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Plant-Soil Feedback: Bridging Natural and Agricultural Sciences

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Keywords

Biodiversity conservation, Climate change, Crop rotation, Plant root traits, Productivity, Sustainability

Highlights

- Plant-soil feedback research evolved disparately depending on the focal system
- Our framework integrates plant-soil feedback in agricultural and natural systems
- Learning from natural systems can guide towards more sustainable agriculture
- Learning from agricultural systems can assist restoration of natural systems

Trends

- Plant-soil feedback has been extensively studied in both agricultural and natural systems, with increased activity in recent years, but a framework for integrating the concepts and principles developed in these systems is lacking.
- Interactions between soil biota and plant leaf and root traits has become an important tool in understanding PSF in wild plants, but this understanding has not yet been utilized in agricultural crop rotations.

- Soil inoculations with microbial strains are increasingly being used for steering the soil microbiome in agriculture but might also offer a promising method of restoration of degraded systems, and for controlling the spread of invasive species.
- Increasing evidence shows that plant-soil feedback can play important roles in mediating ecosystem responses to forecasted climate change and extreme weather events.

Abstract

In agricultural and natural systems researchers have demonstrated large effects of plant-soil feedback (PSF) on plant growth. However, the concepts and approaches used in these two types of systems have developed, for the most part, independently. Here, we present a conceptual framework that integrates knowledge and approaches from these two contrasting systems. We use this integrated framework to demonstrate (1) how knowledge from complex natural systems can be used to increase agricultural resource-use efficiency and productivity and (2) how research in agricultural systems can be used to test hypotheses and approaches developed in natural systems. Using this framework, we discuss avenues for new research towards an ecologically sustainable and climate-smart future.

Plant-Soil Feedback in Natural and Agricultural Systems

A new vision for the sustainable management of agricultural and natural systems is needed to address population demands for food production and ecosystem service and declining ecosystem health [1,2]. Combining insights from research in agricultural and natural systems has potential to considerably improve our understanding of both systems [3–5]. Research on plant-soil-feedback (PSF), has gained attention in agriculture and in natural systems in the past ten years and the opportunity is ripe to integrate knowledge across these systems for improved food provision and ecosystem outcomes [6,7].

Wild and cultivated plant species both influence root-associated organisms, such as soil-borne pathogens, beneficial symbionts, and saprotrophs that break down plant litter. These organisms can, in turn, affect plant performance either negatively or positively. The sum of these negative and positive interactions determines the sign and strength of PSF. While PSF has been widely studied across agricultural and natural settings, research has evolved in markedly different directions depending on the focal system (Box 1, see also Online Supplementary Material Table S1). Few attempts have been made to formally integrate recent developments in PSF research in agricultural and natural systems. Here, we present a conceptual framework to fill this gap, with the aim of better predicting PSF and solve important challenges facing agriculture and biodiversity (Figure 1). We propose that conceptual and theoretical advances from research in diverse and complex natural systems can be used for the development of more sustainable agricultural practices. We also propose that lessons from simplified agricultural systems can be used to guide our understanding of PSF mechanisms in natural ecosystems. We also highlight how our framework can help move toward an ecologically sustainable and 'climate-smart' future, and propose new avenues for future research and discovery.

Bridging the Gap

Agricultural and natural systems vary substantially in terms of aboveground diversity, plant functional traits and soil biota (Figure 1). Plant domestication in agriculture selects the most productive species with resource-acquisitive traits. However, in natural systems plant species encompass the whole trait economics spectrum, including resource-conservative species [8]. That said, in both systems plant functional traits influence the effects of plants on soil organisms [3,9], and the functional traits of soil organisms (within and across taxonomic groups), and their abundance, influence the direction and strength of feedback in plants [10,11]. Consistencies between the effects of plant and soil organism traits provide the basis for our framework towards bridging PSF knowledge from agricultural and natural systems.

The conceptual approach to researching plant-soil interactions recently shifted from plant strategy frameworks [12] to more quantitative approaches using specific plant functional traits and soil food web characteristics directly linked to ecosystem functions [3,9,13–17]. These targeted approaches are useful in PSF research, particularly when applied to plant root and litter traits. For example, it was recently found that, across a large number of grassland species, plants with high specific root length and low levels of mycorrhizal colonization have more negative PSF than species with opposing traits [18]. Litter traits (e.g., C:N ratio) also influence rates of decomposition and nutrient release with feedback effects on plant growth [19,20]. Crop species that have been selected for growth rather than defense, or have lost associations with belowground mutualists because of the use of synthetic fertilizers, may in turn possess leaf and root traits that make them more prone to the build-up of negative PSF than their wild relatives (Figure 1). Identification and quantification of functional links between plant traits and PSF, and moving beyond metrics of evolutionary history and soil nutrient status [21,22], offer a promising means for evaluating the magnitude and direction of PSF (Figure 1).

It is well known that the build-up of species-specific soil pathogens and root herbivores reduces crop production in agricultural systems (Figure 1) [11], yet at the same time can promote plant succession and the maintenance of plant diversity in natural systems [10,23]. Plants also associate with a range of mutualists, including fungal endophytes, mycorrhizal fungi and growth-promoting bacteria, which are all important drivers of PSF. For example, we know from natural systems that arbuscular mycorrhizal fungi (AMF) can increase plant diversity when promoting subordinate species but decrease diversity when promoting dominant species [24]. In agricultural systems, tillage and fertilization decreases fungal biomass and disrupt AMF networks resulting in nitrogen leaching from soil with negative feedback to plant productivity [25]. Clearly, a better understanding of the functional role of soil organisms in driving the direction and magnitude of PSF is needed to better use PSF as a management tool in both agricultural and natural systems.

Plant-Soil Feedback in Agricultural Systems: Improving Sustainability and Productivity

Insights from natural systems, which contain the full complexity of diverse plant and soil communities, can help to tackle the grand challenges facing sustainable agriculture, such as disease control, nutrient retention (Figure 2), and resistance to extreme climatic events (Box 2). Ecologists are accustomed to look across a range of communities, trophic levels and species, in interaction with their environment, over a range of different temporal and spatial scales. Coverage of this depth and breadth offers an opportunity to test the generality and context-dependent nature of PSF, which can in turn be applied to managing agricultural systems (see Online Supplementary Material Table S1).

Optimizing Cropping Systems

Recent studies on wild plants have shown that interspecific PSF varies considerably among plant species in both sign and magnitude [26,27]. The range of species covered by this work offers a lens in which to test the generality of ecological theory, and develop more systematic approaches to rotation planning to maximize positive PSF effects (Figure 1). Accumulating datasets of interspecific PSF can be used to predict how sets of plant traits for specific genotypes and soils can condition the soil community to induce positive interspecific PSF (Figure 1). This could be tested with crop species and used to design efficient crop rotation and intercropping systems (Figure 2), by promoting positive interspecific PSF temporally (i.e., positive soil legacy for successive crop) and spatially (i.e., increasing productivity through belowground facilitation). One of the emerging patterns shown in natural systems is that grasses induce positive effects on broad-leaved plants through PSF [28,29]. This provides a basis for targeted testing of the benefits of rotating grain crops with broad-leaved crops in agriculture, the duration of such legacy effects, and for building a more in depth understanding of the soil organisms involved.

A primary means by which crops affect soil communities is via organic inputs. While inputs of organic material can influence disease suppression and nutrient cycling in agro-ecosystems [17,30], the mechanisms are not always well understood. In natural systems, recent studies show that the type of litter input can strongly affect the capacity of soil communities to decompose organic compounds [20,31] and results in decomposer communities becoming specialized to specific litter types [32]. The concept that emerges is that the type, rate and timing of different organic inputs into the soil are important drivers of decomposer communities. Managing litter inputs in agricultural systems therefore offers an opportunity to steer the composition of the soil community in specific directions over multiple cropping years [33]. Moreover, using a trait-based approach, it has been shown that decomposition rates depend strongly on physiological and enzymatic traits of different microbial taxa [34]. As such, manipulating microbial community traits can be a tool to boost decomposition processes in agricultural systems, although further research is needed to test this idea.

Disease Resistance and Pest Control

Minimizing losses of crops to pests and diseases is a key challenge in agriculture. Application of pesticides is commonplace, but is not always effective, and is a major public health concern. In natural ecosystems, wild plants are dependent on the activity and function of their rhizosphere communities for defenses against soil pests and diseases [11,35]. Over evolutionary time, plants developed intimate relationships with beneficial soil microorganisms, taking advantage of their ability to inhibit plant pathogens [36,37]. Agricultural practices using pesticides and synthetic fertilizers alter the balance between beneficial and pathogenic rhizosphere organisms with consequences for plant defense [38]. From studies in natural ecosystems, we can learn how plant trait-based approaches might be used to improve crop resistance to soil pests and diseases [39,16]. For example, traits which influence the phenolic profile of roots are important predictors of defense against root herbivores [39,40]. Hence, targeting specific chemical root traits through conventional breeding or genomic engineering might maintain yield under pathogen pressure in agricultural systems [41]. Exciting opportunities for new crop defense solutions also exist through re-introduction of wild plant traits into domesticated crops, and for exploring the coevolution of defense mechanisms with microbial communities in wild relatives in their native habitat [35,42].

Many of the changes in plant traits during domestication have led to impaired sustainability of agricultural systems [43,44]. Research in natural systems has shown that plant traits and beneficial microbial isolates (i.e., AMF and nitrogen-fixing bacteria) from wild plants have a greater ability to control soil pathogens than those in domesticated plants [45]. This suggests that inoculation with wild relative soil can also assist in controlling crop pathogens. However, inoculated microbial strains are sometimes difficult to establish, either due to competitive interactions with the resident microbial community or because they require more time to establish than allowed by short term crop cultivation [46]. One way to overcome this problem is to give beneficial microbes from natural ecosystems a ‘head start’ in agricultural soils using inoculated seeds [47]. Similar to natural systems [20,32], incorporating specific crop residues into the soil may also reestablish the natural balance between plant beneficial and pathogenic microbes in domesticated plants [33]. From natural ecosystems, we know that AMF can protect plants against environmental stresses and improve plant defense [48–51]; knowledge that could be used in optimizing AMF inoculations in agriculture.

Resource-Use Efficiency

From natural ecosystems, we know that plant effects on the cycling of nutrients is a major driver of PSF [52]. These nutrient-driven PSFs depend on plant resource-use traits, and the input of organic plant compounds (root exudates, litter) into the soil [53]. To increase resource-use efficiency in agriculture (i.e., the amount of biomass or grain yield produced per unit of nutrient), we can make use of PSF effects via nutrient cycling as observed in natural systems.

First, resource-use efficiency may be targeted by closing the nutrient cycle. High nutrient inputs from external sources and considerable losses of nutrients through leaching and gaseous N emissions have disrupted nutrient cycling in many agro-ecosystems [4]. In natural ecosystems, the nutrient cycle is more closed, with plant residues being decomposed and these nutrients being taken up again by plants or otherwise immobilized [20,54]. Closing the nutrient cycle in agro-ecosystems requires leaving crop residues on the field and making better use of soil decomposer communities involved in litter-mediated PSF (Figure 2) [3]. Increasing resource-use efficiency in agriculture can furthermore benefit from utilizing plants with N-uptake traits that complement each other – insights that have largely been developed in natural systems [55,56]. In agricultural systems, recent work shows that increased production can be realized by using cover crop mixtures in rotation with the main crop (Figure 2, [57]). Legumes have been used as monoculture intercrops for hundreds of years to improve soil fertility but recent PSF knowledge can be used to refine such agricultural practice to better increase productivity and sustainability. For example, interactions between legumes and nitrogen-fixing bacteria can be enhanced in plant species mixtures, thereby increasing plant productivity and tissue quality at the community-level [58] while simultaneously promoting soil carbon storage (see Box 2).

Second, plant breeders are starting to use breeding strategies where mutualistic soil organisms are one of the direct targets of the selection process [59] (Figure 2). For example, new techniques have been developed for modifying the plant genome in alliance with root-associated microorganisms through a novel technology that enables the transmission of endophytic microorganisms to the next generation of crop [60]. Optimizing plant associations with mutualistic soil organisms can in turn help increase nutrient uptake [52,61] and maintain sufficient uptake also under less optimal conditions (e.g., positive effects of mutualists under dry conditions; Box 2) [58]. It is important to note that litter-mediated PSF as discussed above and microbial-mediated PSF involving AMF interact and can have synergic impacts – litter decomposability might have stronger positive effects on PSF strength when AMF are abundant [62]. Taken together, actively utilizing nutrient-mediated PSF in agricultural management could enhance nutrient-use efficiency, reducing the loss of nutrients from the system and the need of copious synthetic fertilization.

Plant-Soil Feedback in Natural Systems: Managing Biodiversity and Ecosystem Functioning

Insights from agricultural systems, that are relatively less complex than natural systems and more easily manipulated, can provide testing grounds for the effects of soil community manipulations on plant growth, which can help to build our toolbox and understanding and managing PSF in natural systems (see Online Supplementary Material Table S1). Findings from agricultural systems on how PSF influences species facilitation and complementarity also help in predicting vegetation responses to shifts in resource availability and perturbations of the soil habitat, and in turn how restoration of degraded systems can be undertaken.

Deciphering Complex Plant-Soil Interactions

In agricultural systems, the concept and application of ‘domesticating microbial communities’ is gaining traction [63]. Many of the biological agents used in agriculture have been identified using screening approaches or resulted from fortuitous observations [63,64]. PSF experiments are particularly well suited to identifying these potential agents because PSF experiments often include information about soil organisms and plant responses to those organisms [65,66]. Similar to agricultural systems, PSF studies in natural systems have just begun exploring more systematic approaches for identifying potential growth-promoting and growth-suppressing soil organisms that might be used in ecosystem restoration. In many cases PSF will be driven by complex soil communities, which will be more difficult to describe. However, from a plant-management perspective, it is only important that culturable pathogens or symbionts with observable effects on target plant species are identified [63]. Whether individual species of soil organisms or whole communities drive PSF, the adoption of genetic sequencing by soil scientists in the next several years can be expected to increase the identification of PSF mechanisms.

Recently, we have seen additional approaches emerge, focused on the signaling that occurs between plant and soil organisms [67]. These new approaches have revealed complex interactions among plant genotypes, soil types, management approaches and soil organisms, with endophytes and mycorrhizal fungi both causing a range of positive to negative effects on different plant species as a function of species identity, plant health and resource availability [36]. Despite growing interest and promising results in agricultural systems, there are several knowledge gaps for using targeted plant-soil biota manipulation in maintaining or restoring the diversity and stability of natural ecosystems. It is likely that a complex network of soil organisms, not just a single organism, determines PSF [68] and that PSF is contingent on management and other site-specific traits (Figure 1). New studies to build a common understanding of the interaction between management, plant traits, and the key players in soil community are needed.

Ecosystem Restoration after Disturbance

Agricultural studies are now focusing on specific management or engineering of soil communities to obtain desired soil community composition and function [4]. Remarkably, while there is an overwhelming amount of information on PSF effects and the specificity of these effects in agricultural systems [7,27,28], so far this knowledge has rarely been used to manage natural soils, i.e. to restore degraded ecosystems (see [69]). Here, we argue that ecologists working within natural systems should apply this knowledge for practical soil management and engineering of soil communities and learn from the lessons of agricultural research in engineering soil microbes for a specific desired aboveground community composition.

Many natural ecosystems are degraded or disturbed due to human activities and restoration of these systems is an important goal. Here, the focus is often on reestablishment of particular key plant species [70] and reduction of unwanted plant species such as exotics, invasives or ruderals (Figure 2). The potential benefits of using soil inoculations in management of natural ecosystems, is nicely highlighted by a recent large field experiment on former arable land in the Netherlands. Inoculation with a small amount of soil collected from underneath natural plant communities was able to alter the composition of the soil community to more closely resemble the natural state, which in turn led to the establishment of vegetation with more target species and fewer ruderals [71]. Importantly, inoculation with soil collected from different donor ecosystems led to different soil communities and vegetation in the recipient plots several years after application [71]. The longer-term consequences are still a matter of speculation, but this example shows that inoculation with soil communities can be used to steer natural ecosystems.

Similar to weed control in agricultural systems, the restoration of natural systems often aims to suppress invasive species and support target species. Suppression of plant growth can be obtained via negative PSF (e.g., through soil pathogens), while supporting the growth of target species can be obtained via positive feedback (e.g., through beneficial organisms such as mycorrhizal fungi) (Figure 3; [23,60]), both of which could be manipulated through inoculation of soil organisms. The USDA ARS EBIPM Area Wide Program is currently testing the ability of the fungal strain *Pyrenophora semeniperda* to decrease cheatgrass (*Bromus tectorum*) growth without affecting winter wheat [72,73]. Similarly, *Methylobacterium* spp. was recently tested for its ability to increase native but not weed growth in coastal sage-scrub communities in California [74]. Closer integration of PSF work in natural systems offers an opportunity for exploring the robustness of these biocontrol programs, and opens the opportunity for more widely using soil organisms in ecosystem restoration of natural communities.

Multifunctionality of Plant-Soil Feedback

In recent years, it has been increasingly advocated that understanding the ecosystem consequences of environmental change requires the integrative study of multiple ecosystem functions (i.e., multifunctionality, [75]). In agricultural systems, this approach has successfully been applied to estimate the sustainability of management practices [76]. For example, recent work in agricultural model systems suggests that increasing soil biodiversity has a positive effect on decomposition of plant material, soil nutrient cycling, plant diversity and productivity [4,77]. There is active exploration of how agricultural management might be able to target and directly engineer a desired soil community that increases ecosystem multifunctionality, by stimulating soil biodiversity and specific beneficial organisms (e.g., after isolation of particular microorganism species) [4]. So far, the application of using PSF for promoting ecosystem multifunctionality in natural systems have received little attention but the approaches developed in agricultural systems seems encouraging in addressing this challenge.

Natural ecosystems provide multiple functions such as carbon storage and water purification, which alongside other ecosystem services have been valued at 125 trillion USD/year in 2011 [78]. Ongoing global changes are however jeopardizing ecosystem multifunctionality, often through changes in plant composition and diversity [79]. While emphasis has already been put on the role of plant diversity and functional traits in driving multiple ecosystem functions [3,9], soil organisms also determine plant diversity and are direct drivers of multifunctionality [68,80]. Experimental microcosm work supports this idea, showing that the diversity of soil decomposers can control effects of plant diversity on plant productivity and nitrogen uptake [81]. Further, soil food web composition has been linked to multiple ecosystem functions across different European land use systems [15], with for example earthworms favoring carbon immobilization and AMF and bacteria enhancing nutrient cycling. PSF has also clearly been linked to climate mitigation and adaptation (Box 2). Despite these advances however, a formal framework for linking PSF to multifunctionality in natural ecosystems systems is lacking. Filling this missing link, and identifying synergies involved across functions, is important for the management of ecosystem functioning and associated services provided to humanity.

Concluding remarks and future challenges

Developing sustainable agriculture to meet demands for crop production and biodiversity conservation in face of global climatic changes is an important challenge of the 21st century. While many questions remain (*see* ‘Outstanding Questions’), major advances in agricultural and natural systems have improved our understanding of linkages and feedback between plants and soil organisms, which in turn have brought us closer to meeting this challenge.

Our review demonstrates how the recent developments in PSF research across agricultural and natural systems can assist in developing more targeted approaches in managing plant-soil organism interactions (Figures 2 and 3, and summarized in Online Supplementary Material Table S1). Targeting positive PSF effects is key to improving the sustainability of food production whilst maintaining productivity. This can be achieved by adding organic inputs to close the nutrient cycle, and to steer the decomposer community with the aim of increasing soil nutrient availability. As we show in this review, promoting biodiversity and enhancing ecosystem functions (i.e., carbon storage, decomposition, nutrient availability, invasive control) in natural systems can also be attained through manipulation of soil biota guided by the knowledge from agricultural systems about soil organism identity and function. Engineering plant-soil biota interactions, through soil inoculation, genome editing, and/or plant trait selection offers a promising avenue to rapidly manipulate the direction and strength of PSF and tackle the grand challenges in both natural and agricultural systems in the future. However, as with any form of engineering our natural environment, obvious care has to be taken of potential unwanted side effects of introducing new organisms and organism traits into an open system [82,83]. Assessing the risks of changing nutrient cycles and trophic interactions will be required before initiating ecosystem engineering and this risk assessment will likely benefit from bridging knowledge from both systems.

By looking ‘over the fence’ we see large potential for joining concepts and methodology across these disparate fields for future research (Box 3). Building a common understanding of the organism traits that mediate how PSF drives resource-use efficiency and resistance to soil diseases and climatic extremes (Box 2) is an important next step. Furthermore, developments in trait-based ecology for soil organisms are promising to better understand the functional role of species and groups of soil organisms. Only if we know the functional attributes of the plant and soil organisms involved, can we make adequate predictions of how ecosystems will respond to human interventions, environmental change, and extreme climatic events. Joining forces across disciplines offers a unique opportunity to expedite the trajectory towards a sustainable and climate-smart future of plant-soil life on Earth.

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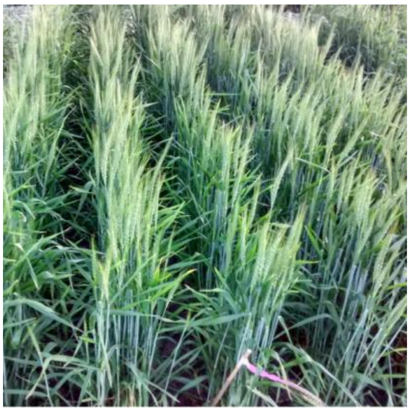
Outstanding Questions

- What disciplinary and institutional bridges need to be built to ensure that knowledge on plant-soil feedback from natural ecosystems can be translated into sustainable agricultural practices?
- Can plant-soil feedback be used to enhance nutrient use efficiency and reduce synthetic fertilizer use across a range of rotational cropping system types? What role do plant root and leaf litter traits play mediating these effects, and can traits for optimal rotations be selected for in new crop varieties?
- Agriculture has embraced microbial management techniques to promote beneficial soil biota and suppress soil pathogens, but the results to date have been idiosyncratic. How can PSF research be used to understand, identify and develop more robust microbial-based management approaches for managing productivity losses in crops?
- Can soil inoculations be used to assist restoration of disturbed or degraded ecosystems, and in combatting the spread of invasive plant species across a range of different ecosystems and contexts? Which species of soil organisms play key stone roles in driving plant community dynamics in natural systems?
- What are the risks associated with ecologically engineering of agricultural and natural systems? Can introducing soil organisms or plant traits initially absent from the system cause adverse effects on non-target plants or soil organisms and negatively impact ecosystem functioning?
- How constant are plant-soil feedbacks over time, within and between growth seasons, and how are plant-soil interactions influenced by legacies that are already present in the soil?

- How can we more widely use plant-soil feedback to improve the resistance and resilience of natural and agricultural systems to climate change?

Box 1. Trends in Plant-Soil Feedback Research in Agricultural and Natural Systems



Agricultural Systems – Repeatedly growing the same crop can deplete soil nutrients and can lead to the build-up of plant-species specific soil pathogens and root herbivores [84]. This phenomenon of negative plant-soil feedback (PSF), also known as ‘soil sickness’ or ‘soil fatigue’ [11,85], has led to the practice of crop rotation [86]. In agricultural systems PSF has traditionally been mostly studied from a temporal point-of-view, by focusing on decline of crop productivity over time (i.e., intraspecific feedback) and on soil legacies and the ability of a crop or a cover crop to succeed another crop (i.e., interspecific feedback) [7]. But, less emphasis has been given to interspecific feedbacks in a spatial context as would occur in multi-cropping [87]. Recently, increasing progress has been made in developing screening methods for soil pathogens and in identifying the active taxa and their host-specificity [88], yet little is known about complex community interactions and trophic relationships among soil organisms. These gaps in knowledge have impaired our understanding of how to make use of PSF in improving agricultural sustainability, i.e., increasing resource-use efficiency, reducing fertilizer application, and combatting pests and diseases.

Natural Systems – PSF research in natural systems has a shorter history than in agricultural systems, but has seen a steep increase in activity over the past two decades [7,89]. In natural systems, PSF research has focused more on the community context at larger spatial and temporal scales, testing its role as driver of population dynamics [90], community assembly and succession [91], plant-competitive interactions and the maintenance of plant diversity [92,93]. PSF has also been suggested as a driver of the plant diversity-productivity relationship [94]. Recently, PSF research in natural systems has also incorporated litter feedback, i.e., how variation in litter input and decomposition among plant species feeds back to growth of conspecific and heterospecific plants [19]. Finally, progress has been made in our understanding of how plant traits can explain the variation in strength and direction of PSF and in the use of novel technology such as remote sensing to quantify these in the field [18,95]. Extending trait-based approaches to soil organisms has been suggested as a promising avenue [96] but so far has seen little follow-up. Despite these developments, our predictive ability of PSF in natural systems is low and we lack a thorough understanding of how to use PSF knowledge in ecosystem restoration and conservation.

Box 2. Plant-Soil Feedback as a Tool to Mitigate Climate Change Impacts in Agricultural Systems

Keeping Carbon in the Soil – Soils store large quantities of the Earth's carbon (C) and climate change could transform soils from C sinks to sources [97], thus creating a positive feedback to atmospheric CO_2 concentrations and further climatic changes. Importantly, PSF could reduce C losses from the soil and release of CO_2 into the atmosphere. Indeed, from natural systems we know that increasing plant diversity or the abundance of legumes can increase productivity but also C inputs into the microbial community, which results in increased soil C storage [98]. This suggests that developing species-diverse crop, intercrop or cover crop cultures (Figure 2 and 3) would increase plant productivity while minimizing adverse impacts on the soil C budget. Photo: CIAT, International Center for Tropical Agriculture

Reducing Nitrous Oxide Emissions – Nitrous oxide (N_2O) is an important greenhouse gas, and is tightly linked to the availability of soil mineral nitrogen (N). In agricultural systems, N_2O emissions are problematic because of inputs of large amounts of N fertilizers. It has been shown that in grasslands soil fungi can function as N sinks due to their extensive hyphal network that allows high N absorption [25]. As such, fungi can reduce N_2O emissions by immobilizing N in the soil. Moreover, most fungi lack the gene that encodes for the enzyme nitrous oxide reductase, promoting N_2 production rather than N_2O [25]. In agriculture, promoting fungal-dominated communities can be an important management practice to reduce N_2O emissions. This could be achieved by including plants with conservative resource-use traits in intercropping cultures (Figure 2) [9]. Another option would be to use novel crop phenotypes inoculated with fungal endophytes [59]. Photo: Surinder Saggar.

Resisting to Extreme Climatic Events – Soil fungi are particularly resistant to climate perturbations and can mediate plant community responses to drought, warming and elevated CO_2 [49]. From natural systems we know that subordinate plant species with conservative resource-use traits can promote ecosystem resistance to climate change through positive, fungal-mediated PSF [99]. More specifically, it has been shown that subordinate species can enhance mycorrhizal root colonization under drought to better resist water stress and continue taking up soil N whose mobility is reduced under drought [47]. This suggests that using species with resource-conservative traits in crop rotations and species-diverse intercropping and breeding crops to promote mycorrhizal associations (Figure 2) have the potential to better adapt agricultural systems to climatic extremes. Photo: Pierre Mariotte

Box 3. Avenues for Future Research

Perspectives in agricultural systems

- While there has been mounting research in natural systems on how particular plant traits might influence the direction and magnitude of PSF, these approaches have not yet been adopted in agricultural research. New experiments are needed to optimize trait combinations for crop rotations [5]. Trait-based crop rotations could improve soil resource-use efficiency and, by that, promote sustainable agricultural by reducing the excessive use of fertilizers and pesticides.
- Increasing breeding efforts for optimal rotations are needed. Exciting and unexplored avenues exist in assessing the differential feedback responses from crop wild relatives in their native environment, and using this knowledge as a basis for selection of traits involved in nutrient acquisition and disease resistance in domesticated varieties.
- Spatial crop diversification (e.g., intercropping) is quickly becoming recognized as an important strategy to sustainably intensify agriculture, and integrating the principles of PSF could further improve intercropping schemes. For example, optimizing plant facilitation by using knowledge on interspecific PSF holds promise for improving a range of agricultural services, such as sustainable resource-use and dietary diversity.

Perspectives in natural systems

- Soil inoculations may assist in restoring degraded ecosystems and control invasive plant species, but the underlying mechanisms are still largely unknown. From research in agricultural systems we know that inoculation with beneficial microbial agents is often not successful because of the large number of competing microorganisms in the rhizosphere that suppress the inoculation agents. Much remains to be understood in how to manipulate complex soil communities in natural systems and under which conditions inoculations would be successful.

- To date trait-based approaches in PSF research have largely focused on differences between species that associate either with bacterial- or fungal-dominated soil communities (e.g., input of fast vs. slow decomposing litter). Less is known about how morphological, chemical, and physiological root traits affect soil organisms, and even less so, how traits of soil organisms relate to plant fitness. A better understanding of which plant and soil organism traits drive PSF has potential to greatly contribute to the management of natural ecosystems, although this has not yet been recognized.
- PSF research in natural systems has largely focused on individual plant growth or population responses; only few studies have considered the ecosystem consequences. Little is known about how PSF influences the multiple functions of natural ecosystems (e.g., nutrient retention, decomposition, carbon storage) and the associated services these functions provide, including water purification and soil erosion control.

Figure 1. Bridging Plant-Soil Feedback in Natural and Agricultural Systems. Conceptual framework bridging knowledge on plant-soil feedback (PSF) research derived from natural and agricultural systems, illustrating the plant and soil components underlying the disparate patterns of PSF. Arrows in the root-soil subsystem represent effects of plants on soil organisms, and vice versa, with red arrows for negative PSF and blue arrows for positive PSF. Intraspecific feedback affects individuals of the same species, while interspecific feedback affects individuals of other species. Natural systems show high plant diversity and trait variation compared to often mono-specific agricultural systems. Wild plants from natural systems show a variety of growth and nutrient acquisition strategies [9], whereas domesticated species from agricultural systems have generally been selected and bred for very fast growth and rapid nutrient acquisition often at the cost of defense against pathogens and herbivores [43]. These trait spectra are largely based on aboveground investigations, whereas much less is known on the belowground trait spectra. In natural systems, the soil food web is taxonomically and functionally diverse and encompasses complex trophic relationships, while soil food webs in frequently disturbed agricultural systems are less diverse and often dominated by root herbivores, pathogens, and fast-growing bacteria and their consumers [25]. Moreover, natural systems are characterized by relatively closed nutrient cycles where plant litter is decomposed and mineralized into plant-available nutrients [20,53]. This contrasts with nutrient cycles in traditional agricultural systems, which are often open and leaky: nutrient losses through crop harvesting, leaching, or gaseous emissions are compensated by inputs of organic or synthetic fertilizers. Triangles represent soil pathogens while circles represent soil mutualists; different colors represent soil taxonomic diversity. Interactions between soil organisms are represented by black lines and highlight the level of soil food web complexity.

Figure 2. Improving Agricultural Sustainability. Insights from plant-soil feedback (PSF) research in natural systems (see italicized green text), characterized by complex and diverse plant and soil communities, can help achieve the grand challenges sustainable agriculture is facing. Arrows in the root-soil subsystem represent effects of plants on soil organisms, and vice versa, with red arrows for negative PSF and blue arrows for positive PSF. Triangles represent soil pathogens while circles represent soil mutualists; different colors represent soil taxonomic diversity. (1) *Optimizing cropping systems*: Positive interspecific feedback, i.e., facilitating effects of one plant species on neighboring species mediated by changes in the soil, are well known from natural systems. In agricultural systems, optimizing the sequence of crop species that maximize positive interspecific PSF could improve the efficiency of crop rotation schemes. (2) *Disease resistance and pest control*: Root defense traits are essential drivers of plant resistance to root pathogens and soil disease in natural systems and breeding or genetically modifying crop species to favor root traits similar to wild species can improve plant resistance in agricultural systems. Inoculation with beneficial soil organisms, such as mycorrhizal fungi or growth-promoting, disease-suppressing bacteria, obtained from natural systems but screened for their ability to also perform well in agricultural systems, can also stimulate crop production and minimize yield loss due to soil diseases (3) *Resource-use efficiency:* Learning from natural systems, breeding crops to promote associations with soil mutualists (i.e., positive PSF) and enhancing complementarity of plant traits in intercrops or cover crops can improve plant nutrient uptake and soil nutrient retention in agricultural systems. Further, positive litter feedback by leaving crop residues on the soil surface or incorporating them into the soil can increase soil nutrient availability for the next generation of crops and reduce the need for synthetic fertilizers. Photo: Shiva Bakhshandeh.

Figure 3. Enhancing Diversity and Ecosystem Functions in Natural Systems. Insights from plant-soil feedback (PSF) research in agricultural systems (see italicized orange text) can assist the restoration and conservation of natural ecosystems. Arrows in the root-soil subsystem represent effects of plants on soil organisms, and vice versa, with red arrows for negative PSF and blue arrows for positive PSF. Triangles represent soil pathogens while circles represent soil mutualists; different colors represent soil taxonomic species diversity. (1) *Deciphering complex plant-soil interactions*: Knowledge of positive and negative interactions between soil organisms in 'simplified' agricultural systems can be used in engineering the soil communities of natural systems to promote species diversity and ecosystem stability, for example by inoculating soil organisms that promote subordinate plant species or suppress the dominant species. (2) *Restoration after disturbance*: Recent advances in our understanding of specific interactions between crop species and soil mutualists and pathogens can be used in the targeted restoration of natural ecosystems. For example, positive interspecific PSF (i.e., through mutualists) driven by the addition of selected plant species or by soil inoculation can promote foundation or rare species while negative PSF (i.e., through pathogens) can be used to reduce the abundance of invasive or ruderal species. (3) *Multifunctionality*: Experimental manipulations of soil community composition in agricultural systems showed that increasing soil biodiversity or the abundance of certain groups of species can enhance multiple ecosystem functions. Similarly, increasing soil diversity or inoculating particular soil organisms (orange triangles and circles) could further promote the complex network of positive feedback between plant and soil organisms and improve multiple functions of natural ecosystems. Photo: Pierre Mariotte.

Glossary

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

AMF networks: underground network of arbuscular mycorrhizal fungal hyphae that connects individual plants and transfers water, carbon and nutrients.

Ecosystem services: benefits that humans derive directly or indirectly from ecosystems.

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

Endophytes: organisms, often fungi or bacteria, that live within a plant and gain carbon from the host plant. Endophytes can have positive or negative effects on plant fitness.

Foundation species: species with a key role in structuring a community by creating or maintaining habitat that supports other species.

Functional traits: quantifiable morphological, physiological, biochemical, or phenological characteristics of individual organisms that are relevant to relationships with other species and how they interact with the environment.

Intercropping: agricultural practice growing two or more crops simultaneously in the same field.

Phenolic profile: the profile of phenols, a class of chemical compounds, produced by plants and microorganisms that varies between and within species.

Plant economics spectrum: gradient of plant functional traits, based on the resource acquisition strategy of the plant, ranging from traits associated with slow growth and conservation of resources to fast growth and rapid turnover of resources.

Rhizosphere communities: microorganisms and micro- and mesofauna living in the narrow region of soil in direct contact with the plant root.

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

Soil food web: community of all organisms living in the soil often forming a complex network of trophic interactions.

Sustainable agriculture: agricultural management with the aim of meeting today's food challenges in an environmentally responsible manner and without compromising the long-term productivity of the system.

Trophic level: position occupied by a living organism in a food chain. In the soil food web, trophic levels include root herbivores, decomposers, consumers, and predators.