Trends in Ecology & Evolution

Review

An Underground Revolution: Biodiversity and Soil Ecological Engineering for Agricultural Sustainability

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Soil organisms are an integral component of ecosystems, but their activities receive little recognition in agricultural management strategies. Here we synthesize the potential of soil organisms to enhance ecosystem service delivery and demonstrate that soil biodiversity promotes multiple ecosystem functions simultaneously (i.e., ecosystem multifunctionality). We apply the concept of ecological intensification to soils and we develop strategies for targeted exploitation of soil biological traits. We compile promising approaches to enhance agricultural sustainability through the promotion of soil biodiversity and targeted management of soil community composition. We present soil ecological engineering as a concept to generate human land-use systems, which can serve immediate human needs while minimizing environmental impacts.

Trends

Recent evidence showed that soil biodiversity supports several ecosystem functions simultaneously, underpinning its crucial role in ecosystems worldwide.

To enable the proper functioning of ecosystems, soil biodiversity has to be enhanced and maintained.

Our analysis indicates that the sustainability of agricultural ecosystems can be restored by stimulating soil life and internally regulated ecosystem processes.

To face the immense global problems related to a growing human population and deterioration of the global biosphere, targeted manipulations of soil organisms become necessary in addition to promoting soil biodiversity.

Targeted approaches through soil ecological engineering to maximize the contribution of soil biological processes to sustainable ecosystem functioning can help to provide food security while minimizing negative environmental impacts.

Soils and Ecological Intensification

Soils are among the most biologically diverse habitats on Earth. It has been estimated that 1 g of soil contains up to 1 billion bacteria cells comprising tens of thousands of taxa, up to 200 m fungal hyphae, and a wide range of nematodes, earthworms, and arthropods [1]. Land-use intensity is constantly increasing on a global scale, with adverse effects on soil ecosystems. One quarter of soils worldwide face degradation [2] and an increasing number of studies have shown that intensive land use threatens **soil biodiversity** (see Glossary), with some groups of soil biota severely affected in very intensive systems [3,4]. Simultaneously, land-use intensification and associated reductions in soil biodiversity contribute to several environmental problems, such as the eutrophication of surface water, reduced aboveground biodiversity, and global warming [5], and can negatively affect human well-being [6]. To combat the negative consequences of human land use, **ecological intensification** has been proposed as an approach to integrate ecological processes into land-management strategies to enhance **ecosystem service** delivery and reduce anthropogenic inputs [7]. However, the role of belowground biodiversity in ecological intensification has been unclear.

In this review, we apply the concept of ecological intensification to soils (Figure 1, Key Figure) and we present soil biological engineering as a concept to enhance usage of internal ecosystem processes for sustainable soil management. We first highlight how soil organisms contribute to **ecosystem functioning**, especially in their capacity to enhance a multitude of ecosystem processes simultaneously. We demonstrate that enhanced soil biodiversity and specific changes in soil **community composition** can complement each other to increase overall

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Key Figure

Schematic Model Applying the Concept of Ecological Intensification [7] to Soils

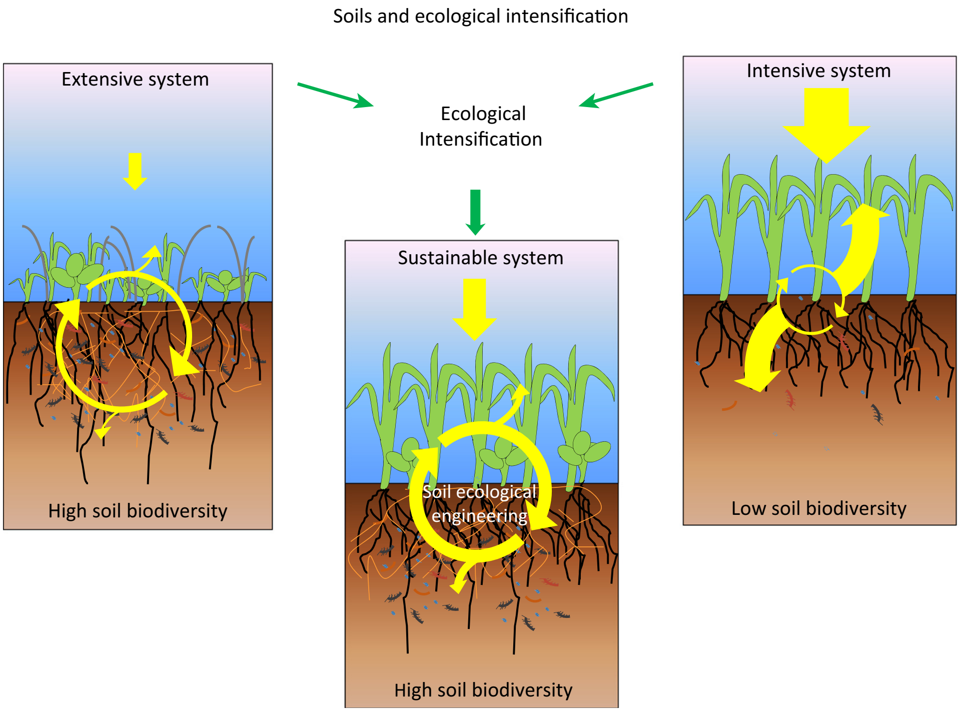

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Figure 1. Yellow arrows show the relation of resource inputs, losses, and internal regulatory processes performed by soil biota (indicated by colored shapes in the soil) in relation to management intensity. The extensive system has a rich soil life and is characterized by low resource inputs and outputs, a high rate of internal regulatory processes, and low productivity. The intensive system has a depleted soil life, is characterized by high resource inputs, high losses, a low rate of internal regulatory processes, but high productivity. Ecological intensification ideally combines traits of both systems and leads to a sustainable system that has a rich soil life and is characterized by moderate resource inputs, a high rate of internal regulatory processes, low nutrient losses, and high productivity. Soil ecological engineering further optimizes the internal regulatory processes performed by soil biota to maximize ecosystem service delivery.

ecosystem sustainability and **ecosystem stability**, in terms of the long-term, environmental friendly delivery of crucial ecosystem services. Second, we show how current land-use practices and agricultural intensification affect belowground processes in positive and negative ways and, in most cases, ignore them. Finally, we present management options to foster soil biodiversity and engineer soil community composition in managed ecosystems (e.g., agricultural systems) to enhance and maintain ecosystem productivity, stability, and sustainability.

Soil Biota and Ecosystem Function

The role of soil organisms in ecosystem functioning has been long recognized and it is well known that soil biota are of pivotal importance for nutrient and carbon cycling in natural ecosystems (Figure 1). Soil fauna and **saprotrophic fungi** fragment and decompose organic matter, making organically bound nutrients available for further processing through the entire soil food web and for plant uptake [8,9]. Micropredators, such as nematodes or protozoans, further

Glossary

Arbuscular mycorrhizal fungi (AMF): soil fungi living in a mutualistic relation with most land plants and, in many cases, providing benefits to plants and ecosystems.

Community composition: proportion of different organisms relative to the total in a given habitat.

Ecological intensification: the attempt to integrate ecosystem services provided by biodiversity into crop production systems.

Ecosystem function or process: a biological, geochemical, or physical process occurring in an ecosystem.

Ecosystem multifunctionality: simultaneous performance of multiple ecosystem functions.

Ecosystem service: benefit that humans derive from ecosystems.

Ecosystem stability: the resistance and resilience of ecosystems to disturbance or stress, such as through environmental change.

Ecosystem sustainability: the ability of an ecosystem to maintain its potential for self-regulation in the long term.

Microbiome: the entity of microorganisms inhabiting a certain habitat, such as the soil or rhizosphere.

Saprotrophic fungi: fungi deriving their energy from nonliving organic material.

Soil biodiversity: the variety of living organisms inhabiting soil.

Soil microfauna: soil-inhabiting invertebrates with a maximum size of 0.1 mm.

regulate the availability of plant nutrients through complex feeding activities [10,11]. Plants, assisted by mutualistic organisms, use the mineralized nutrients to build up organic matter, which eventually re-enters soil to be decomposed again. Although the soil fauna has been shown to have profound impacts on soil ecosystems and to regulate many important soil processes, the key steps in the major elemental cycles are ultimately conducted by soil microorganisms. Soil microorganisms comprise a major fraction of the total living soil biomass [12]. Much progress has been made in elucidating their functional roles in recent years. Various processes in the nitrogen cycle are exclusively performed by microbes (e.g., fixation of atmospheric nitrogen into plant available ammonium; nitrification of ammonium into nitrogen oxides; or denitrification of NO_3 into N_2O and N_2). These processes are of key importance for ecosystem functioning because the availability of nitrogen determines plant productivity [13] and excess nitrogen can cause environmental problems, such as water eutrophication, decreased water quality, global warming, depletion of the stratospheric ozone layer, among others [14].

Several processes in nitrogen cycling are still not well understood. This is perhaps best exemplified by the discovery that a recently identified microbial guild mediates the soil sink capacity for the greenhouse gas N_2O [15] or that bacteria responsible for anaerobic oxidation of ammonium (anammox) can make an important and hitherto overlooked contribution to nitrogen losses in agroecosystems [16]. Moreover, recent work indicated that plant-symbiotic **arbuscular mycorrhizal fungi** (AMF) can reduce not only the amount of plant nutrients leached from soil [17], but also the amount of N_2O emitted from soil through denitrification [18,19]. Given that AMF are also well known for their ability to improve plant nutrition and to efficiently scavenge for soil phosphorus resources [20], these fungi have the potential to enhance nutrient-use efficiency in agricultural systems [21].

In addition, soil biological processes ultimately determine the potential of soils to sequester carbon. Soils contain the 'biggest pool of organic carbon on Earth, exceeding atmospheric and biospheric carbon pools [22]. Therefore, the factors that control carbon storage and release from soils are of fundamental importance [23]. Investigating a range of different land-use types across several European countries, Cramer *et al.* [24] found that soil microbiological indicators explained 82% of the variation in soil carbon cycling. It is generally assumed that, with higher proportions of fungi in soil, the potential for carbon sequestration increases [25]. In addition, Tardy *et al.* [26] reported that bacterial and fungal diversity explain significant portions of carbon mineralization.

Finally, the burrowing, casting, and nesting activities of earthworms, enchytraeids, and soil arthropods, as well as biochemical compounds released by all kinds of soil biota, have been shown to influence soil aggregation and soil structure [27,28]. A range of meta-analyses highlighted the beneficial effects of soil organisms on ecosystem productivity. Sackett *et al.* [29] found that an increase in soil fauna increased plant productivity by 35% across ecosystems, and bacterivorous **microfauna** were found to contribute to enhanced plant nutrition [30]. Another meta-analysis found that earthworm abundance was generally related to enhanced crop yields [31] and AMF have been shown to enhance wheat yields [32], although this may not be the case in fertile soils.

Soil Biodiversity versus Soil Community Composition

Although much is known about specific functions conducted by specific functional groups, it is unclear how widely functions are distributed among different taxa. It has been a long-held view that soil microbial communities comprise such high diversity and such a high level of functionally redundant organisms that changes in microbial community composition would not translate into changes in functioning [33]. However, recent studies showed that community composition matters. For example, Strickland *et al.* [33] found that geographically distinct microbial communities have distinct rates of carbon mineralization. Other studies investigated the process of denitrification, where nitrogen oxides are reduced to the strong greenhouse gas N_2O and subsequently to unreactive N_2 gas. These studies showed that denitrification was directly linked to the composition and abundance of denitrifying soil communities. The proportion of denitrifying bacteria lacking the genes encoding proteins involved in N_2O reduction was shown to relate to the proportion of N_2O from total soil denitrification [34]. Moreover, a reduction in the diversity of denitrifying communities could be shown to reduce total denitrification activity in soil [35]. These examples provide proof of principle that microbial community composition can affect ecosystem functions.

There is an ongoing debate about the extent to which functional redundancy occurs in soil communities. Nielsen *et al.* [36] reviewed studies investigating soil biodiversity–ecosystem functioning relations and found that, at low levels of soil biodiversity, additional species often improved ecosystem functioning, while at higher-diversity levels, effects of species richness on functioning were less frequent. They also found that community composition often had stronger effects compared with species richness. These insights imply that, for the proper functioning of ecosystem processes, a basic toolbox of organisms with certain functional characteristics is necessary, while further increases in soil biodiversity give no direct benefits, suggesting functional redundancy among species. However, agricultural land-use systems usually have a lower (sometimes much lower) level of soil biodiversity compared with less intensively used or natural ecosystems [3,37]. Therefore, the loss of a small number of species or functional groups in such systems could more easily hamper ecosystem functions [38] compared with natural ecosystems. Griffiths *et al.* [39] showed that the functional capabilities of less-diverse soil communities were less resistant to stress compared with diverse communities, although, under no-stress conditions, few functional differences between communities were observed. Moreover, some ecosystem functions are provided by microbial consortia and different functional groups of soil biota have been shown to complement each other in supporting plant productivity [40]. Hence, simplification of soil food webs and the loss of particular soil biota can directly and indirectly affect the functioning of remaining soil biota.

In the study by Wagg *et al.* [41], soil biodiversity and community composition were manipulated by filtering soil through different meshes of declining size. A successive reduction in soil biodiversity led to the successive decline in some of the measured ecosystem functions, such as plant diversity. Other functions, such as litter decomposition, were maintained at a constant degree at higher levels of biodiversity but declined sharply after a certain mesh size, indicating that the performance of this function depends on particular groups of organisms (i.e., ‘keystone species’). Similarly, Schimel [42] proposed to categorize ecosystem functions into physiologically and phylogenetically ‘narrow’ (e.g., nitrification) and ‘broad’ processes (e.g., organic matter decomposition). For some functions, soil biodiversity per se seems to be important, while for others, the presence of certain organism groups (i.e., soil community composition) is crucial. This highlights the difficulties of applying a unifying concept (such as soil biodiversity) to different ecosystem functions, because the underlying mechanisms are likely to vary from function to function. However, the stochastic effects of soil biodiversity can directly provide benefits for ecosystem functioning. It has been shown that increasing levels of soil biodiversity can reduce the ability of a pathogen to colonize the soil [43]. With changing environmental conditions, such as through climate change, the ability of a particular organism to perform its function might be hampered. With high biodiversity, the probability is higher that a partly redundant organism can take over the function under the new environmental conditions (i.e., the insurance effect of biodiversity, *sensu* Yachi *et al.* [44]). Therefore, similar to aboveground biodiversity, soil biodiversity might have direct implications for ecosystem stability under environmental change, such as global warming [45].

Taken together, the above findings suggest that, to maximize the beneficial effects of soil organisms on ecosystem functioning, both soil biodiversity per se and the presence of specific key organism groups have important roles, depending on the function considered.

Ecosystem Multifunctionality

Disentangling the variety of interactions and precisely evaluating which organisms provide which functions under which conditions and how different organisms interact, is a daunting task (Box 1). While technology to detect and quantify soil organisms in high phylogenetic resolution is developing rapidly [12,46], knowledge of the ecological significance of this information is incomplete and ecological theory is lagging behind [47]. However, advanced analytical methods, such as interaction networks, might help us to understand the underlying processes leading to specific net ecosystem effects [48]. Moreover, by adopting conceptual advances from aboveground ecology, important conclusions about the importance of soil biota for overall ecosystem functioning (i.e., multifunctionality) can be drawn (Box 1). First, evidence for the positive effects of soil biodiversity on ecosystem multifunctionality comes from three recent studies that manipulated soil biological complexity in microcosms [41], larger mesocosms [49], and in outdoor lysimeters [21]. We reanalyzed these three studies to compare ecosystem multifunctionality at high and low soil biodiversity.

All three studies found a higher level of ecosystem multifunctionality, defined as a measure of the simultaneous performance of multiple ecosystem functions, with higher soil biological diversity (Figure 2A). However, there was considerable variation in the extent of multifunctionality at high soil biodiversity levels and multifunctionality values of individual experimental units at high soil biodiversity were low in some cases. This indicates that, even at high soil biodiversity levels showing increased average ecosystem multifunctionality, biological communities can be functionally limited (Figure 2A). To have maximum effect on ecosystem multifunctionality, soil community composition will have to be additionally optimized (Figure 2B). Although the evidence is striking that soil biological dynamics have a fundamental role in the sustenance and productivity of natural ecosystems and for local, as well as for global nutrient and energy cycling processes (Figure 1), they remain mostly overlooked in managed ecosystems, such as in agriculture.

Box 1. Soil Complexity and Ecosystem Functions

Soil organisms not only influence a range of ecosystem functions, but also interact with each other directly and indirectly through competitive, facilitative, mutualistic, pathogenic, or predatory effects [97]. Different ecosystem functions trade off against each other [98] and feedback on soil organisms. In addition, all interactions are shaped by environmental factors, such as climate, geomorphology, and land use, adding to the complexity of the system and making all interactions highly context dependent. To understand this multitude of interactions fully is a daunting task. Reductionist experiments investigating effects of single groups of soil organisms on specific functions are important to understand mechanistic backgrounds. However, they do not serve to address the complex interplay between different organisms and ecosystem functions. Ecological network studies aim to decipher the underlying species interactions. Combining ecological network analysis and food-web theory with biodiversity–ecosystem functioning research to detect correlative patterns in soil communities and ecosystem functions may help to elucidate these complex processes [48]. Research showed that more diverse species communities often lead to a higher level of functioning for specific processes [69]. Moreover, it has been recognized that diverse species communities affect several ecosystem functions simultaneously [99]. Most studies focused on biodiversity effects on one or few specific functions, but effects on overall ecosystem functioning are not well understood and may be under- or overestimated.

To quantify the overall effect of soil biodiversity on ecosystem functioning, generalizing approaches are necessary. Multifunctionality indices have been applied to soil studies to provide a quantitative measure of soil biodiversity effects on multiple ecosystem functions simultaneously [100]. Such indices allow general inferences about net effects of soil biodiversity on ecosystem functioning and provide a useful tool to summarize the highly complex and interactive processes in soil ecosystems.

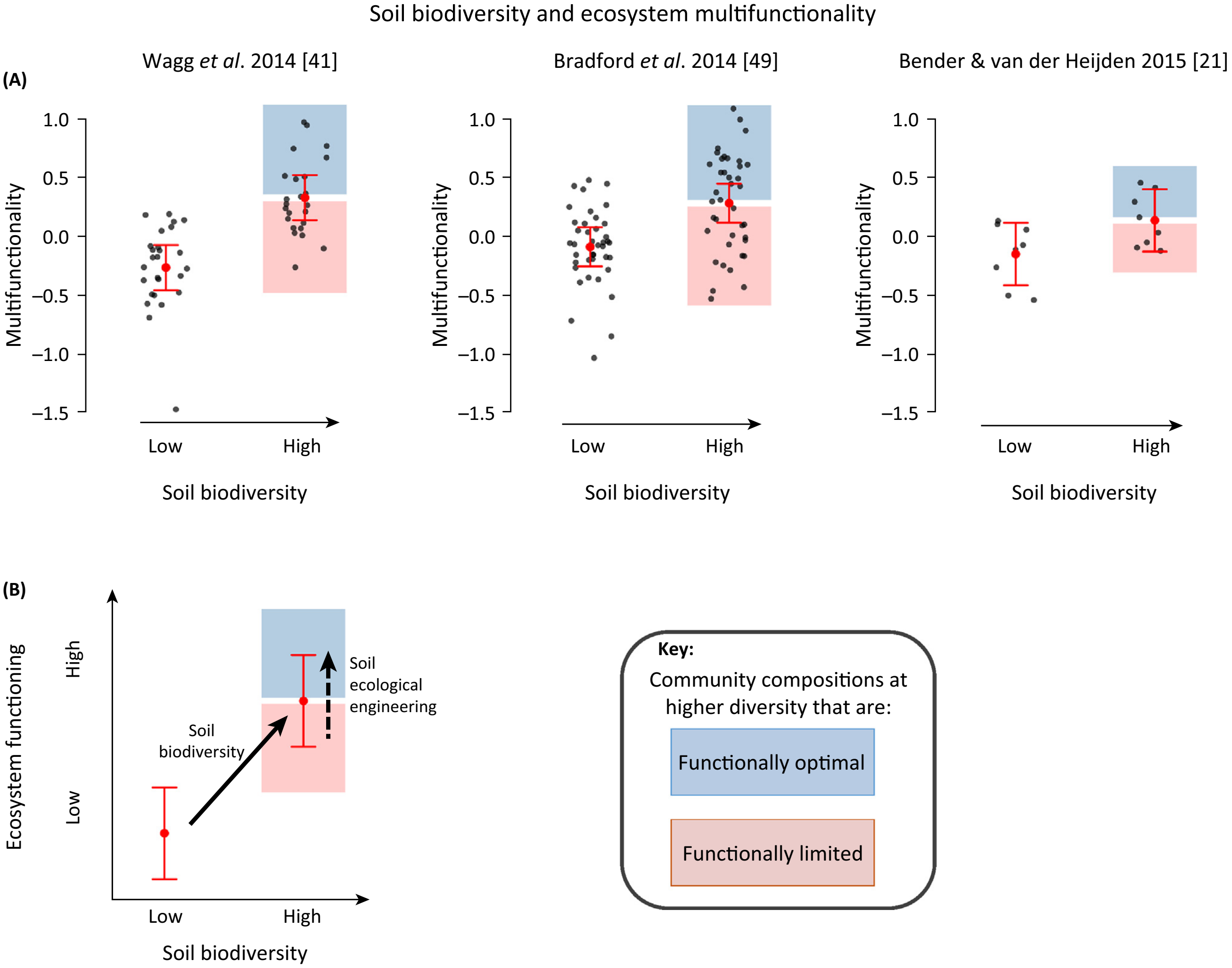

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Figure 2. Effects of Soil Biodiversity on Ecosystem Multifunctionality. The results shown in (A) are based upon three studies that manipulated soil biodiversity and measured several ecosystem functions [21,41,49]. In each study, the differences between the soil biodiversity treatments were significant (two-sided students-t-test; $P < 0.001$ for [41] and [49], $P < 0.05$ for [21]). Red dots represent mean values, error bars represent 95% confidence interval (CI) for the difference between means. Data points shaded in blue and red indicate functionally optimal and functionally limited soil biological communities at high soil biodiversity levels, respectively. Soil biological engineering could further improve the functionality of soil communities and amplify positive effects of soil biodiversity on ecosystem multifunctionality (B). See the supplemental information online for methodological details.

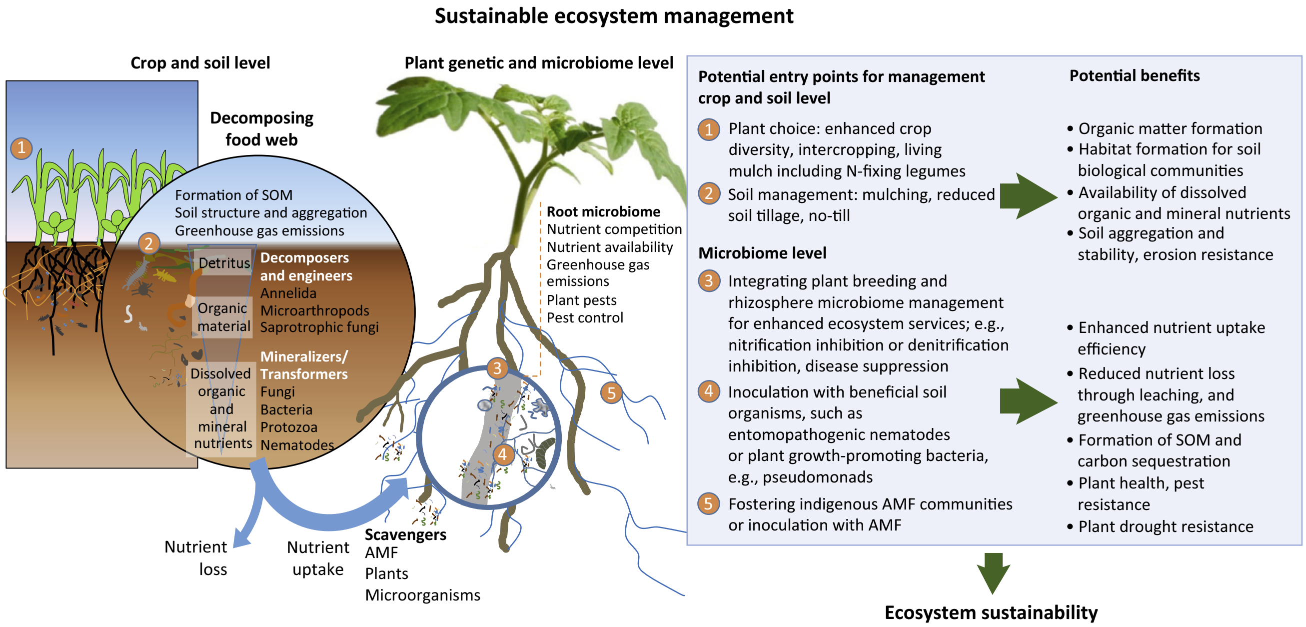
Human Land-Use and Soil Ecosystem Services

Land-use intensification usually interferes with soil internal biological processes and, in agricultural systems, human activities often replace such internal processes with external inputs. For example, biological nitrogen fixation has sustained life on Earth for thousands of years, but modern agricultural practices are based, in huge part, on industrially produced mineral fertilizers [50]. Generally, intensive agricultural practices are considered to lead to simpler soil food webs comprising smaller-bodied organisms and fewer functional groups [3]. Agricultural management practices, such as intensive soil tillage, repeated and intensive fertilization, application of pesticides, and low plant diversity, have been shown to have adverse effects on several groups of soil organisms, including AMF [4], earthworms [51], and microarthropods [52], and to reduce overall soil microbial biomass [53].

Human land use is a major cause of severe environmental problems [5]. Evidence is increasing that, in addition to direct management effects, there are also indirect effects via soil biota providing crucial ecosystem functions [41,54] (Figure 1). Conservation agriculture and organic farming approaches attempt to reduce negative impacts on biodiversity and soil biota [4,37,55]. However, in many cases, more sustainable land-use systems do not achieve yield levels of intensive systems [56]. It appears that optimization of supporting services, such as nutrient cycling or soil formation, trades off with provisioning services, such as crop yield. Given the constantly growing human population and changes in human diet towards higher meat consumption, food production will have to be doubled within the next few decades [57]. Therefore, yield declines through trade-offs between supporting and provisioning services will have to be minimized. A major challenge for the next decades will be to develop strategies and tools to optimize sustainability while maximizing yields.

Engineering Soil Biodiversity for Ecosystem Sustainability

To maximize benefits from ecosystems for human requirements, strong interventions in natural processes are necessary. It has become clear that the 'green revolution' has reached its limits for further yield increases in developed countries [58] and the adverse effects of human land management appear to exceed the capacity of the Earth [59]. Foley *et al.* [57] stressed that global agriculture requires revolutionary approaches to meet the challenges of food security and environmental sustainability. In line with this call, we propose to start an 'underground revolution' by integrating knowledge on how the biological systems and diversity of soils operate in human agroecosystem management. We must go a step beyond generic biodiversity-function relations. For instance, blindly enhancing soil biodiversity infers random inclusions of more species. Maintaining more of everything in an unspecified manner might also include a greater diversity of undesired organisms, such as pathogens [60] or weeds [55]. Thus, we propose a targeted soil biological engineering approach to improving ecosystem functioning and services.



Potential entry points for management crop and soil level

① Plant choice: enhanced crop diversity, intercropping, living mulch including N-fixing legumes

② Soil management: mulching, reduced soil tillage, no-till

Microbiome level

③ Integrating plant breeding and rhizosphere microbiome management for enhanced ecosystem services; e.g., nitrification inhibition or denitrification inhibition, disease suppression

④ Inoculation with beneficial soil organisms, such as entomopathogenic nematodes or plant growth-promoting bacteria, e.g., pseudomonads

⑤ Fostering indigenous AMF communities or inoculation with AMF

Potential benefits

- Organic matter formation
- Habitat formation for soil biological communities
- Availability of dissolved organic and mineral nutrients
- Soil aggregation and stability, erosion resistance

- Enhanced nutrient uptake efficiency
- Reduced nutrient loss through leaching, and greenhouse gas emissions
- Formation of SOM and carbon sequestration
- Plant health, pest resistance
- Plant drought resistance

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Figure 3. Summary of Different Approaches for Local Ecosystem Management from a Soil Ecological Perspective. Entry points include crop, soil, and microbiome management. Numbers in orange circles indicate potential entry points for ecosystem management.

Table 1. Overview of Selected Ecosystem Functions that Can Be Improved by Soil Biological Management Strategies

Ecosystem Function	Soil Biological Management Strategy	
	Enhancing Overall Soil Biodiversity	Targeted Soil Ecological Engineering
Pest control	+	+
Plant nutrient uptake		+
Reduction of nutrient losses		+
Soil formation	+	
Carbon sequestration	+	+

To achieve maximum effects, management strategies have to apply at multiple scales, from soil and plant community management to plant genetic and rhizosphere **microbiome** management (Figure 3). These management strategies can be categorized on the one hand as strategies enhancing general soil biodiversity in an untargeted way and, on the other hand, as targeted manipulations of soil community composition with the aim to specifically affect certain ecosystem processes that are beneficial for sustainable food production in the short or long term (Table 1). Here, we present specific research areas that, from our point of view, require further attention:

Understanding and Application of Soil Management Practices that Conserve the Soil Biological Potential while Allowing Economic Farm Management

While agricultural soil management, such as tillage, often has adverse effects on soil biota, it eases weed control and promotes the decomposition and mineralization of organically bound nutrients [61]. Soil management practices that minimize negative effects on soil biota while providing the desired agricultural benefits (e.g., no, or reduced soil tillage, and strip tillage) need to be further developed. Such conservation tillage practices are often most successful in combination with other measures, such as cover crops and mulches [62]. The application of organic residues and composts have also been shown to reduce pest incidence [63] and weed pressure, and to favor soil biota [55]. In addition, applications of biochar to agricultural soils to improve soil properties and plant performance received much attention over the past decade and have also been shown, for example, to enhance nitrogen fixation and AMF abundance [64]. Moreover, practices conserving the soil biological potential can enhance or maintain soil organic matter content and, therefore, can contribute to long-term soil preservation [65].

Development of Diverse and Efficient Crop Species Mixtures and Crop Rotations that Favor Higher Soil Biodiversity and Can Make Use of Complementary Biodiversity Effects

Enhancing crop diversity spatially (e.g., intercropping) or temporarily (e.g., crop rotation or cover crops) has been proven to have several beneficial effects on ecosystem processes [66]. For instance, the selection of specific cover crops has been used to enhance the abundance of soil biota that increase the yield of the subsequent crop [67]. Moreover, by planting diverse mixtures of rice cultivars in a field study, rice pathogen incidence was reduced to such low levels that farmers did not have to apply fungicides, while yields strongly increased [68]. Enhanced crop diversity might exert similar beneficial effects on soil biota and belowground ecosystem processes. However, there is a severe lack of studies addressing this issue in an applied agronomic context. The targeted combinations of crop varieties with different traits in relation to ecosystem functioning also exploiting niche-complementarity effects [69,70] theoretically opens up a range of possibilities to manage ecosystem services in cropping systems and to reduce the dependence on external resource inputs.

Integrating Plant Breeding and Rhizosphere Microbiome Engineering

Several studies indicate that plants can shape their root endophytic and rhizospheric microbial communities [71]. This feature has also been shown for crop plants [72] and theoretically provides the option to breed crops to acquire soil microbes that provide specific services [73]. For example, some plants can inhibit the transformation of ammonium into nitrate (nitrification) by affecting nitrifying microbes. This potentially improves the nitrogen availability of the plant and can also reduce nitrogen losses from soil through leaching and denitrification [74]. The integration of knowledge about how plants regulate the composition of the root microbiome into crop breeding strategies could greatly contribute to agricultural sustainability [75]. For example, the recruitment of root symbionts, such as AMF or rhizobia, is mediated through carbon allocation and root exudation of specific compounds [76,77]. Selecting crops for the high production of such compounds could maximize symbiotic benefits. Selection for the plant microbiome can also contribute to disease suppression [78] or to altered plant traits, such as flower time [79]. Plant breeders have largely ignored such processes and it is now a key challenge to integrate root traits and associate microbiomes in future breeding programs [80], especially since several modern plant cultivars have partly lost their ability to associate with beneficial soil biota [81]. Action is urgent because the development of new cultivars is often time consuming and can take decades, especially if multiple traits are involved [82]. The adoption of transgenic methods could also be an option to engineer plant effects on rhizosphere communities.

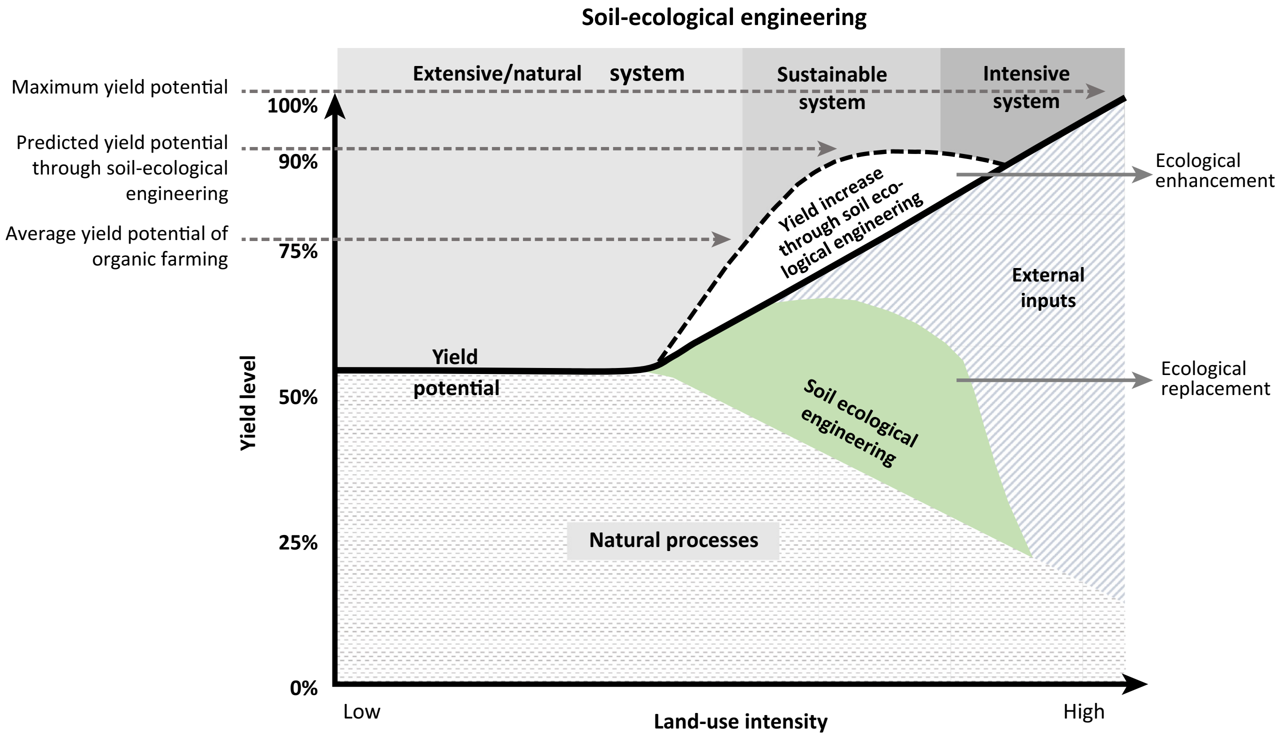

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Figure 4. Conceptual Model Showing the Contribution of External Resource Inputs and Natural Biological Processes to An Ecosystem Function (yield), in dependence of Land-Use Intensity. At low land-use intensity, yield is low and sustained by natural biological processes. With increasing land-use intensity, dependence on external resource inputs increases and the contribution of natural biological processes decreases. Yield is highest under intensive management with a high level of external resource inputs. Soil ecological engineering (green) complements the contribution of natural biological processes and can partly replace external resource inputs, therefore either maintaining yields while reducing external inputs (ecological replacement) or enhancing yield without enhancing external inputs (ecological enhancement). For example, the yield gap of organic farming systems (e.g., 25% lower yields on average in organic farming [56]) might be reduced to 10% when soil ecological engineering approaches are applied in conjunction with reduced external resource inputs.

Biofertilizer Application and Biocontrol

The application of organisms contributing to improved plant performance is an already widely applied technique in many subtropical countries, where fertilizer resources are often limiting [83,84]. Inoculation of seedlings or soils with AMF propagules is, in addition to fostering indigenous AMF communities, an option to profit from beneficial effects provided by these fungi. However, the success of AMF inoculations in temperate soils might be highly variable and plant species and soil type dependent [85]. It is already standard practice to inoculate soybeans with nitrogen-fixing bacteria, which can completely replace the need for nitrogen fertilization [86]. The use of biocontrol agents to control agricultural pests receives much attention, especially in organic farming. It has been shown that a range of microbial phyla, such as *Pseudomonas*, *Bacillus*, and *Trichoderma*, can induce systemic resistance of plants against pathogen attacks [87,88]. A major limitation of bacterial inoculations is often the poor survival of the organisms introduced into soil. However, new formulations for the successful establishment of bacterial inoculants are being developed [89]. The application of microfaunal species, such as entomopathogenic nematodes, has also great potential to reduce pest incidence [90,91]. However, introducing non-indigenous organisms to soil requires profound knowledge of the consequences for endemic species communities [92]. Recent developments in sequencing-based methods from soil or root samples to identify species and even specific isolates will make it possible to follow the fate of microorganisms introduced into soils [93] and will allow risk assessment.

Soil Ecological Engineering

It is obvious that current human land-use practices cannot be maintained in the long term without the deterioration of the integrity of the Earth [59]. Approaches, such as conservation agriculture and organic farming, which aim to promote internal regulatory processes, on average render lower agricultural yields compared with conventional systems [56,62]. We propose ‘soil ecological engineering’ as an approach combining management practices enhancing overall biological diversity in human land-use systems with targeted manipulations of soil biota to deliver specific desired functions, enhance overall ecosystem service delivery, and minimize yield gaps (Figure 4). The discrepancy between high agricultural yields and ecosystem sustainability can only be overcome by strong modifications of ecosystem processes. While the approaches of the green revolution focused on external manipulations of ecosystems, we argue that internal ecosystem manipulation has enormous potential to enhance ecosystem performance (Figure 1), yet with lower environmental consequences.

Concluding Remarks and Future Perspectives

Our review demonstrates that soil organisms have the potential to enhance sustainable ecosystem functioning. We are now beginning to realize the potential below our feet and its importance for plant productivity and environmental sustainability. Humans are taking much from the soils of the Earth, and a one-sided focus on high production in agricultural settings has resulted in the successive deterioration of the fundamental properties of those soils, including the biological potential for self-regulation. Philippot *et al.* [94] proposed going ‘back to the roots’ whereby they recommended that we should observe and learn from natural plant–soil systems, where rhizosphere processes and microbial interactions are more evolved than in anthropogenic controlled cropping systems. Similarly, we propose to go back to the roots of agriculture, relying more on internal regulatory processes compared with contemporary agriculture. Combining targeted soil biological approaches with state-of-the-art technological advances in agricultural science (e.g., precision agriculture for tillage and weed control [95] or optimized nutrient and water addition [96]) could serve to reduce external resource use to a minimum while yields could be maintained or even increased. A major challenge over the next decades will be to sustain the human population and the integrity of the Earth simultaneously (see Outstanding Questions). Our planet is a closed system and we have to use the potential

Outstanding Questions

What is the impact of soil biodiversity on ecosystem multifunctionality and agricultural sustainability in real-world systems?

Which soil management strategies provide agricultural benefits while fostering beneficial soil organisms?

To what extent can soil ecological engineering compensate for external anthropogenic inputs?

Can soil biological processes help to overcome trade-offs between supporting ecosystem services (e.g., soil formation) and provisioning ecosystem services (e.g., yield)?

By which mechanisms do plants recruit their root microbiome? How can this knowledge be used to manipulate ecosystem processes?

How do diverse mixtures of crop varieties affect soil biological communities?

How can soil ecological engineering be implemented into farm management and agricultural policy?

we possess in the most efficient way. Soil ecological engineering might provide a critical step towards achieving this goal.

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Supplementary Information

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