

Opinion

Plant Functional Traits: Soil and Ecosystem Services

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Decline of ecosystem services has triggered numerous studies aiming at developing more sustainable agricultural management practices. Some agricultural practices may improve soil properties by expanding plant biodiversity. However, sustainable management of agroecosystems should be performed from a functional plant trait perspective. Advances in functional ecology, especially plant functional trait effects on ecosystem processes and services, provide pivotal knowledge for ecological intensification of agriculture; this approach acknowledges that a crop field is an agroecosystem whose ecological processes influence soil properties. We highlight the links between plant functional traits and soil properties in relation to four major ecosystem processes involved in vital ecosystem services: food production, crop protection, climate change mitigation, and soil and water conservation, aiming towards ecological intensification of sustainable agricultural and soil management.

Introduction to Functional Traits of Plant–Soil Relationships in Agroecosystems

Concerns over the continuing global loss of biodiversity, and the associated decline of **ecosystem services** (see [Glossary](#)), have triggered numerous studies aiming at developing more sustainable agricultural management practices. Many studies suggest that, compared with conventional agriculture, agricultural practices based on ecological intensification of agriculture improve soil properties by expanding plant biodiversity in cropping systems [1–3]. The positive relationships between biodiversity and ecosystem functions in many ecosystems suggest that increasing plant diversity in managed ecosystems could enhance multiple ecosystem services simultaneously [4,5]. For **agroecosystems**, a link between biodiversity and ecosystem services has recently been demonstrated in multispecies cover crops [6,7]. These results offer a justification for the practice of some farmers to sow a range of varieties and/or species to provide multiple ecosystem services [8]. **Functional diversity** of multispecies cropping systems includes multicropping systems (more than one crop cultivar or species are grown simultaneously), agroforestry systems (including both annual and perennial crops), cover crops (crops comprising several non-harvested species such as catch crops to reduce nitrate leaching and green manure), and intermediate or break crops cultivated to produce forage or biomass energy (e.g., methanisation, biofuel) [9]. To define and manage ecosystem services provided by multispecies cropping systems, functional plant effects on agroecosystem functioning should be understood and included in agricultural management practices [10]. Some functional plant traits, including leaf traits [e.g., specific leaf area (SLA), carbon (C):nitrogen (N) ratio] and root traits involved in nutrient acquisition (e.g., specific root length, carboxylate and proton exudation), may have different effects on resource acquisition, C storage, and pathogen communities in soils [11,12]. However, the effects of functional plant traits and their diversity on soil functions are far from being fully understood [13,14].

Trends

Agroecological studies build on the concept that, by understanding ecological processes, agroecosystems can be managed to produce more biomass more sustainably, and thus protect natural resources.

Many studies in agroecology suggest that some agricultural practices can improve soil quality and restore agroecosystems by enhancing plant biodiversity.

Functional plant traits to assess ecosystem processes and services can be used towards sustainable management of agroecosystems.

Knowledge of the links between functional plant traits and soil carbon dynamics and sequestration, soil structural stability and soil erosion, soil nutrient dynamics and availability, and the abundance and diversity of soil microbial pathogens is essential for the development of agroecological principles.

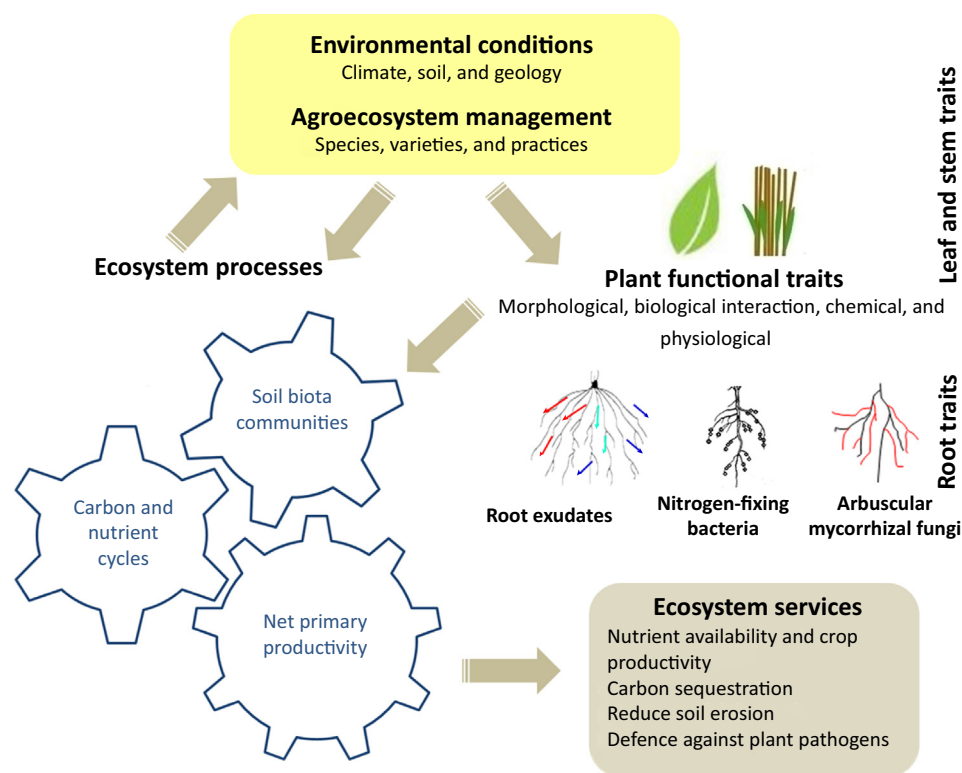
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In the past decade, considerable progress has been made in ecology based on the concept of **functional traits** [15]. These traits are defined as ‘morpho-physio-phenological traits, which impact fitness indirectly via their effects on growth, reproduction and survival’ [16]. Relationships between traits associated with the response of organisms to environmental factors such as resources and disturbances (response traits), and traits that determine effects of organisms on ecosystem functions (effect traits), have recently been studied for several processes and ecosystem services [17] (Figure 1). The effects of plant functional traits on soil properties (i.e., structure of biota communities, physical and chemical properties) is considered to be an important regulator of key ecosystem processes and services, for example soil C dynamic and sequestration, increased soil structural stability and reduction of soil erosion, soil nutrient dynamics and availability, and the abundance and diversity of soil microbial pathogens [7,17,18].

Advances in functional ecology provide pivotal knowledge for **agroecology** or ecological intensification to soil management, and these acknowledge that a crop field is an ecosystem whose ecological processes influence ecosystem services. We focus here on the influence of functional plant traits on four ecosystem processes modulating soil properties and that are considered to be pivotal for the provision of ecosystem services in agriculture (called here agroecosystem services) [10]. The ecosystem processes considered are (i) nutrient dynamics and availability, (ii) fungal communities and soil-borne pathogen dynamics, (iii) C sequestration, and (iv) soil erosion. These processes are associated with the following agroecosystem services: soil fertility, sustainable fertilisation and food production, crop protection against



Trends in Plant Science

Figure 1. Relationships between Plant Functional Traits, Ecosystem Processes, and Services in Agroecosystems. Plant functional traits are selected by climate, geology, soil conditions, and practices of agroecosystem management.

Glossary

Agroecology: ‘the ecology of sustainable food systems’ which considers a crop field as an ecosystem whose biogeochemical cycling and biodiversity are influenced by the landscape, including ecological processes such as nutrient cycling, predator/prey interactions, competition, and facilitation. Agroecological studies build on the concept that, by understanding ecological processes, from crop field to landscape scale, agroecosystems can be managed to produce more biomass while reducing the environmental impact of agricultural practices on biodiversity conservation, natural resources, and ecosystem services.

Agroecosystem: an ecosystem, including biotic and abiotic factors and their interactions, that is managed for agricultural production. Agroecosystems can present a low biodiversity, such as cropping system with few or only one crop in rotation, or be more biodiverse, such as polyculture cropping or intercropping system.

Ecosystem service: an ecosystem process which confers either direct or indirect benefits to humans. We focus on the goods that are directly used by humans (e.g., food, energy, and fibre) and the ecological processes affecting the provision of these goods (e.g., pollination, soil fertility) that are related to human health.

Functional diversity: the value, range, and relative abundance of the functional traits of the organisms in communities that respond to the environment and influence ecosystem functioning. Functional diversity also includes the richness of functional types, which refers to a non-phylogenetic group of species functioning in a similar way with respect to environmental variation or presenting similar effects on ecosystem properties. Functional diversity measures could bridge the gap between ecosystem functioning and community ecology.

Functional traits: quantifiable morpho-physio-chemical-phenological traits of individual organisms that present a response to the variation of environment and its effects on growth, reproduction, organism survival, and ecosystem processes. This non-taxonomic

fungal pathogens, mitigation of climate change, and soil and water conservation [19]. We specifically discuss how knowledge of the links between functional plant traits and the four previously-mentioned vital agroecosystem processes and services is essential for the development of ecological intensification of cultivated soils.

Impacts of Functional Plant Traits on Nutrient Dynamics and Availability to Improve Soil Fertility

For about half a century, the intensive use of fertilisers owing to the increasing demand for food has caused major environmental issues, especially for water quality (freshwater eutrophication causing biodiversity loss) and human health (drinking water contaminated by nitrate) [19]. One approach to reduce synthetic fertiliser use is to increase recycling and availability of nutrients in agroecosystems. Aboveground litter and root traits are important drivers of nutrient dynamics and soil fertility. Plant functional traits that are involved in nutrient dynamics and availability are physiological root traits that modify nutrient speciation, and biochemical traits of litter (above- and belowground) that influence its decomposition and nutrient release. Most studies examining the effect of plant functional traits on nutrient dynamics focus on N and phosphorus (P) [11,12,20].

Effects of rhizosphere-related traits on soil P availability in cropping systems were reviewed recently [7]. Roots may chemically mobilise poorly available forms of P in soil. Crop **phosphorus-mobilising species** improve P nutrition for themselves as well as for neighbouring non-P-mobilising species by releasing protons (effective in alkaline soils to solubilise Ca phosphate), and/or carboxylates (effective in all soils by decreasing P sorption on Al- and Fe-oxides and hydroxides, and solubilising Ca phosphate) into the rhizosphere to solubilise both inorganic P (Pi) and organic P as well as acid phosphatases or phytases, which hydrolyse carboxylate-mobilised organic P and phytate, respectively, to release Pi [18]. Intercropping with P-mobilising crop species (e.g., legumes such as faba bean, lupin, lentil, and chickpea) improves P nutrition of neighbouring non-P-mobilising species [11]. Chemical traits of crop residues associated with functional plant diversity of agroecosystems would influence nutrient availability; for example, cereal residues have lower N and P concentrations, and thus potentially slower mineralisation compared with residues with higher P and N concentrations that stimulate soil nutrient recycling [21,22]. N and P concentrations positively influence aboveground litter-decomposition rates. Root N concentration, root respiration, and specific root length, which are all correlated, positively influence root decomposition, in contrast to root dry matter content and lignin: N ratio [11], whereas N and P concentrations and tissue density affect stem decomposition [23]. However, these trait effects that are known for plants from forest ecosystems are increasingly studied for crop residues in agroecosystems [24–26]. Functional plant traits are good predictors of N cycling in agroecosystems [27]. Nitrification is strongly impacted by root traits (specific root length, root N concentration, and the affinity for NH_4^+ of the root uptake system) linked to plant N cycling. **Root exudates** constitute an important functional trait in N cycling because their release enhances microbial mineralisation of organic matter (OM) which may increase nutrient availability. This process of rhizosphere priming, which is often effective in N-poor soil, involves the stimulation of microbial mineralisation of organic N, thereby increasing N availability [28]. However, exudation traits can also stimulate microbial biomass and cause microbial N immobilisation, consequently reducing N availability [29]. A rhizosphere priming effect was confirmed by a comparison with bulk soil, showing that gross N mineralisation rate in the rhizosphere was increased by 10–52% as a result of greater microbial oxidative enzyme activity [30]. However, rhizosphere priming of soil N and, especially, how it can be modulated by organic exudate (also called rhizodeposit) quality, still remain elusive [29]. We need to better understand the effects of morphological and exudate traits on rhizosphere priming effects and N availability. Effects of both litter N and P concentrations on litter decomposition reflect the coupling of P and N in plant–soil microbial decomposer interactions,

approach allows trait effects on ecosystem processes and services to be quantified, and intraspecific variation to be included.

Mycorrhiza: a structure arising from colonisation by a mycorrhizal fungus of the roots of a host plant (the majority of vascular plant species can form such a symbiotic structure), either predominantly inside the roots (as produced by arbuscular mycorrhizal fungi) or predominantly outside the roots (as produced by ectomycorrhizal fungi). The fungus provides nutrients and water as well as protection against pathogens for the plant in exchange for a supply of carbon by the plants.

Niche complementarity: ecological niche of functionally distinct species structured with respect to resource partitioning [e.g., soil depth, chemical nitrogen (N) and phosphorus (P) forms] and that can coexist in the community. Niche complementarity can positively influence ecosystem functioning such as net productivity.

Phosphorus-mobilising species: species with root traits that are able to chemically mobilise poorly available forms of P.

Plant–soil feedback: changes to soil properties that are caused by plants which in turn influence the performance of plants.

Root exudation: the release from roots of exudates into soil, comprising low molecular weight organic compounds (e.g., carboxylates), protons, and enzymes (e.g., acid phosphatase) which influence microbial communities as well as nutrient dynamics and availability.

Soil aggregates: groups of soil particles that bind to each other more strongly than to other surrounding particles. Soil aggregates are formed mainly by physical forces, while stabilisation is caused mainly by organic matter (OM), clays, iron and aluminium oxides, fine roots, and fungal hyphae. The spaces between aggregates provide pore space for roots to explore and for the movement of water and air.

Soil aggregate stability: refers to the ability of soil aggregates to resist environmental stress (e.g., wet–dry cycles) without breaking.

Soil aggregation: the result of physical stabilisation due to biological and chemical processes.

and stress the importance of this coupling for C and nutrient flow in eco- and agroecosystems [31]. Fresh OM of crop residue mixtures may prime the breakdown of recalcitrant soil organic matter (SOM), and thus reduce the soil organic N and P fractions and increase N and P availability [32]. Moreover, the effects of plant functional traits on litter and SOM mineralisation and nutrient release can be variable. These effects depend on initial soil properties and notably on competition for energy and nutrient acquisition between the microorganisms specialised in the decomposition of fresh OM and those feeding on polymerised SOM (SOM decomposers and SOM builders). Emerging trends show that the balance of these interactions leads to a litter priming effect [32]. Further investigations are thus essential to gain a better insight into N and P cycling and to ensure sustainable fertilisation of cropping systems.

Plant functional traits influencing the functional traits of soil fauna communities and biomass should also be considered in understanding indirect plant–soil processes that are involved in nutrient dynamics. The influence of functional traits, particularly SLA, leaf dry matter content, C:N and N:P ratios, and P concentration of aboveground litter on soil biodiversity and litter decomposition was recently demonstrated in grasslands and forests [33,34]. These plant traits can promote bacterial and fungal communities, as well as soil fauna, which results in a positive feedback on plant growth by litter decomposition and maintains a high P availability [33]. Soil fauna influenced by the functional diversity of plant species and SOM could improve nutrient availability [12]. A recent meta-analysis highlighted that the soil fauna biomass can increase plant productivity across ecosystems by 35%, notably by improving nutrient availability (effect size between treatments with high soil fauna biomass compared with treatments containing a lower soil fauna biomass) [35]. Bacteria-feeding nematodes increase nutrient availability and reduce nutrient leaching [36]. The main plant functional traits impacting on nematode abundance are root and leaf glucosinolate concentrations, which are high in Brassicaceae [37]. The relationships between plant functional traits and soil fauna which modify microbial communities by consuming bacteria and fungi, thereby increasing nutrient dynamics, need to be quantified to manage nutrients cycling in agroecosystems and sustainable fertilisation.

Plant functional traits that improve nutrient availability can influence species interactions and negatively impact on plant fitness and biomass productivity by increasing competition for light (plant species selected from fertile soils can be taller and have more leaf area) or allelopathy [38]. This effect, known as negative **plant–soil feedback**, can have a negative impact on ecosystem processes and services, and should also be considered in agroecosystem management. Biochemical, physiological, and morphological above- and belowground litter traits involved in nutrient dynamics and availability in agroecosystems should be considered in several soil and climate contexts to model nutrient dynamics in agroecosystems and to perform sustainable fertilisation.

Functional Plant Traits Affect C Dynamics and Sequestration in Soil

More than two-thirds of the organic C stored in terrestrial ecosystems is contained in SOM [39]. However, this soil C is vulnerable to losses, and this has important implications for soil biodiversity, productivity, and climate feedback [40]. Because soil C sequestration is a vital ecosystem service to mitigate climate change, a sound understanding of the underlying processes and mechanisms controlling soil C levels is required. In this context, elucidating the influence of plant functional traits (i.e., litter traits and physiological root traits) on C decomposition and C stabilisation in soil has become a major environmental challenge [41]. Specific leaf area and litter N concentration are negatively correlated with soil organic C (SOC) concentration, while leaf dry matter content is positively correlated in a Mediterranean old field succession [42]. These traits influence the decomposition rate of leaves and the accumulation of aboveground litter [43,44], and thus affect the balance of C in soils. Recent studies have highlighted controversial effects of plant functional traits on SOC concentration [45]. Emerging

trends showed that aboveground litter N concentration is positively correlated with SOC content [46]. Litter with a high N concentration is mineralised, thus producing more microbial residues, which are then strongly bound to the mineral soil matrix, leading to an increase of stable SOC content [47,48]. SOC content in turn is influenced not only by climate and soil properties (in an oceanic climate by mean annual temperature, soil pH, and soil moisture content) but also by the community abundance-weighted mean leaf N concentration (under N-rich vegetation) [49]. The relationship between plant functional traits and SOC may be complex because it depends on soil properties and the functional structure of microbial communities. Soil properties influencing the protection of OM (physical, chemical, and biochemical protection) against biological breakdown (known as SOC stabilisation) can influence the plant trait effects on SOC mineralisation and thus soil C concentration [50]. Plant trait effects on SOC decomposer organisms can be affected by spatial inaccessibility of SOC to decomposer organisms as a result of occlusion, intercalation, hydrophobicity, and encapsulation and/or SOC stabilisation by interaction with mineral surfaces (Fe-, Al-, Mn-oxides, phyllosilicates) and metal ions [50]. However, mineral protection of soil C can be counteracted by root exudates [51]. In addition, recent studies also indicate that the impact of litter functional traits on SOC stabilisation must be balanced by the soil C saturation level [52]. This new concept suggests that soils have a finite capacity to store C within relatively stable pools in the mineral soil matrix. Accordingly, the effect of litter quality on stable SOC (i.e., mineral-associated SOC) would be a function of the C saturation deficit such that (i) litter quality would affect stable SOC stocks only when there is a saturation deficit, and (ii) the capacity to store additional stable SOC in soils receiving high-quality litter would saturate at a lower litter input rate than in soils receiving low-quality litter [52]. Mineral nutrient additions including N fertilisers can also enhance microbial biomass and litter mineralisation, thereby modifying litter trait effects on SOC by increasing the transfer of plant litter to total SOC and stabilised SOC [53].

Plant resource economics with respect to interspecific trait variation among species, both within and across organs, is referred to as the 'plant economics spectrum'; it can influence C and nutrient cycling in ecosystems [54]. The contrasting decomposabilities of different plant parts suggest a major role for the relative inputs of organ litter as a driver of C cycling [34]. Fine root litter decomposes approximately 2.8-fold slower than leaf litter derived from the same species [34]. Belowground litter represents an important driver of ecosystem OM dynamics and soil C sequestration. Root traits constitute the main factors that influence SOC [55]. In particular, physiological root traits are notably underinvestigated owing to technical difficulties [54]. Chemical traits (lignin, C and N concentrations) of fine roots (≤ 2 mm in diameter) [56] constituting the main source of OM input into the soil can be considered as the main drivers influencing root decomposition and C in soil [11,57]. The effects of these chemical traits on fine root decomposition can be more important than the effect of climate [58].

To better understand the dynamics and drivers of C in soil, root traits should be combined with traits of arbuscular **mycorrhizal** fungi (AMF), given that AMF can facilitate long-term humus build-up through production of melanised hyphae that resist decomposition [59]. Ectomycorrhizal roots and hyphae decreased soil respiration rates by up to 67% under field conditions in two separate field exclusion experiments, and thus limit SOC mineralisation [60]. Labile soil carbon released from roots mediates the soil microbial community and can increase litter and SOC mineralisation [61]. Likewise, information on exudates is crucially important, but hard to obtain. The approach to use leaf manganese concentration as a proxy for carboxylate exudation is very promising because this leaf trait is much easier to measure than carboxylate release [62]. An increase in SOC content is generally observed in agroecosystems with a fungus-dominated community. Root traits impact the growth of microbial functional groups, such as high lignin and low root N concentrations, which stimulate fungal growth and promote soil C sequestration [63]. These microbial groups differ in their metabolism because fungi

respire less C per unit fungal biomass C gained, resulting in higher C-use efficiency in fungi than in bacteria [39]. The effects of above- and belowground plant traits on ecosystem processes and services need further study on the response traits to different soil contexts, climate, and cropping systems to model the effects of plant functional traits on SOC and thus manage C sequestration in agroecosystem and climate change mitigation (Figure 1).

Fine Root and Mycorrhizal Fungal Traits Influence Soil Aggregation and Stability to Conserve Soil

Soil aggregation results in the formation and stabilisation of soil structure. **Soil aggregates** are important for root growth and for ecosystem processes and services such as C storage, resistance to erosion, and surface water protection [64]. Soil aggregation is a complex process which is controlled by a range of abiotic factors such as texture, and is mediated by traits of plants and soil biota as well as their interactions [65]. Root length density and root diameter strongly influence soil stability, in other words the ability to resist breakdown when subjected to disruptive forces. Fine roots constitute an important factor in **soil aggregate stabilisation** [66]. Root traits influence soil porosity and water infiltration, notably root mass density and root diameter, and thus reduce runoff and soil erosion [66,67]. Rooting depth is the most important trait to stabilise soil on slopes [68]. Plant root and mycorrhizal interactions are a crucial force in driving soil aggregation, but their effects on soil aggregation differ according to morphological and physiological traits [55] and have not been fully elucidated so far [65,69]. Fine root and mycorrhizal fungal traits should be considered in the formation of soil aggregates because they promote the encounter of soil particles and bring soil material together [65]. Furthermore, exudates from roots and hyphae influence the initial formation of aggregates [70]. In particular, glomalin, a fungal glycoprotein released by arbuscular mycorrhizal fungi into soil during hyphal turnover and after the death of the fungus [71], has been identified as a key soil-binding agent and is strongly related to aggregate stability in various soils [65]. The effect of fine roots on soil aggregation increases in the presence of mycorrhizal fungi [72]. Indirectly, mycorrhizal fungi may also affect soil aggregate stability through their host plants by accelerating the development of their root network [73] and by serving as a distribution vector for associated bacteria, which participate in the formation and stabilisation of micro-aggregates [74]. Root traits are important drivers of ecosystem processes and services in soil protection and water quality, and should be included in sustainable agroecosystem management. In addition, the burrowing, casting, and nesting activities of soil invertebrates influence soil aggregation and soil structure [75], providing a link between plant functional traits and the structure of soil fauna communities. These should be considered in soil conservation [76].

Soil erosion management also requires understanding the effects of plant functional traits on hydraulic roughness and sediment trapping [77]. Many studies highlight candidate plant species that increase hydraulic roughness but without characterising plant functional traits [78]. Aboveground functional traits are principally involved in this hydrological process [78]. We need to study the effects of several stem and leaf traits such as leaf and stem densities, plant community weighted stem and leaf area (SLA), and stem specific density on hydraulic roughness [79]. In the context of intense soil erosion, intercrops, multispecies cover crops (intermediate and permanent), hedges, and agroforestry systems should be designed using a plant functional traits approach to reduce soil erosion and conserve water.

Functional Plant Traits and Arbuscular Mycorrhizal Fungi Affect Soil-Borne Microbial Pathogens

The use of pesticides to control plant parasites and diseases has generated serious environmental problems. Pest management that tends to rely more on ecosystem processes by including plant trait effects on soil-borne microbial pathogen can provide an alternative to both reduce the use of fungicides and improve crop quality [3]. Functional plant traits influence belowground plant pathogens and their antagonists [80]. Study of litter and microbial

interactions involved in plant–soil feedback (i.e., the effects of plants on soil biota that subsequently affect plant performance, with consequences for ecosystem functioning) highlights the relative importance of traits in controlling plant–soil feedback intensity, and its effects on the composition and abundance of root–pathogens and/or mycorrhizal fungi [81]. The effect of litter decomposability on plant–soil feedback decreases when pathogens are abundant, and increases with the relative abundance of mycorrhizal fungi. Therefore, this positive plant–soil feedback by mycorrhizal fungi results in increased nutrient availability [81]. In severely nutrient-impoorished soils of some natural ecosystems, plants with non-mycorrhizal P-mobilising strategies involving carboxylate release [82] coexist with mycorrhizal plants; mycorrhizal fungi may provide their hosts with protection against pathogens, thus promoting coexistence of different P-acquisition strategies [14]. Plant–soil feedback should be understood at the plant community scale because plant community composition shapes soil-disease suppression via changes in abiotic soil properties and the abundance of bacterial groups [83]. Understanding the ecological function of mycorrhizal plants in these nutrient-impoorished soils may allow us to better manage nutrient-poor agroecosystems, and may need to be considered in the management of crop protection more generally.

Does Functional Diversity Influence Ecosystem Processes and Services?

Functional diversity influences various ecological processes, and offers several ecosystem services, but its effects on the intensity of ecological processes (i.e., synergetic effects) are controversial [17]. Grime [84] developed the 'mass ratio hypothesis' proposing that the effect of functional plant trait on ecosystem properties strongly depends on the relative contribution to the total biomass or abundance of those plants. Accordingly, ecosystem processes such as C and nutrient cycling would be determined by aggregated traits of dominant species [42,43,85]. Only few studies have highlighted a positive influence of functional divergence on ecological processes [17]. A positive effect of functional diversity for several traits was shown for C cycling, aboveground net primary productivity, and soil C sequestration in a herbaceous ecosystem [86]. The effects of functional diversity on ecosystem processes would be explained by complementary resource use between plant species [87] or by increased biomass productivity of the plant community, thus increasing soil C content [88]. High-diversity mixtures of perennial grassland species store 500% and 600% more soil C and N, respectively, than do monocultures [88]. The positive effect of functional diversity is explained by increased C and N inputs via greater root biomass, and greater root biomass accumulation to greater soil depth, resulting from the presence of highly complementary functional groups [89]. This functional diversity effect on soil N availability would be due to the increased N retention [90]. Higher plant diversity increases rhizosphere C input into the microbial community, resulting in both increased microbial activity and C storage; C inputs are greater than decomposition rates for existing soil C [91]. Soil fauna can also have a positive effect on functional diversity. Earthworms change the interactions between the intercropped species mainly by reducing competition for nutrients; earthworms decrease the amount of organic P and increased Pi availability [92]. The positive effects of functional diversity on plant productivity can be explained by spatial niche differentiation associated with the ability of different species to access different sources of water and nutrients in the soil profile, notably in nutrient-deficient soils [89,93]. Negative effects of functional diversity on ecosystem processes are basically the opposite processes to those listed above that show positive effects (e.g., priming vs negative priming; mobilisation vs immobilisation). However, these negative effects of functional diversity highlighted in ecosystems can be positive in agroecosystems by establishing appropriate agricultural practices to mitigate competition via appropriate space among rows when sowing, seed density, and asynchronous timing of sowing [9]. Although the impact of plant diversity on ecosystem processes and services has been highlighted within a plant community [89,94], understanding the role of functional diversity of root traits on the physical belowground environment remains a

Box 1. Can We Design Multifunctional Agroecosystems for Sustainable Soil Management?

Agroecosystems should be multifunctional because they should offer multiple services such as enhancing sustainable crop productivity, nutrient availability, and carbon sequestration, or reducing soil erosion [10]. Some plant functional traits can promote several agroecosystem processes and services, and enhance for example C sequestration and reduce soil erosion. Some traits of fine roots can contribute both to aggregate stability and SOC [55]. By contrast, some agroecosystem processes and services depend on contrasting traits. For example, the increase in nutrient availability is influenced by low C:N and C:P ratios of litter, while soil erosion mitigation by aboveground litter is driven by high C:N and C:P [20,78]. Detailed knowledge of several plant trait effects on soil properties and ecosystem processes and services is of major significance to allow several functional plant traits to be combined in the design of multifunctional agroecosystems for sustainable soil management.

challenge [55]. Functional diversity effects should be further studied for several ecosystem processes, and in various soils and ecosystems, to understand its controversial effects.

Concluding Remarks and Future Challenges

Pivotal knowledge of the effects of plant functional traits on soil properties, ecosystem processes, and services comes from studies on the functional ecology of natural ecosystems. However, this is only a first step to understand the effects of plant functional traits on agroecosystem functioning and to improve ecological intensification of agriculture. The complexity of functional plant trait effects on ecosystem functioning is process-dependent, and soil C and nutrients are influenced by initial soil properties. The challenge to manage ecosystem processes and services in agroecosystems based on a plant functional trait approach is to consider intraspecific variation and the phenotypic plasticity of plant traits. This will be done by characterising response traits to various soil properties (physical, chemical, and biological) and climate with the goal of modelling plant trait effects on ecosystem processes and services. The perspective is to gain insight into the interactions between functional traits of plants, microorganisms, and soil faunal communities in various soil and climate contexts and cropping systems. A list of candidate plant traits that improve soil properties, agroecosystem functioning, and ecosystem services should be compiled, focusing on several growth stages and different soil properties, climates, and agricultural practices. The main challenge is to precisely identify the effects of plant functional traits and their diversity on soil properties and ecosystem processes and services in different soil contexts, climates, and agricultural practices to design ecosystem services in sustainable cropping systems (Box 1).

Outstanding Questions

What are the relationships between plant functional traits and agroecosystem processes and services?

What are the effects of climate, initial soil properties, and agricultural practices on the responses of plant functional traits and agroecosystem processes and services?

Does functional diversity influence agroecosystem processes and services?

How can we model the effects of functional traits on agroecosystem services based on generic crop, biogeochemical, and hydrological models to design multifunctional agroecosystems?

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