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Soil biodiversity promotes key ecosystem functions by its complex structure and interactions – state and perspectives

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Abstract

The biodiversity of soil microorganisms and fauna supports many ecosystem functions in terrestrial ecosystems, such as decomposition, aggregation of soil organic matter or mobilization and recycling of nutrients. These processes are linked to the functional traits (e.g. life strategy, body size, metabolic capabilities) as well as frequently occurring mutualistic interactions (e.g. mycorrhiza symbiosis) of soil organisms. The high vertical and horizontal diversity of soil food webs maintains and stabilises ecosystem functions. As part of the German Biodiversity Assessment ('Faktencheck Artenvielfalt'), a group of experts summarized the available knowledge on the state and role of soil biodiversity in Germany. Here, we highlight the role of biodiversity in soils as a driver of ecosystem multifunctionality and buffer against perturbation by human activities, e.g. by mediating the storage and release of greenhouse gases. Through their outstanding contribution to decomposition of dead organic matter, soil organisms control the carbon balance of terrestrial ecosystems, and thus can contribute to climate protection. We further discuss the multifunctionality of soil organisms as a basis for stable ecosystem functioning. Taken together, soil biodiversity, through its emerging properties, is as a key player in processes that govern terrestrial systems, and as such needs to find more consideration in ecosystem sustainability and restoration.

Keywords soil microorganisms | soil fauna | diversity | decomposition | mineralization | soil aggregation | greenhouse gases | functional traits | multifunctionality | multitrophic interactions

1 From soil biodiversity to ecosystem functions

The ecosystem functions (ESF) provided by soil communities are of pivotal importance for the biogeochemical cycles in terrestrial habitats, e.g., in forests, grasslands, and arable land (FAO 2020). The biodiversity of microorganisms and fauna is a prerequisite for the maintenance and stability of soil ESF (Garland et al. 2021, Geisen et al. 2019, Wagg et al. 2021). Due to this role, the natural soil-related ESF are considered in European and Federal Soil Protection Acts (European Commission 2023). In the corresponding German law (Bundes-Bodenschutzgesetz - BBodSchG),

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two main functions regarding the community of soil organisms are emphasized: (1) their role in water and nutrient cycles, and (2) their contribution to filtering and buffering as well as to substance transformation, in particular in the context of groundwater protection. Overall, soil biodiversity supports several ESF simultaneously, underpinning the crucial role as an essential basis for human life (Wall et al. 2015).

The ESF are strongly dependent on the functional traits of organisms, i.e. **functional diversity** (Heemsbergen et al. 2004). This refers to characteristics of organisms that influence one or more aspects of the functioning of an ecosystem (Tilman, 2001). For a better understanding of these relationships, species are divided into functional groups with similar life strategies (Ferris & Tuomisto, 2015). From the diversity within such a functional group, conclusions can be drawn about the degree of utilisation of available resources and the complementarity of ESF, e.g. in microorganisms-mediated conversions in nutrient cycles (Chen et al. 2019). Conversely, the functional diversity within, but also across functional groups (see "cooperative diversity" below) determines important ESF such as resource utilisation. However, functional biodiversity influences not only ESF, but also interactions between organisms. Symbioses of nitrogen-fixing microorganisms of the genus *Rhizobium* in nitrogen-deficient soils can promote the growth of legumes, which in turn increases the abundance of this group of bacteria in soils. The associated positive and negative effects on ecosystem processes then also change the ESF at the landscape scale (Taylor et al. 2020).

The relationship between soil biodiversity and ESF does not only exist at the level of individual species and functional groups, but also in **morphological diversity**, which is often regarded as an important component of functional diversity (Motiejūnaitė et al. 2019, Bonfanti et al. 2024). Soil ecosystems, with their three-dimensional matrix of different microhabitats, result in a wide range of space-related biotic characteristics (Giller 1996). This is reflected in the enormous range of size groups in soil organisms (microorganisms, micro-, meso-, macro-, and megafauna), determining the access to a given soil pore space. The differences in body size and life strategy have a strong influence on ESF, i.e. the extent to which different organisms contribute to ecosystem functions (Montagna et al. 2018, Angst et al. 2024, Bonfanti et al. 2024). However, how these interactions play out at different spatial scales, from soil pores to soil aggregates to soil horizons, and at the macroscale of the ecosystem, is still poorly understood (Guerra et al. 2020).

Another special feature of soil ecosystems is that ESF are often provided by consortia of microorganisms and fauna that each taxonomic group alone would not be able to realize. This **'cooperative' diversity** alters ESF such as litter decomposition and mineralisation. A vivid example is the resource utilisation by microorganisms as their complementary enzymatic equipment makes decomposition processes possible in the first place (Gessner et al. 2010, Garcia-Palacios et al. 2013). Moreover, the removal of functional groups of the fauna, experimentally manipulated by selective exclusion according to body size, causes a sharp decline in decomposition processes (Nieminen & Setälä, 1997). Soil detritivore fauna like earthworms and millipedes are known to facilitate decomposition processes, by fragmenting, redistributing, and altering the chemical composition of organic matter, thereby increasing the surface area and microbial access of organic matter (Gessner et al. 2010, Angst et al. 2024, Bonfanti et al. 2024). Thus, the intensity of this ESF depends on certain groups of organisms, i.e. "key taxa", and their loss can have a direct impact on the functioning of the remaining soil organism community (Wagg et al. 2014).

Soil ecosystems also harbor a great **diversity** in **symbiotic relationships** between plants and microorganisms. The soil microbiome consists of a large number of different groups, categorised as Bacteria, Archaea, fungi, protists, and viruses, covering the belowground parts of plants (>1000 species per plant; Hassani et al. 2018, Philippot et al. 2013). Fungi form mycorrhiza with roots, which provides the plant with additional nutrients and water; in return, the fungus receives energy-rich food from the host. Almost all land plants, including crops, are associated with mycorrhizal fungi (Brundrett & Tedersoo, 2018). Also soil bacteria interact positively with plants and their root systems, primarily in the protection against pests and diseases below- as well as aboveground (Latz et al. 2012, Ristok et al. 2023). Positive effects on root growth are also known to reduce the susceptibility to water deficiency (Cho et al. 2008). These multiple positive interactions of plants with the soil microbiome form the basis for their growth and fitness, paving the way for a diverse vegetation, hence also for ESF provided aboveground.

Finally, **trophic diversity** within soil food webs determines the material and energy flow in the soil ecosystem. Due to their high complexity, species that have the same trophic level and similar diet as well as a comparable function in the food web may be aggregated to feeding guilds, aiding researchers to understand the mechanistic roles these guilds play in complex food webs (Heijboer et al. 2018). Key characteristics of a guild are food preference, body mass, microhabitat specialisation, and hunting mode (Potapov et al. 2022). Soil food webs have a high vertical diversity, i.e. complexity across trophic levels. Omnivory, which strongly influences

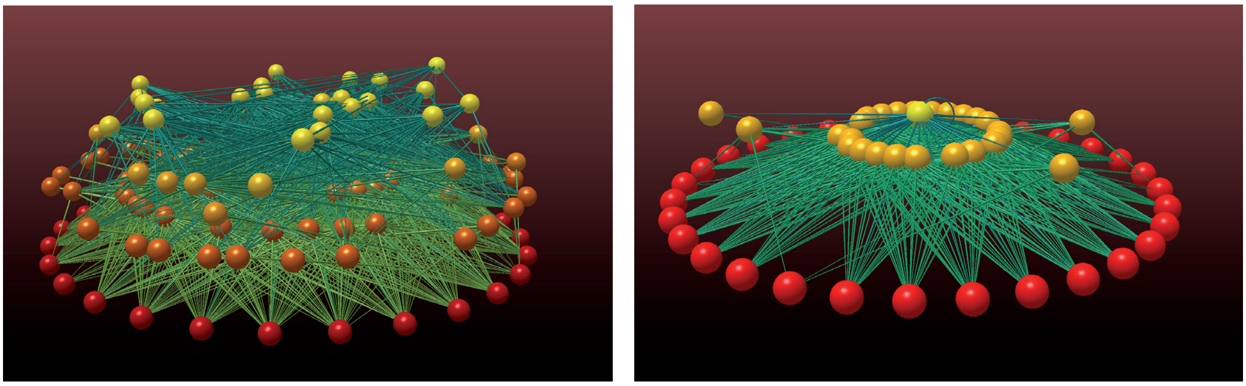

Figure 1. Connectedness web visualizing the differences in horizontal and vertical diversity of feeding relationships (binary links) of the soil food web in an arable land across depth. Left – top soil (0-10 cm) with a biodiversity of 138 different taxa and right – mineral soil (60-70 cm) comprising 60 different taxa. Red spheres - bacteria and fungi, orange spheres - bacterial- and fungal feeders (protists, nematodes, springtails, mites), light orange - plant feeders (nematodes, mites, insects) and yellow - omnivores and predators (nematodes, mites, insects). Investigated was the 0-10 cm horizon of a Luvisol grown with maize in a temperate climate. Data from Scharroba et al. (2012) and Pausch et al. (2016) graphic created with Foodweb3D - picture courtesy B. Lang.

carbon and nutrient flow, is particularly characteristic (Potapov et al. 2022). Soil food webs also display a high horizontal diversity within a trophic level, which refers to all aspects of species diversity (species richness, evenness, functional traits) (Gessner et al. 2010). The connectedness web in Figure 1 represents the trophic links in an arable soil, ranging from microorganisms over micro- and meso- to macrofauna. This view illustrates how the vertical and horizontal diversity of the food web can change along the soil profile. While the network in the topsoil at 0-10 cm comprised 138 different taxa, there were only 60 taxa at 60-70 cm. At depth, the higher trophic levels were represented by fungal- and root-feeding nematode taxa. These differences in horizontal and vertical diversity reflect the heterogeneity of abiotic (e.g. texture, moisture, O_2) as well as biotic (e.g. litter, root exudates) factors within the deep transect, leading to trophic assemblages that differ in diversity, composition and connectivity. These multitrophic interactions form an important base for soil ESF such as decomposition and nutrient mineralization. Similar to the multifunctionality of ecosystems, new research approaches describe ‘trophic multifunctionality’ as the simultaneous support of several trophic functions by the food web (Potapov, 2022).

2 Soil biodiversity fosters decomposition and mineralization

The functional diversity of soil organisms is essential for decomposition processes and thus for the availability and mobilisation of nutrients. Soil organisms use plant-, animal- or microbe-derived organic material as resources (Heemsbergen et al. 2004, Hättenschwiler et al. 2005). During decomposition, nutrients (nitrogen, phosphorus, sulphur, etc.) are mineralised, i.e. converted into an inorganic chemical form that can be used by plants and microorganisms. A large biodiversity of both, soil microbial and animal decomposers contributes synergistically to these decomposition processes. Ensuring this natural nutrient balance driven by soil communities is of importance for a sustainable plant biomass production in arable land (Geisen et al. 2019) and determines global food production (Fonte et al. 2023). Soil communities ultimately optimize nutrient utilisation and reduce nutrient losses by plants (Leimer et al. 2016).

In particular forest ecosystems are characterised by a high diversity and recalcitrance of plant litter, i.e. a wide variation in the chemical composition and quality of leaf and needle substrates. This requires a high functional diversity of the microbial community when decomposing the substrate (Gessner et al. 2010). Microbial nutrient recycling, which maintains the forest’s internal nitrogen recycling, is considered one of the most economically valuable ESF (Costanza et al. 1997). However, the structure and thus also the function of the soil microbiome is strongly influenced by environmental boundary conditions (Purahong et al. 2016). Studies in 150 forest soils in three German regions revealed that regional (climate, soil type) followed by local (e.g. main tree species) factors are particularly effective here (Kaiser et al. 2016, Richter et al. 2018).

In addition to microorganisms, the soil fauna plays a fundamental role in these processes. The primary decomposers within the group of macrofauna (e.g. earthworms, isopods, milipeds) break down dead organic material and drive its sequestration into the soil carbon pool (Angst et al. 2024, Bonfanti et al. 2024). They also convert a substantial part into faecal material, altering the decomposition rates in comparison to the original substrate (Frouz et al. 2015, Joly et al. 2020). Secondary decomposers (e.g. springtails) further process the plant material that has been shredded and pre-digested by primary decomposers. This mechanical comminution as well as the mixing of organic and mineral material promotes microbial mineralization, and is therefore an important ESF of the soil fauna (Blume et al. 2010).

The contribution of the so-called "grazers" within the secondary decomposers is also significant. These include the soil microfauna, i.e. protists and nematodes (Gao et al. 2019, Ruess, 2024) as well as parts of the mesofauna, such as springtails and mites (Scheu, 2002). Grazing keeps bacteria and fungi at high productivity and decomposition performance (Bonkowski et al. 2009, Gessner et al. 2010). Without grazing, microorganisms generally go into an inactive state and the mineralisation rate decreases (Paul, 2014). The soil fauna further contributes to the nutrient supply of plants in another way - through the excretion of nitrogenous waste products, especially ammonium. Recent studies indicate that earthworms and in particular nematodes provide agriculturally relevant amounts of nitrogen (Lang & Russell, 2022, Fonte et al. 2023). For nematodes, the additional release of ammonium is estimated at 32-38% of the annual nitrogen mineralisation in arable land (Whalen et al. 2013). However, this supply of plant-available nutrients by the soil fauna has hardly been considered in the soil nitrogen balance, i.e., the focus remains on microbial processes (e.g. Koch & Sessitsch, 2024, Lewin et al. 2024).

In summary, the interplay between microorganisms and fauna in soils is essential for the two ESFs decomposition and mineralisation. Nevertheless, little is known about the quantitative impact of the functional diversity of soil organisms on these important ESFs. There is still a considerable need for research in this area. Soil habitat complexity, small-scale heterogeneity, and three-dimensional structure, together with the difficulties in taxonomic delineation and the broad ecology of soil organisms, require an expansion of the classical ecological toolkits (White et al. 2020).

3 Ecosystem functions of soil organism communities related to climate change

The activity of soil organisms in soil organic matter formation and degradation impacts our climate. Carbon taken up from the atmosphere by plants is only slowly released back as CO_2 (Schmidt et al. 2011), as approximately 85% of the carbon on land is stored in soil organic matter (Crowther et al. 2016, Friedlingstein et al. 2022). This soil organic matter improves plant growth and water retention in the topsoil, thus enabling a productive vegetation that is resilient to disturbances (Huang et al. 2024). It is stabilised in soils, e.g. by binding to mineral soil particles, but also by physically preventing decomposition in soil aggregates. In this way, a large proportion of climate-active carbon – atmospheric CO_2 - is removed from the atmosphere in the long term (over years to decades). If soils remain undisturbed over long periods of time, a balance is established between the formation and decomposition, thus the amount of carbon remaining as soil organic matter no longer increases (Vaidya et al. 2024).

The interaction of plants, soil fauna, and soil microorganisms is essential for formation and stabilisation of soil organic matter by ensuring a balanced regulation of this carbon pool (Filser et al. 2016, Angst et al. 2024) (**Fig. 2**). Hence, soil communities are actors that influence climate change and contribute significantly to its buffering (Paustian et al. 2016). Microorganisms in particular are considered as a carbon pump in soils (Lange et al. 2015, Schmidt et al. 2011, Zhu et al. 2020), which, depending on external factors, can accumulate carbon from plants in the soil but also release it back into the atmosphere (Fig. 2). The ESF formation and stabilisation of soil organic matter is therefore relevant for the development of the climate and can mitigate or accelerate climate change (Canadell et al. 2021, Crowther et al. 2016, van Gestel et al. 2018). Land use plays a key role in this context. For example, arable soils have significantly lower soil organic matter contents than grassland and forest soils (Jacobs et al. 2018, Smith et al. 2021). Soil microorganisms can foster organic matter decomposition, predominantly in a dysfunctional relationship with vegetation, as it is often the case in agricultural soils. Moreover, with rising temperatures as a result of climate change, more soil organic matter is converted back into climate-warming CO_2, which is not compensated for by an increased uptake by the vegetation.

To date, there are no systematic monitoring programs that assess the relationship between carbon storage in soils and the composition and biodiversity of soil communities. It therefore remains unclear to what extent e.g., invasive species as a result of human intervention or climate change, influence this soil-related ESF. Soils with a higher biodiversity generally also have a larger pool of soil organic matter - both biodiversity and soil organic matter content are therefore mutually dependent in mineral soils (Delgado-Baquerizo et al. 2016). Organic soils in wetlands and mires may not always follow this general pattern, requiring more research on this topic in these soil types. Furthermore, it is also likely that only intact soil communities with an active soil fauna and a high proportion of soil fungi, which only develop in sufficient abundance after longer periods of time (years to decades), effectively store carbon (Angst et al. 2022, Morrien et al. 2017).

The most important greenhouse gases - carbon dioxide, methane, and nitrous oxide - are formed by soil (micro-) organisms, but can also be taken up by them from the atmosphere. Soil organisms act as important, and in some cases the only, greenhouse gas sinks on land. All three gases together cause the majority of global warming (IPCC 2021). The main soil organisms for the ESF greenhouse gas sink, i.e. the removal of climate-relevant greenhouse gases from and emission into the atmosphere, are microorganisms, including Bacteria, Archaea, and fungi. Most open lands (grasslands, fields), forests and wetlands (moors and floodplains) can be sinks for carbon dioxide until they remain in an equilibrium of formation and uptake from the atmosphere over long periods of time without disturbance. This state of a soil being a net carbon sink is generally given when a high level of biodiversity occurs (Lange et al. 2015, Dawud et al. 2017). Nonetheless, understanding the mechanistic relationships between soil biodiversity and net carbon storage requires future research (Angst et al. 2024).

Species of certain soil bacteria - so-called “methanotrophs” - are the only sink for methane on land. Methanotrophs live close to the soil surface and are sensitive to a range of measures taken as a part of regular land use. Therefore, the natural sink function for methane provided by soil communities is highly dependent on land management. Sealed and heavily fertilised urban soils, and intensively used grasslands and acres, remove little or no methane from the atmosphere compared to forest soils, which can be considered as the strongest methane sinks per area on the land surface (Kolb 2009, Täumer et al. 2021). Soil communities in grasslands can also act as sinks, although it is unclear how this is related to land management and its specific measures (Täumer et al. 2021, 2022). Many current grasslands in Central

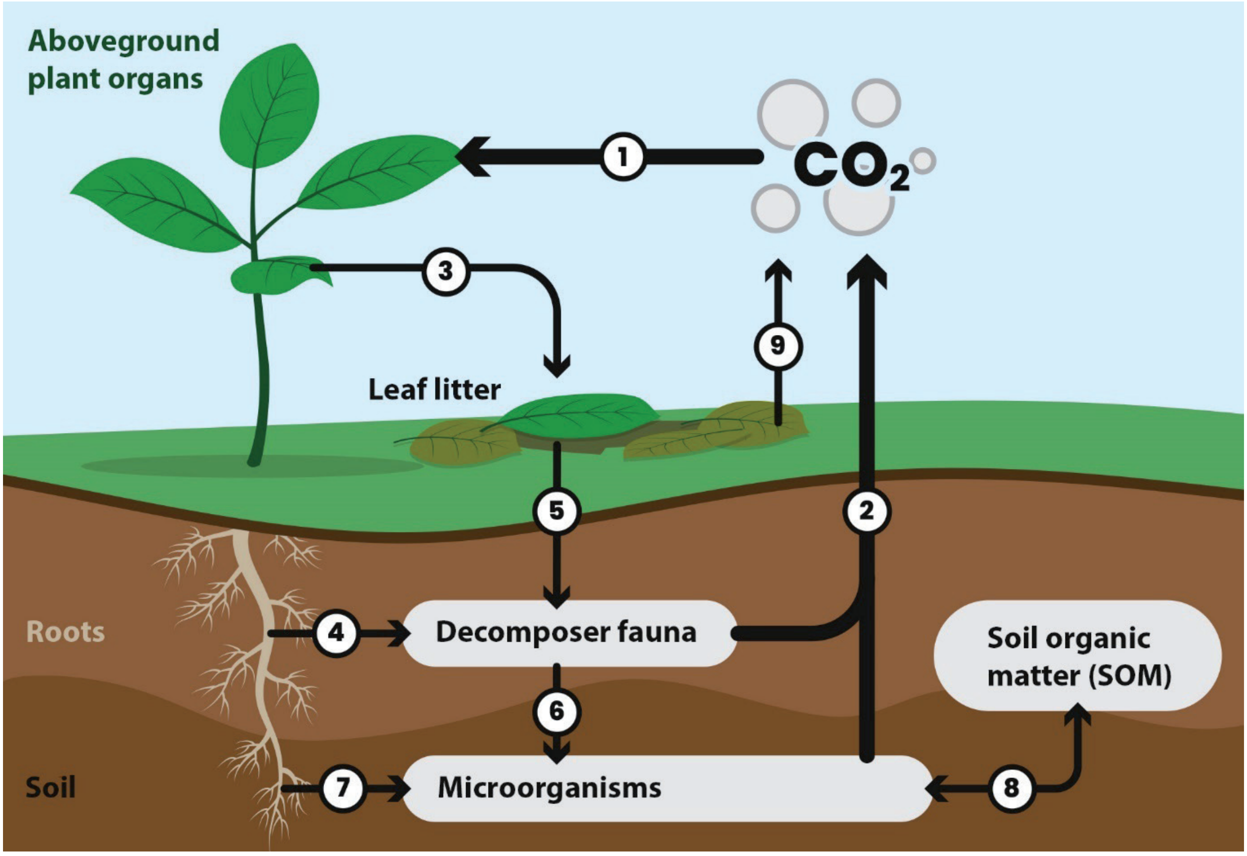

Figure 2. Conceptual interactions of plants, soil fauna and microorganisms in the formation and decomposition of organic matter in soils, and consumption of carbon dioxide (CO_2). The biodiversity of the fauna and the microorganism is complex and differently dependent on habitat type, location, and region. 1. Uptake and formation of plant biomass by photosynthesis.; 2. Turnover of soil organic matter (SOM) and plant biomass by respiration (syn. soil respiration), main actors are microorganisms, fauna, and roots; 3. Carbon allocation by leave litter fall; 4. Decomposition of plant roots; 5. Decomposition of leaf litter; 6. Mineralisation of dead decomposer and leaf biomass; 7. Mineralisation of rhizodeposits; 8. Formation and mineralisation of SOM (= carbon stock); 9. direct mineralisation of leaf litter by fungi.

Europe are former drained peatlands. Rewetting these areas would primarily restore their function as carbon dioxide sinks, yet as a side effect, methane emissions also increase.

Besides carbon, intact and biodiverse soil communities enable the continuous uptake of nitrogen from the atmosphere. This process is essential to supply terrestrial ecosystems with sufficient nitrogen. On the other hand, nitrous oxide is produced when nitrogen is converted by soil (micro-)organisms. In terms of a molecule, it is much more harmful to the climate than carbon dioxide, because it warms the atmosphere 296 times more over a reference period of 100 years (Canadell et al. 2021). Particularly on intensively-used arable land, there are often unpredictable and unwanted nitrous oxide emissions, because too much nitrogen fertiliser is applied at the wrong time, and the unused nitrogen is converted by soil microorganisms (Asad et al. 2022, Yue et al. 2022). In natural grasslands with a species-rich soil community, this climate-relevant process is generally not or only weakly observed (Yu et al. 2022). Soil biodiversity depletion plays a major role in the release of nitrous oxide (Chen et al. 2021), but the mechanisms behind this have not yet been conclusively clarified (Conthe et al. 2018). Arable and forest soils account for a comparable proportion of nitrous oxide emissions nationwide in terms of area. In particular arable soils have the potential to reduce nitrous oxide emissions through optimised nitrogen fertilisation practice (Mathivanan et al. 2021).

The role of interactions of soil microorganisms with soil animals and plants in nitrogen dynamics have hardly been investigated to date. In many specific cases, it remains unclear how human-induced environmental changes quantitatively affect the interactions between soil biodiversity and the terrestrial greenhouse gas balance. It is therefore nearly impossible to predict how biodiversity conservation will affect greenhouse gas emissions. Soil biodiversity is fundamentally involved in the regulation of the climate system through the emission (ESF source) and removal (ESF sink) of greenhouse gases. Systematic studies on this are lacking at national and international level, but have the potential to close a crucial knowledge gap.

4 The importance of plant-microbiome interactions for soil ecosystem functions

The interaction of soil microorganisms with plants is central to stable, biodiverse and resilient plant communities, and the related ESFs provided. The nutrient and water supply, but also the habitability of soils for the various plant species is ensured by these relationships. Over the past two decades, many studies have shown that there are positive interactions between soil bacteria and fungi with all plants studied to date (Hassani et al. 2018). The much smaller microorganisms colonise the insides and outsides of roots and aboveground organs of plants. This assembly of plant host and microorganisms can be understood as a meta-organism, the so-called holobiont, which reacts jointly to environmental changes and human intervention. This phenomenon is also known for humans and animals and is discussed in the context of the "One Health" concept, which aims to combine the protection of the environment with the protection of human health (Banerjee & van der Heijden 2022, Samaddar et al. 2021).

The plant microbiome can ward off disease-causing microorganisms (syn. pathogens) and thus contribute to plant health. It can also support plants in their defense against herbivorous plant pests and stimulate root growth, which in turn reduces susceptibility to water deficiency (Cho et al. 2008). Highly specialised plant-microbiome interactions, such as mycorrhiza (plant - soil fungi) or nitrogen-fixing root nodules (plant - soil bacteria), are particularly at risk from human intervention and soil degradation if, for example, these microorganisms are absent or greatly reduced due to crop breeding and intensive fertilisation. This is typically the case in intensively utilised grassland and arable soils (Beltran-Garcia et al. 2021). In principle, the main aim of crop breeding in recent decades has been to maximise yields, and thus crop plant varieties were developed that no longer interact sufficiently with soil microorganisms. Initial efforts are made to improve these dysfunctional plant-microbiome interactions through modified cultivation systems, but also in plant breeding (Escudero-Martinez & Bulgarelli, 2023).

The interactions of soil microorganisms with plants, which enables a stable nutrient and water supply, further make plants more resilient against climate change related disturbances such as heat waves and droughts (Allsup et al. 2023). This belowground stabilisation of plant communities also fosters aboveground food webs, which depend on resilient and productive vegetation. Conversely, high plant diversity results in functionally diverse soil microbiomes (Lange et al. 2015), e.g., pathogens are less likely to attack plants (Latz et al. 2012). Soil animals also depend on the microbiome living in and on them to survive. Positive interactions of microorganisms with soil animals have been well studied for various earthworm species and springtails (Buse et al. 2014, Lund et al. 2014, Thimm et al. 1998). However, while considerable knowledge on the contribution of microbial communities to stability of soil ESF related to biogeochemical cycling exists (Wagg et al. 2021), the extent to which microbiome interactions with their plant or animal partners stabilizes ESF has not been systematically investigated, but can be considered as generally positive for the fitness plant and animal hosts.

5 Multifunctionality supports stable ecosystem functions

The structural and functional biodiversity of soil organism communities promotes multifunctionality, i.e. multiple ESFs simultaneously (Soliveres et al. 2016, Wagg et al. 2014). However, soil organisms not only influence ESF, but also interact directly and indirectly with each other in competitive, mutualistic, pathogenic or predatory relationships (Wardle et al. 2004). In addition, ESFs have a feedback effect on soil organisms. The importance of multifunctionality integrates all ecological processes in soils and is therefore challenging to summarise, which may explain the diversity of approaches, that have been used in the past (Bender et al. 2016, Garland et al. 2021, Giling et al. 2019). The key to future multifunctionality studies should be to not treat the underlying functions as a black box, but also show and investigate them individually, which will facilitate assessing the overall functioning of ecosystems as well as individual processes, improving the mechanistic understanding of terrestrial ecosystems.

Generally, a decrease in soil organism diversity leads to a decrease in ESF (Bender et al. 2016, Wagg et al. 2014). Soil biodiversity therefore plays a key role in maintaining ESF, and thus increasing multifunctionality (Delgado-Baquerizo et al. 2020). However, individual processes can still be suboptimal, and species replacement may alter ESF processes, and their efficiency and resilience.

Box: Open research topics requiring a joint consideration of soil microbiota and fauna.

Research on the ecology of soil microbiota and fauna often occurs in different scientific disciplines. Our review revealed open topics relevant to soil ESF, that require joint efforts, as they can only be addressed if microbial-faunal interactions are considered in the same study:

1. ***Soil-specific interplay between microorganisms and fauna***: Soil is a complex, small-scaled, three-dimensional habitat, with various boundary surfaces and conditions. Soil organisms interact with each other and drive ESF at multiple spatial scales, ranging from pore-space to landscape-level. Taken together with the huge organismic biodiversity, this calls for an expansion of the classical ecological toolbox – e.g. developing new approaches to quantify contributions of soil fauna and microbiota to carbon storage in soils or in-situ imaging techniques to analyse trophic interactions at the pore space.

2. ***Non-trophic interactions between soil fauna and microbiota***: To which extent non-trophic interactions of microorganisms and fauna (e.g., soil aggregate formation) affect the stability and intensity of soil-related ESF has not been systematically investigated. Nonetheless, it can be assumed that these are decisive for soil ESF.

3. ***Soil microorganisms and greenhouse gas dynamics***: Soil bacteria can act as a biological sink for or source of greenhouse gases, which is especially relevant for carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). It needs to be explored how the overall biodiversity of soil communities, including the many soil animals, are linked to the balance of these critical processes.

4. ***Trophic interactions between soil fauna and microbiota***: Soil fauna that grazes on soil Bacteria, Archaea or fungi modulates the intensity and stability of ESF. These trophic interactions are not yet quantitatively investigated, reducing the capabilities to predict the resilience of soil ESF, especially when affected by climate change, pollutants, or land use. Future experiments may want to test how these (anthropogenic) changes of the environment affect the trophic interactions between soil fauna and microbiota, e.g., through detailed analyses of feeding interactions, via stable isotope, fatty acids, and amino acid analyses, as well as energy flux modelling.

Soliveres et al. (2016) showed in a study on 150 grassland sites in Germany, that high species richness in several trophic groups (multitrophic diversity) has stronger positive effects on ESF, than high biodiversity in a single trophic group. A basic set of organisms with certain functional traits is necessary for the proper functioning of ecosystem processes, while further increases in biodiversity may not provide direct benefits (Nielsen et al. 2011). This has often been called the functional redundancy of species. However, functional redundancy is controversially discussed in the literature, and has mostly been reported for broad ecosystem processes (Eisenhauer et al. 2023). Mutual substitution of functions is limited in soil ecosystems though, due to the pronounced spatial and temporal heterogeneity. Accordingly, in soils with a low number of species or functional groups, such as arable land, ESF are less resistant to stressors compared to diverse communities (Griffiths et al. 2000). This is an important aspect with regard to increasingly occurring stressors caused by global climate change such as droughts, heat waves or heavy rainfall events (de Gea et al. 2023).

The highly diverse soil food webs are a prime example of how organisms interact. With increasing diversity, a trophic or functional group has stronger effects on soil processes, as species related differences in morphological and behavioral traits or physiological adaptations lead to better use of resources. However, in the context of ESF, it is primarily the biomass and the metabolic activity of organisms that have an effect (Ferris & Tuomisto, 2015). This is taken up in concept of the “metabolic footprint’, a trait-based method developed for soil nematodes as a functional attribute for services in the soil food web (Ferris, 2010). This approach is used e.g., to determine the contribution of functional groups to belowground carbon flow (Scharroba et al. 2016, Ewald et al. 2020) and was proposed as a functional descriptor of land use (Mulder & Maas, 2017). This functionality of soil organisms is a key factor in regulating carbon and energy fluxes in soil and is thus decisive for soil-related ESF (Barnes et al. 2018, Potapov, 2022). For example, mature and complex soil communities support high energy flux across soil food webs (Zheng et al. 2023). Also, soil amendment with organic fertilizer or biochar can increase the uniformity of energy flow across trophic level, thereby enhancing ESFs (Wan et al. 2022a, Wan et al. 2022b, Zhu et al. 2023). However, it should be noted, that most current energy flux approaches are based on model calculations. First studies that empirically measure soil energy flow and link it to functional groups, have only recently been made for the soil micro-food web (van Bommel et al. 2025).

Overall, applying an energy flux approach to soil food webs does not only allow integrating multiple ecosystem functions with a “common currency”, but also facilitates studying interactions between aboveground-belowground or across ecosystem boundaries (Barnes et al. 2018, Jochum & Eisenhauer 2022). Moreover, this allows to quantify ESF that are hard to measure under field conditions, such as belowground herbivory and predation (Jochum & Eisenhauer 2022) as well as the integration of taxa of different body sizes and trophic groups in assessments of ecosystem multifunctionality (Potapov et al. 2019).

6 Conclusions

Studies on soil biodiversity, and the ESF derived from it, are often limited to a few or individual known ESF. There is also a lack of systematic integration of the specific conditions in soil ecosystems into ESF concepts. Whether processes follow the same patterns as those described for aboveground ecosystems often remains unclear. However, a comprehensive understanding of these interactions is essential to protect soil biodiversity and multifunctionality through appropriate measures. Since most studies are only focusing on soil fauna or soil microbiota to investigate effects on soil ESFs, there is a systematic gap of knowledge on the relevance of a complementary and supporting interaction of both groups for providing ESFs, and how this interaction affects ESFs such as mineralization or greenhouse gas sink function (see **Box**). As soil ESF are the basis for agricultural and forestry production, resilience to climate change and the stability of terrestrial ecosystems, future conservation measures should aim to ensure a high level of functional diversity of soil organismic communities for a sustainable soil environment.

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