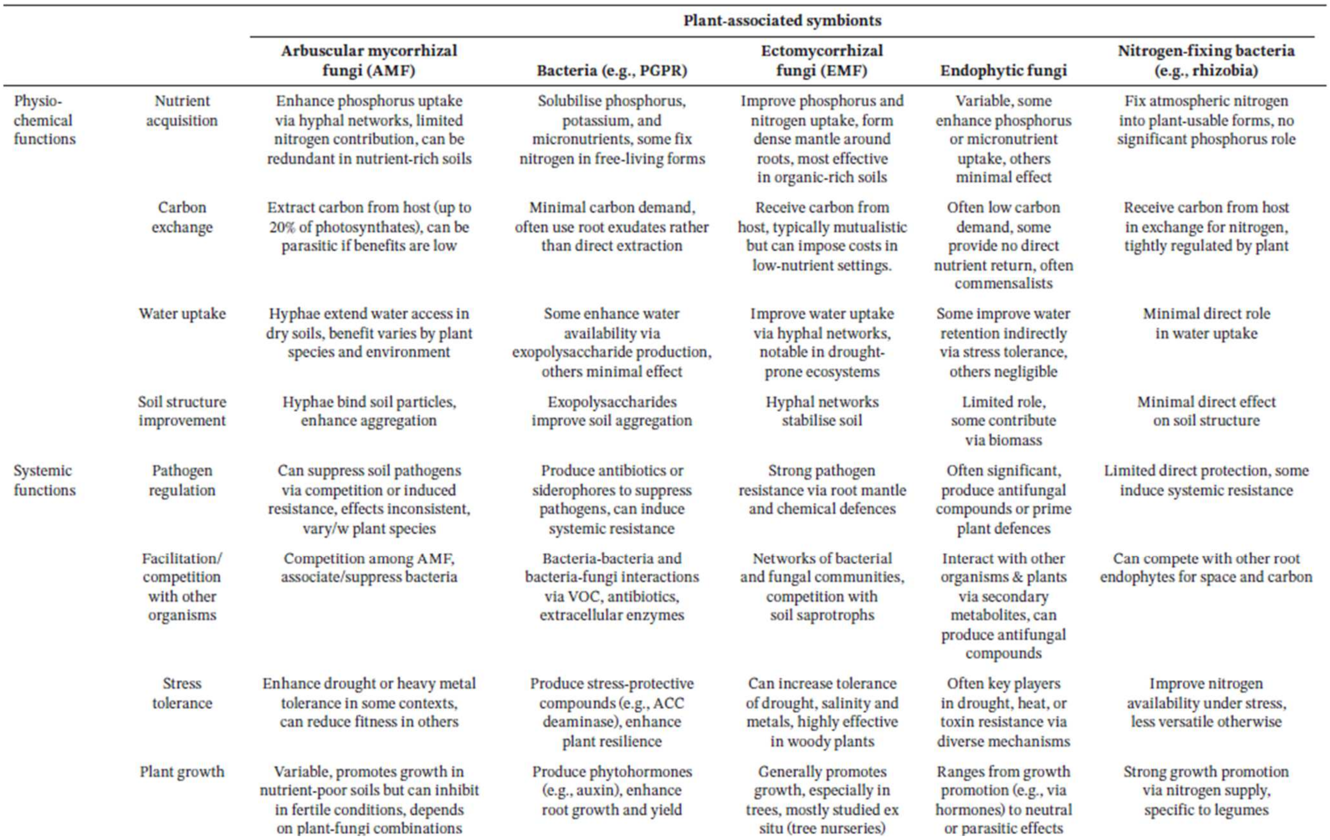


TABLE 1 *- Exemplary functional groups found in most soil food webs, their putative contributions to carbon and nutrient cycling, water retention and soil structure, systemic contributions along the mutualism–parasitism continuum, and estimated abundance and diversity for each group.*



		Plant-associated symbionts				
		Arbuscular mycorrhizal fungi (AMF)	**Bacteria (e.g., PGPR)**	**Ectomycorrhizal fungi (EMF)**	**Endophytic fungi**	**Nitrogen-fixing bacteria (e.g., rhizobia)**
Physio-chemical functions	Nutrient acquisition	Enhance phosphorus uptake via hyphal networks, limited nitrogen contribution, can be redundant in nutrient-rich soils	Solubilise phosphorus, potassium, and micronutrients, some fix nitrogen in free-living forms	Improve phosphorus and nitrogen uptake, form dense mantle around roots, most effective in organic-rich soils	Variable, some enhance phosphorus or micronutrient uptake, others minimal effect	Fix atmospheric nitrogen into plant-usable forms, no significant phosphorus role
	Carbon exchange	Extract carbon from host (up to 20% of photosynthates), can be parasitic if benefits are low	Minimal carbon demand, often use root exudates rather than direct extraction	Receive carbon from host, typically mutualistic but can impose costs in low-nutrient settings.	Often low carbon demand, some provide no direct nutrient return, often commensalists	Receive carbon from host in exchange for nitrogen, tightly regulated by plant
	Water uptake	Hyphae extend water access in dry soils, benefit varies by plant species and environment	Some enhance water availability via exopolysaccharide production, others minimal effect	Improve water uptake via hyphal networks, notable in drought-prone ecosystems	Some improve water retention indirectly via stress tolerance, others negligible	Minimal direct role in water uptake
	Soil structure improvement	Hyphae bind soil particles, enhance aggregation	Exopolysaccharides improve soil aggregation	Hyphal networks stabilise soil	Limited role, some contribute via biomass	Minimal direct effect on soil structure
Systemic functions	Pathogen regulation	Can suppress soil pathogens via competition or induced resistance, effects inconsistent, vary/w plant species	Produce antibiotics or siderophores to suppress pathogens, can induce systemic resistance	Strong pathogen resistance via root mantle and chemical defences	Often significant, produce antifungal compounds or prime plant defences	Limited direct protection, some induce systemic resistance
	Facilitation/ competition with other organisms	Competition among AMF, associate/suppress bacteria	Bacteria-bacteria and bacteria-fungi interactions via VOC, antibiotics, extracellular enzymes	Networks of bacterial and fungal communities, competition with soil saprotrophs	Interact with other organisms & plants via secondary metabolites, can produce antifungal compounds	Can compete with other root endophytes for space and carbon
	Stress tolerance	Enhance drought or heavy metal tolerance in some contexts, can reduce fitness in others	Produce stress-protective compounds (e.g., ACC deaminase), enhance plant resilience	Can increase tolerance of drought, salinity and metals, highly effective in woody plants	Often key players in drought, heat, or toxin resistance via diverse mechanisms	Improve nitrogen availability under stress, less versatile otherwise
	Plant growth	Variable, promotes growth in nutrient-poor soils but can inhibit in fertile conditions, depends on plant-fungi combinations	Produce phytohormones (e.g., auxin), enhance root growth and yield	Generally promotes growth, especially in trees, mostly studied ex situ (tree nurseries)	Ranges from growth promotion (e.g., via hormones) to neutral or parasitic effects	Strong growth promotion via nitrogen supply, specific to legumes

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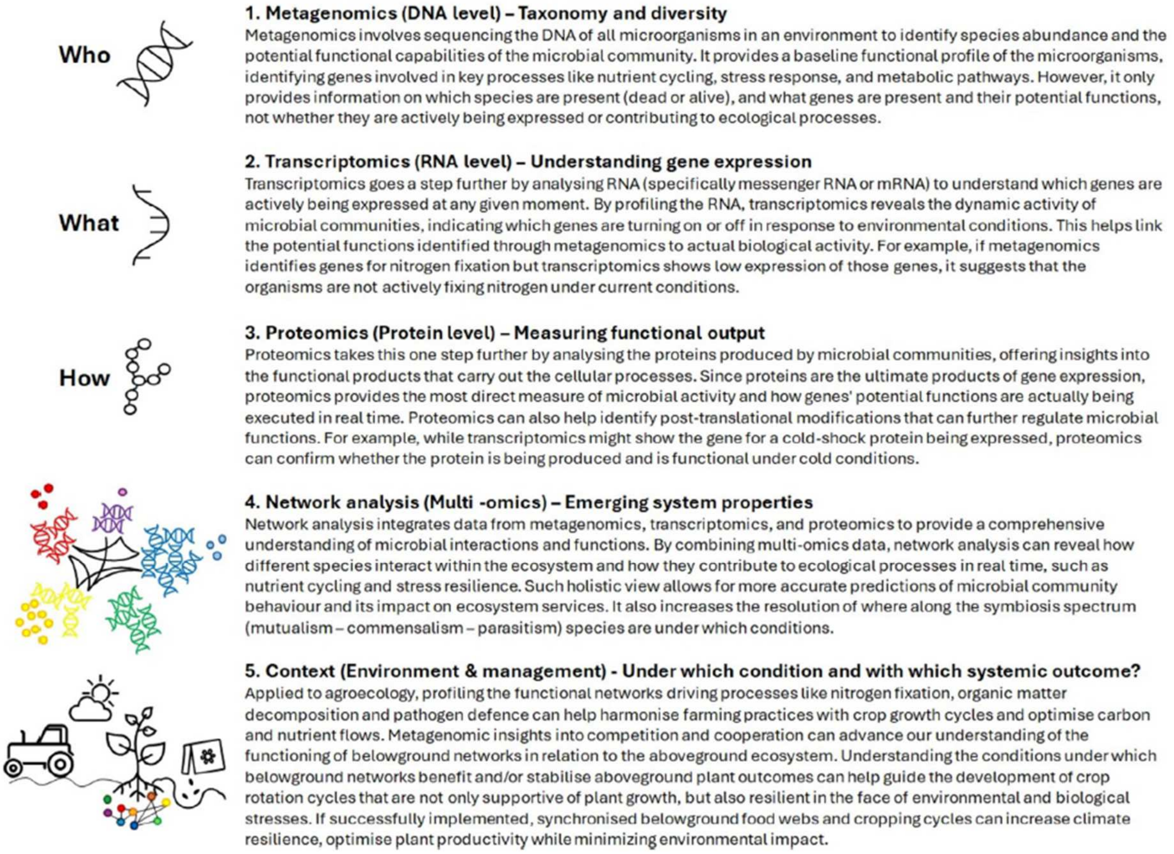
		Arbuscular mycorrhizal fungi (AMF)	**Bacteria (e.g., PGPR)**	**Ectomycorrhizal fungi (EMF)**	**Endophytic fungi**	**Nitrogen-fixing bacteria (e.g., rhizobia)**
Abundance and diversity	Ecosystem distribution	Mostly studied in laboratory, widespread in grasslands, less abundant in forests or nutrient-rich systems, inoculation produces variable results for crops	Ubiquitous in soils and plant tissues, dominant in rhizosphere	Dominant in temperate and boreal forests, rare in grasslands.	Ubiquitous across ecosystems, highly diverse and adaptable	Specific to legumes and some non-legumes, patchy distribution
	Estimated number of species/ examples	~240 species, + more putative OTUs, incl. *Glomus intraradices, Rhizophagus irregularis*	Millions of soil bacteria, e.g., *Pseudomonas fluorescens, Bacillus subtilis*	~10,000 species (mostly Basidiomycota), e.g., *Boletus edulis, Pisolithus tinctorius*	Thousands, but poorly defined group, incl. *Trichoderma harzianum, Piriformospora indica*	~200–300 species, incl. *Rhizobium leguminosarum, Bradyrhizobium japonicum*

		Soil free-living						
		Collembola	**Earthworms**	**Free-living bacteria**	**Free-living fungi**	**Mites**	**Nematodes**	**Protozoa**
Physio-chemical functions	Nutrient acquisition	Fragment litter, enhance microbial N, P release, increase decomposition by fragmenting litter	Mix and mineralize nutrients via gut action, accelerate decomposition via mixing, digestion	Mineralize organic compounds, key in N, C cycles, accelerate decomposition via mixing, digestion	Decompose organic matter, releasing C, N, P, slow decomposition of complex substrates	Shred organic matter, enhance decomposition, aid microbial cycling	Regulate nutrient release via microbial predation, accelerate decomposition via microbial grazing	Mineralize N, P via bacterial predation, boost decomposition via bacterial grazing
	Carbon exchange	Physically break down C-rich litter	Transform C via digestion & casting	Rapidly degrade simple C compounds	Break down complex C (e.g., lignin) via enzymes	Degrade C via fragmentation, fungal grazing	Indirect via feeding on C-processing microbes	Release C via bacterial grazing
	Water uptake	Enhance soil porosity, water infiltration	Burrows improve water infiltration	Exopolysaccharides aid water retention	Hyphae retain soil moisture	Burrowing aids water movement	Minimal, some affect porosity	Minimal, some influence moisture via activity
	Soil structure improvement	Fragmentation, burrowing improve aeration	Burrows & casts enhance aggregation	Exopolysaccharides glue soil particles	Hyphae bind aggregates & stabilise structure	Fragmentation & tunnelling stabilise soil	Burrowing enhances aeration & porosity	Minimal, some aid micro-aggregation

		Soil free-living						
		Collembola	**Earthworms**	**Free-living bacteria**	**Free-living fungi**	**Mites**	**Nematodes**	**Protozoa**
Systemic functions	Pathogen regulation	Limited, graze on fungal pathogens	Reduce pathogens via gut processing	Produce antibiotics & siderophores	Antagonise pathogens via competition, antibiotics	Some suppress pathogens via grazing	Prey on pathogenic microbes, biocontrol	Prey on pathogenic bacteria
	Facilitation/ competition with other organisms	Top-down control?, graze on bacteria & fungi, can compete with other arthropods & mites	Top-down control?, can compete with other soil fauna for food	Competition for resources (C, N, etc.) in microsites, can produce antibiotics	Fungi-fungi and fungi-bacteria interactions via VOC, antibiotics, extracellular enzymes, mycotoxins	Top-down control?, can compete with other soil fauna for microbial prey and root resources/ space, graze on fungal hyphae	Top-down control?, can compete with other soil fauna for microbial prey and root resources/space	Can compete with other soil fauna for bacterial prey
	Stress tolerance	Tolerate drought, pollutants, enhance resilience	Buffer soil against drought & compaction	Form spores & biofilms to survive stress	Resist drought & metals pollution via spores	Some resist desiccation & toxins	Survive stress via cryptobiosis	Survive extremes via cysts
	Plant growth	Enhance nutrient availability, minimal direct effect	Increase nutrient cycling & soil aeration	Increase nutrient mineralization, hormone production, some neutral	Variable, some beneficial via nutrient release, others compete with plants for resources	Increase nutrients through decomposition, some may graze on beneficial fungi	Mixed, beneficial via microbial regulation, but some are parasitic	Aid nutrient release from bacterial grazing
Abundance and diversity	Ecosystem distribution	Common in litter, topsoil, vary by habitat	Widespread, prefer moist, organic soils	Ubiquitous, occur in rhizosphere and bulk soil	Ubiquitous, dominant in organic-rich soils	Ubiquitous in diverse habitats, incl. litter & soil	Widespread, abundant in moist soils	Ubiquitous in moist soils & water films
	Estimated number of species/ examples	~8000 species, incl. *Folsomia candida, Entomobrya nivalis*	~6000 species, incl. *Lumbricus terrestris, Eisenia fetida*	Millions, incl. *Bacillus cereus, Streptomyces coelicolor*	~100,000 species, incl. *Trichoderma reesei, Penicillium chrysogenum*	~40,000 species, incl. *Oribatida* spp., *Tetranychus urticae*	~25,000 species, incl. *Caenorhabditis elegans, Pratylenchus* spp.	~30,000 species, incl. *Amoeba proteus, Paramecium* spp.

FIGURE 2 - *Data pipeline which can help deepen our understanding of belowground networks and emerging ecosystem services. Accurate prediction models for soil biodiversity behaviour, which ultimately can guide the development of multivariate soil health indicators scalable to local contexts, rely on a suite of parameters which in turn require various methods to measure them. These parameters include taxonomic diversity (e.g., species richness, Shannon index), functional metrics (e.g., enzyme activity, gene expression), trophic interactions (e.g., predation, stable isotope tracing) and ecosystem functions (e.g., decomposition, nutrient cycling, plant productivity), measured against the background of varying environmental factors (e.g., soil moisture, pH), and anthropogenic drivers (e.g., land use, pollution). These parameters are integrated into statistical, including machine-learning, models to forecast how soil communities respond to conditions like climate change or land management, and what the systemic outcome in terms of plant productivity is. Long-term field data are crucial for validating these models and capturing dynamic, multi-species interactions over time*



1. Metagenomics (DNA level) – Taxonomy and diversity

Metagenomics involves sequencing the DNA of all microorganisms in an environment to identify species abundance and the potential functional capabilities of the microbial community. It provides a baseline functional profile of the microorganisms, identifying genes involved in key processes like nutrient cycling, stress response, and metabolic pathways. However, it only provides information on which species are present (dead or alive), and what genes are present and their potential functions, not whether they are actively being expressed or contributing to ecological processes.

2. Transcriptomics (RNA level) – Understanding gene expression

Transcriptomics goes a step further by analysing RNA (specifically messenger RNA or mRNA) to understand which genes are actively being expressed at any given moment. By profiling the RNA, transcriptomics reveals the dynamic activity of microbial communities, indicating which genes are turning on or off in response to environmental conditions. This helps link the potential functions identified through metagenomics to actual biological activity. For example, if metagenomics identifies genes for nitrogen fixation but transcriptomics shows low expression of those genes, it suggests that the organisms are not actively fixing nitrogen under current conditions.

3. Proteomics (Protein level) – Measuring functional output

Proteomics takes this one step further by analysing the proteins produced by microbial communities, offering insights into the functional products that carry out the cellular processes. Since proteins are the ultimate products of gene expression, proteomics provides the most direct measure of microbial activity and how genes' potential functions are actually being executed in real time. Proteomics can also help identify post-translational modifications that can further regulate microbial functions. For example, while transcriptomics might show the gene for a cold-shock protein being expressed, proteomics can confirm whether the protein is being produced and is functional under cold conditions.

4. Network analysis (Multi -omics) – Emerging system properties

Network analysis integrates data from metagenomics, transcriptomics, and proteomics to provide a comprehensive understanding of microbial interactions and functions. By combining multi-omics data, network analysis can reveal how different species interact within the ecosystem and how they contribute to ecological processes in real time, such as nutrient cycling and stress resilience. Such holistic view allows for more accurate predictions of microbial community behaviour and its impact on ecosystem services. It also increases the resolution of where along the symbiosis spectrum (mutualism – commensalism – parasitism) species are under which conditions.

5. Context (Environment & management) - Under which condition and with which systemic outcome?

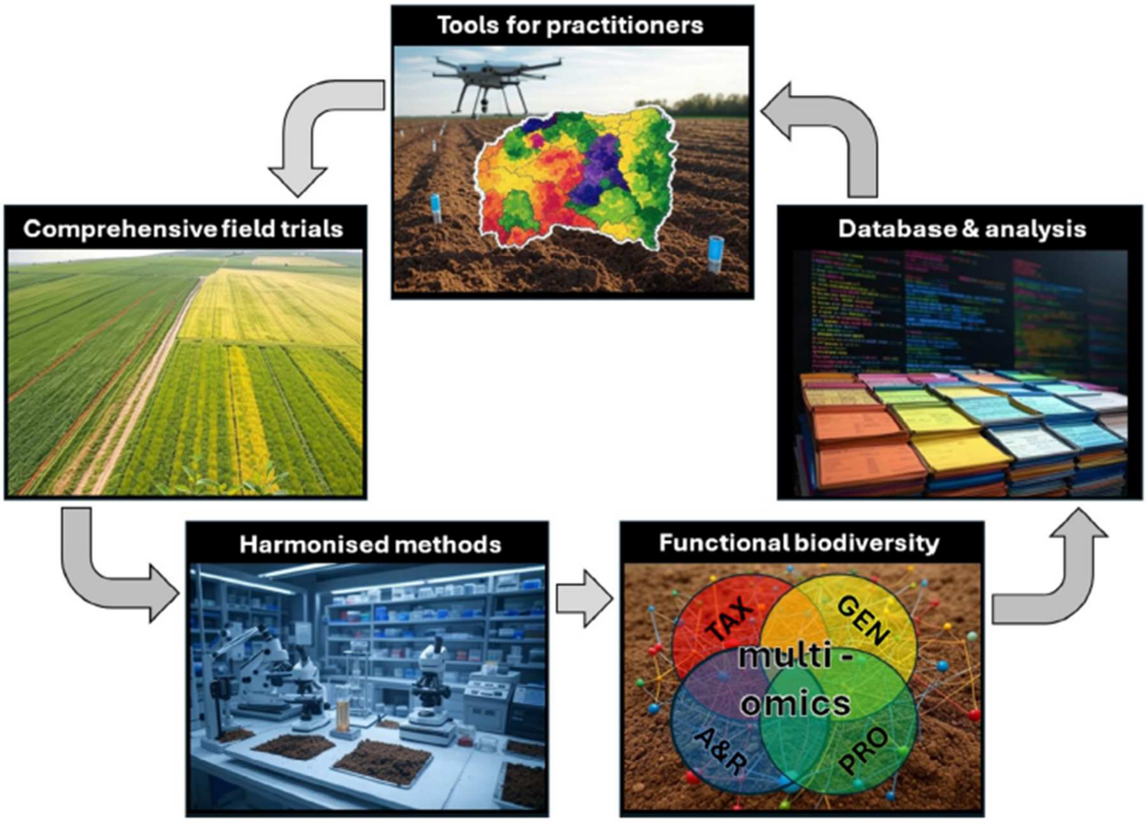
Applied to agroecology, profiling the functional networks driving processes like nitrogen fixation, organic matter decomposition and pathogen defence can help harmonise farming practices with crop growth cycles and optimise carbon and nutrient flows. Metagenomic insights into competition and cooperation can advance our understanding of the functioning of belowground networks in relation to the aboveground ecosystem. Understanding the conditions under which belowground networks benefit and/or stabilise aboveground plant outcomes can help guide the development of crop rotation cycles that are not only supportive of plant growth, but also resilient in the face of environmental and biological stresses. If successfully implemented, synchronised belowground food webs and cropping cycles can increase climate resilience, optimise plant productivity while minimizing environmental impact.

Neglecting any of these organisms can lead to an incomplete representation of soil functioning. Yet, many soil organisms with significant contributions to biogeochemical cycling and organic matter decomposition are under-represented in soil studies and models (Peguero et al. 2019). Nematodes, for example, are mostly famous for their negative impact on plants through root damage and transmission of diseases, but their activity can also increase soil nutrient availability by up to 25% and lead to improved plant growth (Gebremikael et al. 2016; Briones 2018). Similarly, some *Bacillus* species can improve phosphorus bioavailability and thus enhance plant productivity; *Rhizobium* can fix atmospheric nitrogen and convert it into bioavailable forms; some *Pseudomonas* produce antibiotics that suppress plant pathogens; and of course some fungi in the *Glomeromycota* clade can facilitate plant nutrient uptake through their extensive mycorrhizal networks (Bakki et al. 2024; Durairaj et al. 2017; Lindström and Mousavi 2020). And within a broad community of diverse soil organisms, many species can engage in facilitative interactions creating a robust network that buffers against disturbances.

3. Soil Health Concepts Need to Account for Dynamics in Symbiotic Interactions

While researchers, and increasingly also policymakers, agree that soil organisms should be addressed more given their importance in global biogeochemical cycles, caution should be taken when picking out individual taxa as “indicator” or “keystone” species. Focussing on single organisms as if they were isolated entities acting independently in soils may provide mechanistic insights in a limited context, but it is hardly scalable to ecosystems which are governed by multi-species interactions where the ability of specific groups of organisms to support ecosystem processes always depends also on the other organisms present in the food web and on the local pedo- climatic context (Lehmann et al. 2020; Lutz et al. 2023). For instance, the complexity of ecological networks makes other parties (often in different trophic levels) set the context for changing the net effects of competitive interactions, such as when keystone predators exert top-down control in lower trophic levels by alleviating competition, thereby preventing competitive exclusion and contributing to the maintenance of biodiversity (Paine 1966). Studies focusing on individual organisms while isolating their activity from the broader soil biodiversity network, and a bias towards publishing positive rather than negative, or no, effects of an interaction, impede our ability to understand how different organisms with similar functions can co-exist and complement each other, and how soil biodiversity networks can adapt and function under varying environmental and climatic conditions.

FIGURE 3 *- Integrating functional soil biodiversity into agronomic land management is essential for crop productivity, sustainability and resilience. High resolution data acquisition using harmonised sampling and analysis protocols precedes the development of soil health indicators, which can then be used to guide agronomic practices. (As in Figure 1): A&R, adaptability and resilience; GEN, Gene expression; PRO, proteins; TAX, Taxonomy.*



The term "symbiosis" is often used in multi-species interactions. Symbiosis describes a spectrum of interactions covering "mutualism" where both symbiotic partners gain benefits from the interaction, "parasitism" which is when one organism lives at the expense of another, and "commensalism", in which one species obtains food or other benefits from its symbiont without harming nor benefiting the latter (Encyclopaedia Britannica 2023). It is agreed that the character of almost any symbiotic interaction is context-and case dependent, often a trade-off between competition and survival and, by definition, not always mutually beneficial (Bicharanloo et al. 2023; Lutz et al. 2023; Spake et al. 2023). In nature, the interactions between symbiotic partners oscillate between mutualism, commensalism and parasitism, and therefore results can vary widely between studies (Roy-Bolduc and Hijri 2011; Hammer et al. 2011; Gómez et al. 2023). The popular plant association with arbuscular mycorrhizal fungi (AMF), for example, is à priori context-dependent, where AMF colonisation of plant roots can have positive, negative, neutral or no effect on plant and ecosystem performance (Johnson et al. 1997; Neuhauser and Fargione 2004; Cheng et al. 2012; Ryan and Graham 2018; Peng et al. 2024). However, much remains to be discovered about this symbiosis and its environmental context dependency (Moreno Jiménez et al. 2024; Michel et al. 2025), especially because AMF were historically often studied without considering other organisms coexisting in soils and plant roots (Zhang, Feng, et al. 2024). Such a historically AMF-focused view risks overlooking the vast dimensions of diversity in soil and the multitude of interspecies and inter- kingdom interactions. In addition, given that AMF themselves are a comparably less diversified group of fungi (Redecker and Raab 2006) and that AMF themselves harbour endobacteria in their hyphae and spores (Desirò et al. 2014; Zhang, van der Heijden, et al. 2024) highlights the importance of studying AMF in the context of all the other soil organisms. A holistic approach, particularly enabled by new molecular methods, allows consideration of the presence and functions of AMF, their associated microbiome, and communities of other soil organisms together, thereby helping to design adaptation strategies for improved resilience of agroecosystems that go beyond the benefits of single-species studies (Figure 2; Singh et al. 2020). It is therefore imperative to better understand the conditions under which AMF, or any other symbiotic organism, are mutually beneficial for the involved plant species, how these interactions change over time and under variable environmental conditions, and how variability in these interactions relates to soil functions such as nutrient cycling and ecosystem stability. For this understanding, it is important to free research from affirmation bias and confirmation bias (Oswald and Grosjean 2004; Jeng 2006; Hoorens 2014), apply consistent and precise terminology (Neubauer et al. 2024), and be cautious about creating oversimplified narratives which can lead to misinformation and misrepresentation of scientific facts, as is discussed for common mycorrhizal networks in forests (Karst et al. 2023; Irwin 2024).

4. Soil Health in Agricultural Cropping Systems

Enhancing soil functions and beneficial soil biodiversity is especially critical in agricultural cropping systems, but rendered difficult because plant turnover is rapid, often with intensive application of fertilisers, pesticides, and tillage, which can negatively impact the establishment and the functioning of belowground nutrient-cycling networks maintained by diverse organisms, leading to reduced resistance and resilience of agroecosystems (Miyasaka and Habte 2001; Peng et al. 2024). Harnessing the full potential of soil biota for agricultural benefits will likely require a systemic shift away from high- yield, high- turnover cropping systems towards management practices that maintain the soil structure and the soil biome intact (Hartmann and Six 2023). Various options such as permanent plant cover, intercropping, or agroforestry can be implemented to benefit both biodiversity and crop yield/health (Li et al. 2022; Primieri et al. 2022). In line with the concepts of agroecology and One Health, plant diversification could be used as a major lever to activate ecological processes within the agroecosystem, in connection with the associated soil biodiversity (Evans and Leighton 2014; Duru et al. 2015).

Soil biodiversity, which includes free-living fungi, bacteria, nematodes, collembola, mites, earthworms, and protozoa, also plays a pivotal role in enhancing the resilience of agroecosystems, particularly under the pressures of climate change and extreme weather events (Table 1). Resilience in this context refers to the capacity of an agroecosystem to maintain its functions, including crop production, nutrient cycling, and soil structure, and recover from disturbances such as droughts, floods, heatwaves, or storms. Soil biodiversity contributes to resilience through functional redundancy, diverse interactions, and the provision of ecosystem services that buffer against environmental stressors (Durairaj et al. 2017; Peguero et al. 2019; Bakki et al. 2024; Hnini et al. 2024). By these means, soil biodiversity provides functional redundancy, with multiple species performing similar roles (e.g., decomposition, nutrient cycling). This diversity acts as an “insurance policy,” allowing ecosystems to maintain functions even if some species are lost or temporarily impaired due to climate stressors. For example, some heat-resistant microbial taxa respond to high temperatures, as they may occur with heat waves under global warming, by upregulating genes for proteins involved in microbial cell wall degradation and modification. These bacteria sustain their growth through necromass recycling from heat- sensitive taxa. This can buffer against N-shortages from the lacking activity of the dead species and shift microbial N-cycling potential towards N-mineralisation and assimilation under higher temperatures, along with reduced potential for conversions among inorganic N forms (Donhauser et al. 2021). Integrating phylogenetic data into soil management, for example, by selecting crop varieties with divergent traits, could also enhance microbiome functionality and resilience, although in some cases plant identity may override phylogeny (Leff et al. 2018; Jiang et al. 2022; Walkup et al. 2023; Wang et al. 2024). Moreover, climate change can exacerbate pathogen pressure both by weakening plants directly and by altering the growth optima of plant antagonists. Functional soil biodiversity comprises diverse microbial and faunal communities that can directly support crop performance and also indirectly benefit crops by suppressing soil-borne pathogens through competition, predation, and antibiotic production. For example, several bacteria (e.g., Pseudomonas spp.), fungi (e.g., Trichoderma spp.) and protozoa can produce antibiotics or outcompete pathogens, thus protecting crops (Rønn et al. 2012; Radu et al. 2021; Li et al. 2024). Furthermore, higher trophic levels (soil predators) can exert top- down indirect effects contributing to maintaining biodiversity and ecosystem functioning of soil food webs (e.g., Melguizo-Ruiz et al. 2020). Potentially, myriads of these propagating indirect effects on soil food webs can affect soil biodiversity, functioning, and health. Research and management aimed at optimising biodiversity for agroecosystem functioning are therefore paramount.

5. Future Research Needs

In conclusion, addressing knowledge gaps and linking scientific studies to practical applications will require collaborative research across field sites and scientific disciplines, with particular emphasis on five key areas (Figure 3):

5.1. EMBRACING MULTIFUNCTIONALITY IN MULTI- SPECIES INTERACTIONS

Investigating interactions between known symbionts and other soil microorganisms, as well as among multiple co-occurring symbionts, could reveal synergistic effects on plant health and nutrient uptake, and help determine where each interaction lies along the symbiosis spectrum (Shen and Duan 2024). Understanding how these interactions vary across soil types and environmental conditions is essential to develop targeted soil management practices (Hnini et al. 2024). Multi-species interactions can be studied through co-occurrence network analysis, which constructs networks based on significant positive or negative correlations between the abundances of different soil organisms. Network analysis can uncover complex interactions and highlight key clusters or modules within soil communities (Faust 2021; Guseva et al. 2022). However, co-occurrence networks have notable limitations that require cautious interpretation. For example, the inferred relationships are primarily statistical, often capturing indirect effects such as shared environmental preferences, rather than direct ecological interactions like competition or mutualism (Blanchet et al. 2020). Additionally, network construction relies on arbitrary parameters, such as correlation thresholds and *p* value cutoffs, which can influence results and introduce biases (Goberna and Verdú 2022). Compositional data from microbial sequencing further complicates inferences due to relative abundance artefacts and sparsity. Recent advancements address these caveats to improve network reliability, for example by integrating multiple correlation methods (e.g., Pearson, Spearman, and hypergeometric distribution) to reduce spurious associations and enhance robustness (Deng et al. 2012).

5.2. ESTABLISHING AND IMPROVING COMPREHENSIVE FIELD TRIALS

Much of our current knowledge about AMF and other soil biota is based on single-species studies and on laboratory experiments (Lutz et al. 2023; Magkourilou et al. 2024). To bridge the gap between laboratory findings and field applications, it is essential to validate laboratory observations under real-world conditions. To capture the versatility of multi- species interactions, such studies must also span sufficiently long timeframes and data need to be recorded in a temporally explicit manner (Lehmann et al. 2020; Mathieu et al. 2020; Buckley et al. 2021). Conducting long-term studies that monitor changes in AMF and other soil biota interactions over time would provide insights into the stability and resilience of these interactions under changing environmental conditions and throughout different crop growth seasons, which is essential for long-term management and to anticipate how agroecosystems will respond to future climate change.

Designing such long-term field trials requires an integrative and adaptive framework. This includes selecting diverse cropping systems and soil types across different climatic regions to account for spatial variability in soil communities. Replicated plots should be established and maintained over multiple years, ideally across full crop rotation cycles, to capture successional changes in soil biota and their functions. Additionally, monitoring should include seasonal sampling of soil communities, root colonisation, and key soil functions such as nutrient cycling, organic matter decomposition, and soil aggregation. To assess the dynamics of multi-species interactions, both taxonomic and functional diversity should be monitored using a combination of molecular techniques (e.g., metabarcoding, metagenomics) and trait-based approaches. Furthermore, within these trials we should conduct manipulative field experiments of target organisms that can reveal their role in maintaining biodiversity, ecosystem functioning, as well as plant and soil health (e.g., Lensing and Wise 2006; Melguizo- Ruiz et al. 2020). Monitoring environmental variables such as soil moisture, temperature, and nutrient status will enable linkage of biotic interactions with abiotic changes over time. Furthermore, integrating crop yield and health data will help connect belowground biodiversity with aboveground ecosystem services, providing a holistic understanding of agroecosystem functioning. Collaborations with farmers and land managers can facilitate long-term access to sites, increase the relevance of findings, and support co- design of practical solutions. Overall, well- designed long- term field trials are critical for moving beyond reductionist models and towards a systems-level understanding of how complex soil biotic networks contribute to sustainable agriculture under real- world conditions.

5.3. USING TECHNOLOGICAL ADVANCES

Utilising and combining advanced molecular techniques, such as metagenomics and transcriptomics, could help to better understand the complex networks of soil biota and their interactions with plants and soils (Aguiar-Pulido et al. 2016; Perez-Mon et al. 2021). For example, integrating datasets from various-omics technologies could provide important new details on the links between presence/absence of taxa and functional parameters such as nutrient cycling and pathogen defence (Djemiel et al. 2022; Dong et al. 2024). Accessing such combined datasets linking taxonomy and activity across long-term field experiments testing different management practices will enable us to identify which management practices foster functional belowground networks and could reveal new structural insights into soil food-web dynamics and enhance our understanding of biodiversity-functionality links to harness the full potential of belowground biodiversity (Deutschmann et al. 2021; Singh and Rai 2024). Incorporating meta-transcriptomics and in situ techniques such as stable isotope probing could help distinguish active from dormant microbial communities and identify organisms directly involved in specific processes (Fortunato and Huber 2016; Alcolombri et al. 2022). Such analytical pipelines already exist for marine environments, but, until recently, lagged behind in soil science due to the more complex and challenging physical matrix composed of soil as compared to water (Edwin et al. 2024). For example, molecular studies of gut content in animals using metabarcoding and next- generation sequencing can help establish animal–animal interactions and reconstruct food webs (Casey et al. 2019). Given the now almost exponential increase in data from soil microbial studies, developing bioinformatic tools to analyse this vast amount of information will also be important to help identify reliable patterns and relationships between soil organisms and environmental factors. In this regard, machine learning algorithms could be used to develop predictive models that can forecast soil biodiversity behaviour under different conditions and help understand the dynamics of soil networks and their response and contribution to environmental factors and services (Awais et al. 2023). For example, random forests have been used to identify sets of soil organisms that are associated with the consumption of organic matter (e.g., Gavín- Centol et al. 2023) and artificial neural networks can be used to improve assessments of soil health indicators making use of extensive soil datasets and thus support agricultural decision-making (El Behairy et al. 2024).

5.4. HARMONISE METHODS AND DATABASE INTEROPERABILITY

Synthesising already existing data is complicated by methodological differences across studies, including different sampling and extraction protocols for many organism groups, and by sub-optimal database quality for taxonomic and functional classification (Guerra et al. 2020). Expanding and curating high-quality databases for functional soil biodiversity is hence an essential collective effort needed to understand temporal and spatial variability. For ecosystem upscaling, databases also need to be extended to include underrepresented groups of soil organisms and several trophic levels. Standardising extraction methods and sampling protocols across soil organism groups would help reduce variability and bias. Collaboration between plant and soil scientists, ecologists, microbiologists, and data scientists is key for integrating these approaches, while creating open-access platforms for data sharing would enhance cross-validation and minimise redundancy in efforts.

5.5. DEVELOP TOOLS FOR PRACTITIONERS

Remote sensing and data analysis can be used to monitor soil conditions like nutrient levels and microbial activity to identify spatial patterns and temporal trends and relate them back to soil health (Beatty et al. 2021; Vavlas et al. 2024). Precision agriculture technologies, such as soil sensors and drones, can generate comparable field-level data, facilitating targeted agricultural interventions

(Guebsi et al. 2024). Implementing such detailed monitoring across a variety of pedo-climatic contexts could help to upscale high-resolution soil and crop data into land management and fertilisation strategies. Developing user-friendly interfaces and increasing digitalisation could help guide in real time the fine tuning of agricultural interventions to ensure resources are used economically, effectively and sustainably (McFadden et al. 2022). However, developing these tools faces challenges, including integrating heterogeneous data sources such as remote sensing and ground-based sensors, ensuring scalability across varied agroecosystems, addressing high costs and technical expertise requirements, and overcoming limited digital infrastructure in rural areas, which can hinder accessibility and adoption by practitioners (Mizik 2023; Dhillon and Moncur 2023; Wang et al. 2023).

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Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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