Sustainable agroecosystems need integrative biodiversity approaches with more than friendly fungi in the food web

Jennifer Michel[1,2*], Philippe Hinsinger[3], Jordi Moya-Laraño[4], Sara Sanchez-Moreno[5], Iñaki Balanzategui-Guijarro[4], Markus Weinmann[6], Sarah Symanczik[7], Matthias Waibel[7], Jacques Le Gouis[8], Da Cao[9], Dominique Van Der Straeten[9], Hervé Vanderschuren[1,2,10], Cécile Thonar[1,11,#], Pierre Delaplace[1,2, #]

1 Plant Genetics and Rhizosphere Processes Laboratory, Gembloux Agro-Bio Tech, University of Liège, Gembloux, Belgium
2 Transdisciplinary Agroecosystem Platform for Integrated Research (TAPIR), TERRA teaching and research centre, Gembloux Agro-Bio Tech, University of Liège, Gembloux, Belgium
3 UMR Eco&Sols, Univ Montpellier, CIRAD, INRAE, IRD, L'Institut Agro Montpellier, Montpellier, France
4 Functional and Evolutionary Ecology, EEZA, CSIC, Almería, Spain
5 Environment and Agronomy, INIA-CSIC, Madrid, Spain
6 Faculty of Agricultural Sciences, University of Hohenheim, Hohenheim, Germany
7 Department of Soil Sciences, Research Institute for Organic Agriculture, Frick, Switzerland
8 UMR GDEC, INRAE, Université Clermont Auvergne, Clermont-Ferrand, France
9 Laboratory of Functional Plant Biology, Department of Biology, Ghent University, Ghent, Belgium
10 Tropical Crop Improvement Lab, Department of Biosystems, KU Leuven, Heverlee, Belgium
11 Agroecology Lab, Faculty of Sciences, Université Libre de Bruxelles (ULB), Brussels, Belgium
* Corresponding author: jennifer.michel@uliege.be
# These authors contributed equally.

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Highlights

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

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 form 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. Soil services are a function of how these organisms interact with each other, with the aboveground plant species and with the physio-chemical soil matrix. Here, we argue that multiple ecosystem processes, as well as system adaptability and resilience in challenging environmental conditions, rely on diverse plant and soil communities with complex interactions between various actors carrying out complementary functions, rather than on individual flagship organisms on their own. We highlight areas of research which could be deepened 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 of essential terrestrial ecosystems and the services they provide to the human population.

We need to adapt crop species and agricultural practices to produce high quantities of 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 the productivity, diversity, and environmental services of terrestrial ecosystems (FAO, 2020). Soil-based ecosystem services are an overarching concept referring to processes which help foster ecosystem attributes, such as: primary productivity, water purification and regulation, carbon sequestration and regulation, provision of functional and intrinsic biodiversity, and provision and cycling of nutrients (Schulte et al. 2014). Many of these components that sustain ecosystem functioning are based on the activity of soil organisms (De Vries et al. 2013). While some soil organisms have been studied in detail over decades, like arbuscular mycorrhizal fungi (AMF) for example, we here highlight that with the use of new technologies and advances in the analysis of multi-species interactions and microbial networks, we can gain new insights to unravel the complexity of soil biodiversity as a whole, 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 & Duan, 2024). This goes beyond single-species studies because fostering soil biodiversity for the benefit of the whole ecosystem requires functional diversity, niche complementarity and redundancy in a diverse network of co-occurring organisms. Interconnected food webs with many species and trophic and non-trophic interactions also allow flexible adaptation to different climatic conditions and to different plant species and can increase ecosystem resilience and adaptability (Moore et al. 1993; Bascompte 2009; Maes et al. 2024; Shi et al. 2024).

Across temporal and spatial scales, ants, archaea, cyanobacteria, bacteria, earthworms, fungi, nematodes, protists, rotifers, springtails, termites and many more organisms interact to sustain ecosystem services and together constitute the networks that directly drive elemental cycles and disease dynamics. 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 and the phosphorous cycle, for example methane oxidation, and carbon utilization rates vary with phosphorus bioavailability (Luo et al. 2022). These couplings are essential for maintaining ecosystem balance and nutrient availability and depend on a diversity of different soil organisms carrying out complementary processes across time. Neglecting any of these organisms can lead to an incomplete representation of soil functioning. Yet, many soil organisms with significant contribution 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 *Bazillus* species can improve phosphorus bio-availability and thus enhances plant productivity, *Rhizobium* can fix atmospheric nitrogen and convert it into bioavailable organic forms, some *Pseudomonas* produce antibiotics to keep plant pathogens at bay, and of cause 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 & Mousavi 2019).

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 depends always 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). Studies focussing on individual organisms 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. The term “symbiosis” is often used in multi-species interactions. Symbiosis describes a spectrum of interactions covering "mutualism” where both symbiosis partner gain benefits form the interaction, "parasitism" which is when one organism lives at the expense of another, and “commensalism” which is when one species obtains food or other benefits from its symbiont, without either harming or benefiting the latter (Encyclopaedia Britannica, ed). It is agreed that the character of almost any symbiotic interaction is context- and case-specific, 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 & Hijri 2011; Hammer et al. 2011). The popular plant-mycorrhizal association for example is à priori context-dependent, where AMF colonisation of plant roots can have positive, negative or no effect on plant and ecosystem performance (Neuhauser & Fargione 2004; Cheng et al.2012; Ryan & Graham 2018; Peng et al. 2024). However, a lot remains to be discovered about this symbiosis and its environmental context dependency (Moreno Jiménez et al. 2024), especially because AMF were historically often studied without consideration of any other organism simultaneously living in soils and in plant roots (Zhang Y. et al. 2024) and the majority of studies (92%) were conducted in the northern hemisphere (Bennett & Classen, 2020). Such historically geographically biased and purely AMF-focused view risks to overlook the vast dimensions of diversity in soil and the multitude of interspecies and inter-kingdom interactions. Given in addition that AMF themselves are a comparably little diversified group of fungi (Redecker & Raab 2006) and that AMF themselves harbour endobacteria in their hyphae and spores (Desirò et al. 2014; Zhang C. et al. 2024) highlights the importance to study AMF in the context of all the other soil organisms. A holistic approach, notably benefiting from new molecular methods, allows to consider the presence and functions of AMF, their associated microbiome, and communities of other soil organisms together to help design adaptations for improved resilience of agroecosystems that go beyond the benefits of single-species studies (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 the variability of interactions relates to soil functions such as nutrient cycling and ecosystem stability. For this understanding, it is important to free research from positive affirmations and confirmation bias (Oswald & Grosjean, 2004; Jeng 2006; Hoorens 2014), apply clear terminology (Neubauer et al. 2024) and be cautious with the creation of overly simple narratives which can lead to misinformation resulting in the misrepresentation of scientific facts, as is discussed for common mycorrhizal networks in forests (Karst et al. 2023; Irwin 2024).

Securing soil functions and soil biodiversity is especially critical in agricultural cropping systems, but rendered difficult because plant-turnover is rapid, often with intensive application of fertilizers, pesticides and tillage, which negatively impacts the establishment and the functioning of belowground nutrient-cycling networks maintained by diverse organisms, leading to a reduction of both resistance and resilience of agroecosystems (Miyasaka & Habte 2001; Peng et al. 2024). Harnessing the full potential of soil biota for agricultural benefits will likely require a systemic change from high-yield, high-turnover cropping systems towards management practices which keep the soil structure and the soil biome intact (Hartmann & Six 2023). Various options such as permanent plant cover, inter-cropping or agroforestry (Li et al. 2021; Primieri et al. 2022) can be implemented to benefit both biodiversity and crop yield and health (Li 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 & Leighton 2014; Duru et al. 2015).

In conclusion, to fill existing knowledge gaps and bring scientific studies closer to practical implementations, future research could focus on five areas:

i) Embracing the symbiosis spectrum and multi-organism interactions

The interactions between host plants and associated symbiotic microorganisms can fluctuate between mutualism, commensalism and parasitism, depending on the environmental context. To develop soil management strategies with reliable plants-microbe interactions, it is important to understand what triggers shifts across the symbiotic spectrum and how complementary functions can be executed by different organisms in the soil food web to maximise the systems' functional capacity in a variety of pedo-climatic contexts to increase system performance and resilience. Investigating the interactions between known symbionts and other soil microorganisms, and between multiple co-occurring symbionts, could reveal synergistic effects on plant health and nutrient uptake and determine where along the symbiosis spectrum each interaction is placed (Shen & Duan, 2024). Understanding how these interactions vary across different soil types and environmental conditions will be essential for developing targeted soil management practices (Hnini et al., 2024). Multi-species interactions could be studied using co-occurrence network analysis, a method that constructs networks based on significant positive or negative correlations between the abundances of different soil organisms. Network analysis can reveal complex interactions and identify key clusters or modules within the network (Faust, 2021; Guseva et al., 2022).

ii) Improving and establishing comprehensive field trials

Much 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 theory and applicable solutions for field practitioners, it is key to test observations in laboratory studies in the field. To capture the versality of multi-species interactions, these studies also need to run over sufficiently long-time frames and data needs to be recorded temporally explicit (Lehman et al. 2020). 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.

iii) Using technological advances

Utilizing and combining advanced molecular techniques, such as metagenomics and transcriptomics, could help to better understand the complex interactions between soil biota, plants and soils (Aguiar-Pulidoet al. 2016). For example, combining datasets from various omics technologies (genomics, proteomics, metabolomics) could provide important new details on the links between presence/absence of taxa and functional parameters. Linking taxonomy and activity could reveal new structural insights to soil food-web dynamics and enhance our understanding of biodiversity-functionality links to harness the full potential of belowground biodiversity (Singh & Rai, 2024). Furthermore, high-throughput sequencing of environmental DNA and RNA can provide a comprehensive view of soil microbial diversity and activity. Incorporating meta-transcriptomics and in situ measurements like stable isotope probing, could further help to distinguish active from dormant microbial communities and identify organisms actively involved in specific processes (Fortunato & Huber 2016; Alcolombri et al. 2020). Given the almost exponential increase of data from 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 its response and contribution to environmental factors and services (Awais et al., 2023).

iv) Harmonising methods and database interoperability

Synthesizing already existing data is complicated by differences in methodology between 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. Harmonizing extraction methods and specific sampling protocols for different soil organisms would help reduce variability and bias. Collaboration between plant and soil scientists, microbiologists, and data scientists is key for integrating these approaches, while creating open-access platforms for data sharing would enhance cross-validation and minimize redundancy in efforts.

v) Developing 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). Using precision agriculture technologies like soil sensors and drones allows to generate similar data at field level which facilitates targeted interventions in agricultural practices (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).

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