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Opinion

Belowground cascading biotic interactions trigger crop diversity benefits

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Crop diversification practices offer numerous synergistic benefits. So far, research has traditionally been confined to exploring isolated, unidirectional single-process interactions among plants, soil, and microorganisms. Here, we present a novel and systematic perspective, unveiling the intricate web of plant–soil–microbiome interactions that trigger cascading effects. Applying the principles of cascading interactions can be an alternative way to overcome soil obstacles such as soil compaction and soil pathogen pressure. Finally, we introduce a research framework comprising the design of diversified cropping systems by including commercial varieties and crops with resource-efficient traits, the exploration of cascading effects, and the innovation of field management. We propose that this provides theoretical and methodological insights that can reveal new mechanisms by which crop diversity increases productivity.

Highlights

Crop diversification offers numerous synergistic advantages over intensive monocultures via belowground interspecific interactions.

The plant–soil–microbiome interactions that trigger cascading effects underpin the benefits of crop diversification.

Unlocking the potential of cascading effects in diversified cropping systems can alleviate common obstacles in intensive monoculture farming.

Strategically selecting species and varieties that complement and facilitate one another can enhance agricultural productivity with fewer agrochemical inputs.

The benefits of diversified cropping systems

Meeting the food security needs of a growing global population presents a major challenge for agriculture [1,2]. However, the widespread use of conventional farming with often simplified cropping systems has led to detrimental effects on multiple ecosystem services. This includes issues such as nutrient imbalances, degraded soil structure, proliferation of soil pests, loss of wildlife species diversity, and long-term declines in crop yield stability [3–5]. These problems often result from the excessive use of chemical inputs, while overlooking the inherent advantages of harnessing biological processes within crops to efficiently utilize surrounding resources.

Previous studies on natural ecosystems and agroecosystems have shown that increasing plant diversity can enhance productivity and other ecosystem services [6,7]. In agroecosystems, **crop diversification** (see Glossary) strategies, including **intercropping**, **crop rotations**, **cover crops**, and **cultivar mixtures**, implemented at various spatial and temporal scales offer numerous advantages over intensive monoculture farming. For example, crop diversification increases the utilization of available light, and soil water, nitrogen (N), and phosphorus (P). It also helps to suppress pests, diseases, and weeds, enhances soil fertility, improves crop yield and quality, and stabilizes overall agricultural productivity [8–12].

Intercropping and crop rotations are among the most commonly employed diversified cropping systems. The key benefit lies in the maximization of root and rhizosphere processes through species interactions. These interactions mobilize, acquire, and utilize resources more efficiently, making agricultural production less reliant on chemical fertilizers and pesticides. To date, most research on diversified cropping systems has focused on aboveground light utilization and belowground facilitation via root exudates [7,13], which are unidirectional and involve single-process interactions. Belowground facilitation in nutrient acquisition – for example, root-exudation patterns that enhance

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N fixation in legumes via signaling molecules from intercropped maize (*Zea mays* L.) – contribute to overyielding in intercropping systems [14]. In the case of crop rotations, by growing different crops sequentially, a positive **legacy effect** can be created, with better soil conditions for subsequent crops. Deep-rooted crops make biopores (root channels) in the subsoil, facilitating deeper root development in subsequent crops [15]. In addition, legumes cultivated during the first season can enhance the nutrition of subsequent cereals [16]. Cover crops play a role in modifying the composition of root-associated microbiomes that offer protection to the seedlings of subsequent cash crops against pathogens [17].

So far, studies have predominantly focused on isolated, single-process interactions, limiting our ability to fully comprehend the intricate interactions occurring within the complex above- and belowground systems present when cropping is diversified. We contend that there is an urgent need for a systematic approach that comprehensively explores how multiple interspecific interactions operate and how these trigger **cascading effects** both above- and belowground in diversified cropping systems. Our research group has recently developed a systematic perspective and approach aimed at fully harnessing the biological potential of plant–soil–microbiome interactions. This approach entails multi-interface interactions encompassing plant–plant, plant–microbe, and microbe–microbe interactions, which can be strategically leveraged to enhance nutrient-use efficiency and boost crop productivity [13,18]. We further develop this systematic perspective via introducing the cascading effects to examine how interspecific interactions influence overyielding, nutrient uptake, and biomass accumulation in more complex diversified cropping systems. Thus, we propose that plant–soil–microbiome interactions serve as the catalyst for above- and belowground cascading effects that underlie the benefits of crop diversification.

In this Opinion, we begin by defining cascading effects and provide examples of their occurrence in the realms of ecology and microbiology. We then discuss the principles governing the cascading effects associated with crop diversification and provide a case study featuring a maize/faba bean intercrop (representing spatial diversification) and a maize–soybean (*Glycine max* L.) rotation (representing temporal diversification). We then explore the applications of the principles of these cascading effects in mitigating soil biotic and abiotic stresses. This is achieved by harnessing the biological potential of crops through the judicious selection and combination of crop species within diversified cropping systems. Finally, we outline a framework for the application of the principles of cascading effects to achieve sustainable cropping systems, which aim to allow a high yield, high food quality, and high economic benefits but decreased environmental impacts. This systematic approach sheds light on the intricate interactions between plants, soil, and microorganisms in terrestrial systems, making valuable contributions to the management of species and varieties in the pursuit of sustainable agriculture and nature conservation.

Unlocking the potential of cascading plant–soil–microbiome interactions in diversified cropping systems

A cascading effect, in the realm of ecological science, is akin to a domino effect, whereby an initial perturbation sets off a sequence of events within a system. Ecologically, this term has been applied to depict the ripple effects of a primary extinction event, where the loss of a keystone species leads to secondary extinctions [19] or the loss of ecosystem services through a series of trophic changes initiated by an invader [20]. Additionally it is relevant in microbiology, where the presence of sucrose initiates a signaling cascade, triggering solid surface motility and facilitating *Bacillus subtilis* colonization in the rhizosphere [21]. In the context of diversified cropping systems, we posit that their myriad benefits stem from intricate inter- and intraspecific interactions, incorporating feedback loops and cascades, thus highlighting the role of crop diversification in these ecological dynamics (Figure 1, Key figure).

Glossary

Cascading effect: a sequence of events in which each event produces circumstances necessary for the initiation of the next.

Cover crop: a crop grown between periods of regular production of the main crop for the purposes of protecting the soil from erosion and improving soil quality [69].

Crop diversification: a strategy that enhances the diversity of simplified cropping systems in either time or space by introducing additional crops [70].

Crop rotation: the sequential planting of different crops over time [71].

Cultivar mixtures: combinations of cultivars from the same crop species [71].

Hyphosphere: the narrow region of soil around hyphae where the physical, chemical and biochemical conditions differ from those of the bulk soil due to the influence of hyphal exudates [72,73].

Intercropping: the mixed cultivation of two (or more) crop species on the same field at approximately the same time [74].

Legacy effects: factors transmitted from the past that can significantly impact the current and future performance of plants [75].

Plant–soil feedback: interactions between plants and soil, both biotic and abiotic, that result in subsequent effects on plant growth and fitness. These interactions can be negative, neutral, or positive [76].

Rhizobiont: root growth, root exudation, and microbial symbioses are supported by aboveground C fixation. The exchange of C and nutrients between the crop shoot, roots, rhizosphere, and microbiome forms a systematic core of rhizosphere interactions, collectively termed a rhizobiont [18].

Key figure

Principles of cascading plant–soil–microbiome interactions in crop diversification

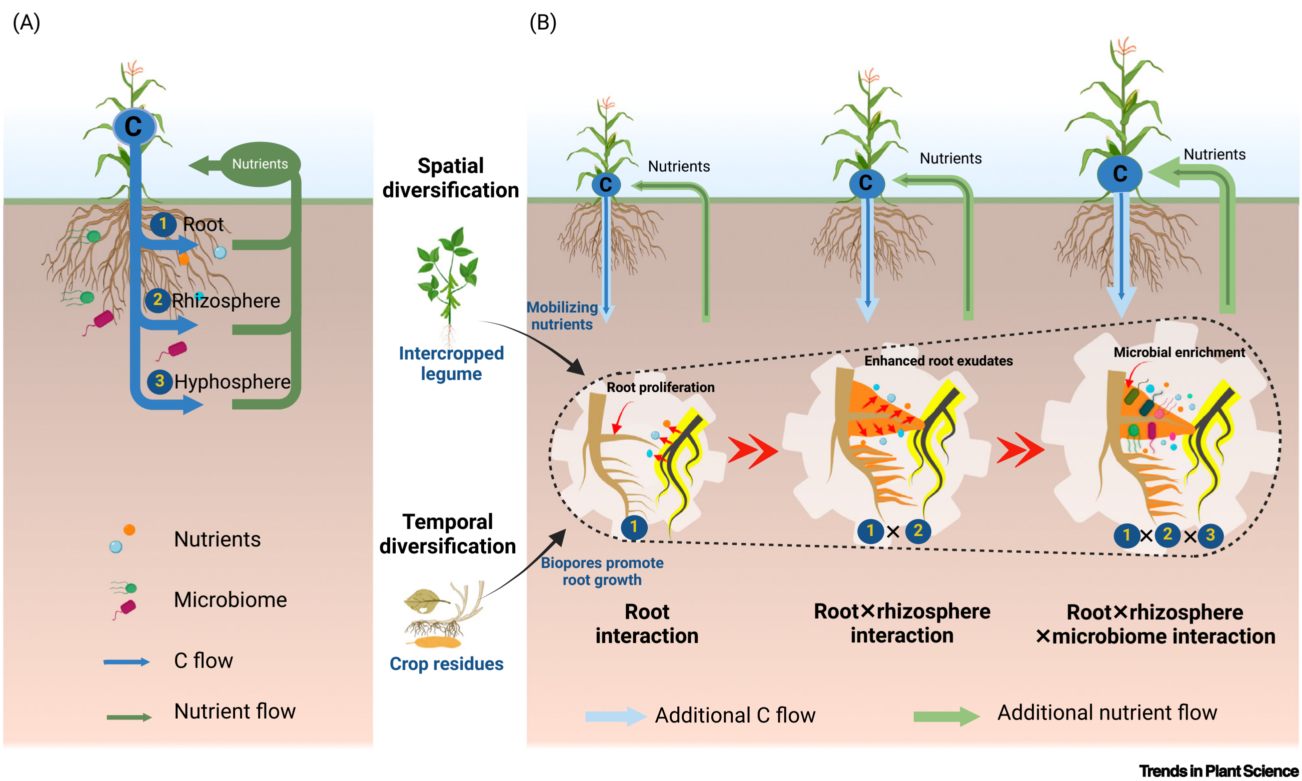

Figure 1. In (A), monoculture maize invests carbon (C) into ❶ the root interface: physical scavenging at the macro- and microscale; ❷ the rhizosphere interface: chemical mining or biological enhancement via exudates; and ❸ the **hyphosphere** interface: hyphosphere microorganisms mobilize nutrients. In (B), for spatial diversification, the intercropped legume mobilizes nutrients, and subsequently the focal maize roots increase root proliferation in response to the mobilized nutrients and then maize invests more C into root exudates that mobilize nutrients, and the enhanced root exudation leads to microbial enrichment. For temporal diversification, crop residues of preceding crops create biopores and promote root growth, triggering the subsequent cascading effects. Figure created with BioRender.com.

The intricate web of interactions involves root growth, root exudation, and microbial symbioses, all underpinned by aboveground carbon (C) fixation. A flow of C from aboveground sources and nutrients moving upward connects the crop shoot, roots, rhizosphere, and microbiome, forming a cohesive system known as the **rhizobiont**. Remarkably, even a small change in root and rhizosphere processes can exert profound effects on the entire system. Within diversified cropping systems, multi-interface interactions abound, including root interactions, root–rhizosphere interactions, root–rhizosphere–microbiome interactions, and above- and belowground interactions. These interactions collectively trigger cascading effects, which ultimately bolster crop productivity during the growing season and in subsequent crops. This knowledge is informative for how to design an effective diverse cropping system.

Here, we synthesize recent advances in the systematic examination of both above- and belowground interactions between different crop species. We emphasize that, in contrast to a monoculture, the proximity of neighboring plants or the preceding crop can induce a cascading effect on the focal plant. This effect sets in motion a series of interspecific interactions, such as enhanced root proliferation, enhancement of rhizosphere processes, and enrichment of microbial communities, all geared towards increasing nutrient acquisition by the focal plant (Figure 1). This heightened nutrient acquisition allows increased aboveground C fixation, which in turn stimulates belowground interspecific interactions. It reinforces root–root interactions related to root morphological traits, rhizosphere processes via root exudates, signaling molecules, and the augmentation of root–rhizosphere–microbiome interactions.

In scenarios of crop diversification, neighboring legume plants can create nutrient patches by exuding P-mobilizing carboxylates and phosphatases that trigger maize to proliferate roots and thus acquire more nutrients. Consequently, more C resources are allocated belowground to synthesize more root exudates, which in turn may mobilize greater quantities of nutrients (Figure 1B). Notably, root-exuded compounds like carboxylates, phytosiderophores, and phosphatases play pivotal roles in nutrient mobilization, enabling access to sparingly soluble nutrients [7]. These root exudates are of paramount importance to various microorganisms and are instrumental in shaping the plant microbiome [22]. Greater root exudation fosters microbial enrichment (Figure 1B), increasing the diversity of beneficial microbes and further enhancing nutrient uptake. For instance, root exudates promote nitrogen-fixing bacteria and can trigger the reassembly of rhizosphere microbial networks, facilitating nutrient uptake in intercropping systems [23,24].

Enhanced nutrient uptake arising from a belowground cascading effect can further trigger above- and belowground interactions. In maize/soybean intercropping, increased light interception during the post-silking stage results in enhanced root growth and P uptake in maize. This is facilitated by the translocation of sucrose to the roots, which stimulates intercropped maize root growth and enhances arbuscular mycorrhizal associations, and this can then bolster P uptake. These examples underscore the pivotal role of both above- and belowground interactions in regulating nutrient-use efficiency in intercropping systems [25].

Examples of cascading effects in diversified cropping systems

We highlight two cases that illustrate the principles of cascading effects: a maize/faba bean intercrop and a maize–soybean rotation (Figure 2). The two crop diversification practices are commonly in agroecological regions and have been extensively investigated for their beneficial impacts on nutrient acquisition and yield. In northwest China, maize/faba bean intercropping is a prevalent practice [26]. Likewise, the maize–soybean rotation is adopted in many parts of the world [11], and both systems have garnered substantial research attention due to their pronounced benefits in terms of nutrient acquisition and yield enhancement.

Faba bean significantly augments the P acquisition of intercropped maize, both in the field and under greenhouse conditions. A 4-year field study revealed a 46% increase in overyielding for intercropped maize and a 26% increase for intercropped faba bean, with both crops exhibiting enhanced P acquisition in the presence of each other [26]. The cascade of effects contributing to enhanced P acquisition in maize/faba bean intercropping stems from the P mobilization by the root exudates released by faba bean, which is better at mining sorbed P than maize is [7] (Figure 2A, Steps 1 and 2).

Maize displays greater root plasticity than faba bean [27], and in response to the patches rich in P that is mobilized by faba bean exudates such as carboxylates and phosphatases, maize roots proliferate vigorously. This increased root growth enables maize to take up the P mobilized by faba bean and subsequently to allocate C resources belowground (Figure 2A, Step 3). This belowground investment supports the production of root exudates, which serve to support P-solubilizing bacteria [28] (Figure 2A, Steps 4 and 5). For instance, in compacted soil conditions, the levels of rhizosphere

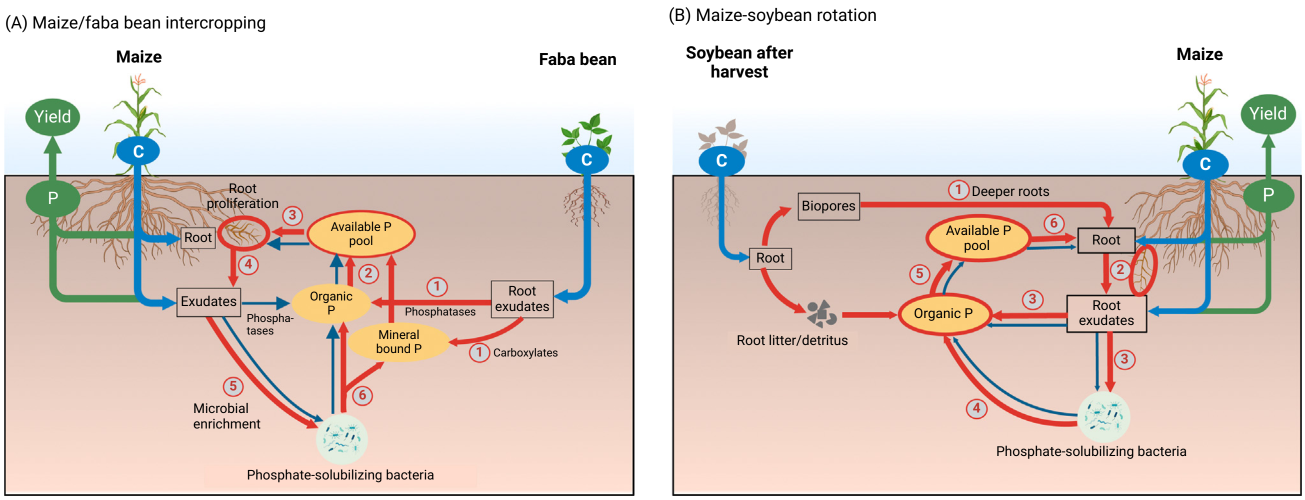

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Figure 2. Typical examples of cascading effects on phosphorus (P) acquisition in maize/faba bean intercropping (A) and a maize–soybean rotation (B). The blue unbroken lines represent how monoculture maize takes up soil P through its roots, with the involvement of root exudates and microbes. The red lines represent how intercropped and rotated maize takes up soil P through plant–soil–microbiome interactions in the presence of neighboring faba bean or preceding soybean. In (A), ❶ the intercropped faba bean releases root exudates that ❷ mobilize sorbed P such as sparingly soluble calcium P, P bound to metal(hydr)oxides, and organic P to available P. ❸ The neighboring maize plants increase root proliferation because of their high plasticity and thus take up the P made available and ❹ import more carbon (C) that enhances the release of root exudates, which ❺ feeds phosphate-solubilizing bacteria that further mobilize sorbed P and ❻ supports mycorrhizal colonization and hyphal exudates that further support phosphate-mobilizing bacteria that access organic P. In (B), ❶ soybean, after harvest, leaves biopores in the soil, which increase the rooting depth of maize in the next season; ❷ more C supports maize to mobilize organic P via the release of phosphatases or ❸,❹ supports P-releasing bacteria. The root litter/detritus from the soybean season is mineralized to release organic P, which increases the organic P pool and can be used by maize in the next season. Figure created with BioRender.com.

carboxylates in maize increases by 17% and several genera of actinobacteria were enriched in the rhizosphere. The abundance of these actinobacteria is positively correlated with carboxylate concentrations, suggesting the selection of P-solubilizing microorganisms in the maize rhizosphere that enhance P uptake [29]. Alternatively, the invested C resources boost mycorrhizal colonization, with hyphal exudates further supporting P-solubilizing bacteria [30].

Legume-based rotations are highly effective, boosting the yield of the main crop by 20% compared with non-legume cropping systems [11]. The cascading effects that are responsible for P acquisition in maize–soybean rotations originate during the soybean season. Here, soybean mobilizes fixed mineral P and leaves behind root pores in the soil (Figure 2B). After soybean harvest, the crop residues, including dead roots, undergo transformation, transitioning into organic P. This organic P reservoir can be accessed by the subsequent maize crop, facilitated by phosphatases or P-releasing bacteria [31]. The soil structure is enhanced by the presence of these root pores, which favor deep root development in the succeeding maize crop (Figure 2B, Steps 1 and 2). Consequently, increased root exudation by maize serves to mobilize organic P, expanding the available P pool (Figure 2B, Step 3). This surge in root exudates attract P-solubilizing bacteria (Figure 2B, Step 4), further enhancing the mobilization of organic P into plant-available forms (Figure 2B, Step 5). Collectively, these interfaces systematically increase the overall P uptake within the rotation system (Figure 2B, Step 6).

Application principles of cascading effect to mitigate soil limitations

We propose that the application of cascading effects in diversified cropping systems is a potent strategy to address soil nutrient deficiencies, alleviate root growth constraints imposed by compacted soil, and overcome microbial barriers in agroecosystems (Figure 3). To achieve

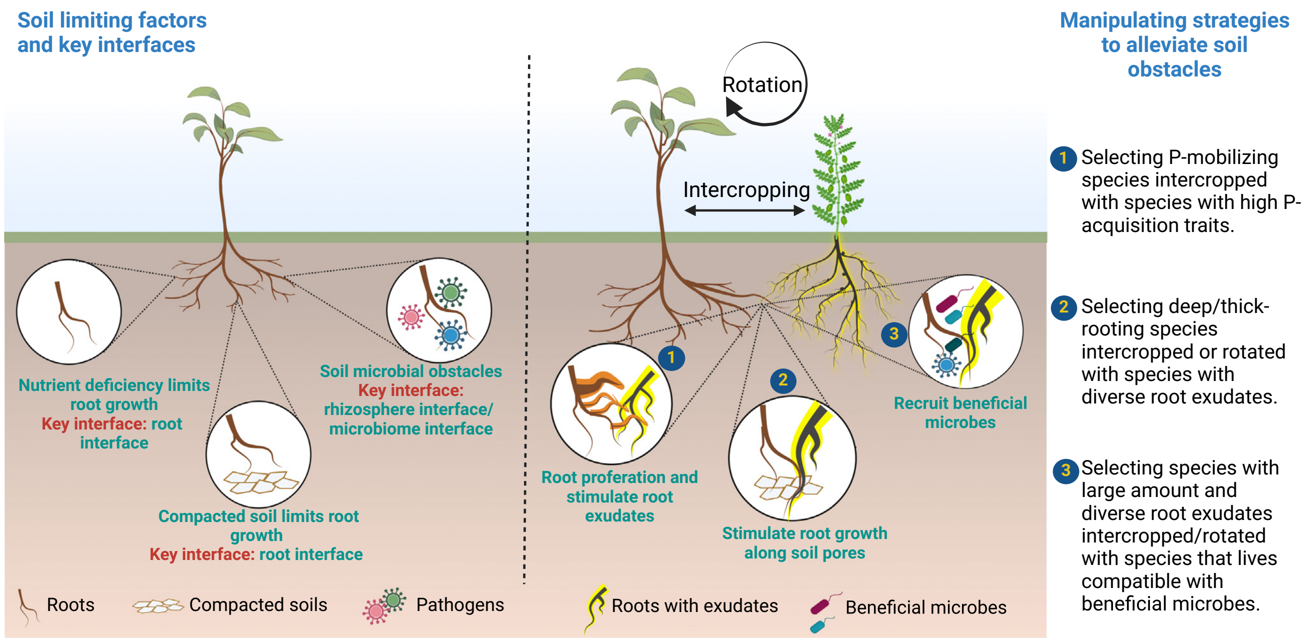

Figure 3. Applying the principles of cascading effects of diversified cropping systems to alleviate soil obstacle factors in agroecosystems. Figure created with BioRender.com.

these objectives, a deeper understanding of how soil biotic and abiotic stresses impact key interfaces, how interspecific interactions influence cascading effects, and how such interactions can lead to improved nutrient acquisition and defense of the crop is paramount. This knowledge can significantly advance root and rhizosphere management strategies aimed at mitigating impacts of soil-related challenges.

Addressing soil nutrient deficiency

Soil nutrient deficiencies often restrict plant growth, with the root interface being the primary concern. Following the principles of cascading effects in spatial diversification, selecting species with strong P-mobilizing traits for intercropping alongside species displaying efficient P-acquisition characteristics (e.g., high specific root length and root morphological plasticity) can substantially enhance P acquisition in intercropping systems. When facilitated neighbors possess root traits that are compatible with species that effectively mobilize sparingly soluble P through mechanisms such as acidification, carboxylate exudation, or phosphatase release, the facilitation of P uptake in intercrops is further enhanced [32]. For instance, the interaction between *Carex korshinskyi* (a P-mobilizing sedge) and *Stipa grandis* (a perennial bunchgrass with high root plasticity) illustrates the potential for enhanced P acquisition. When *S. grandis* is grown with *C. korshinskyi*, it exhibits greater root elongation than other species grown with *C. korshinskyi*, demonstrating complementarity [33].

In the context of root traits and P acquisition, root morphological traits play a substantial role in the apparent recovery efficiency of applied P in intercropping systems. Specifically, root morphological traits contribute significantly more to the increased P uptake (64%) than root physiological traits (27%) or microbiome associations (9%) [34]. This underscores the importance of root trait plasticity in facilitated species for the promotion of P uptake in intercropping systems. Moreover, genotypic variation within crop species, such as differences in carboxylate exudation, root mass fraction, specific root length, and colonization by arbuscular mycorrhizal fungi (AMFs), results in varying P-acquisition efficiencies [35]. Thus, the choice of plant cultivar in intercropping can significantly impact its effectiveness.

An effective approach is to intercrop or rotate crop genotypes known for their strong P-mining capabilities, including rapid carboxylate and phosphatase exudation or a strong association with AMFs. This strategy enhances P-acquisition efficiency in diversified cropping systems. Complementary P uptake can also be achieved by intercropping genotypes with contrasting root functional traits associated with P acquisition, such as pairing a genotype with a high root-exudation capacity with one that exhibits robust root morphological responses to P deficiency [36]. However, there are barriers to the adoption of mixing varieties because of a lack of knowledge of farmers and highly variable overyielding patterns for different variety mixtures. Revealing the drivers of productivity and stability of variety mixtures needs further research [37].

Intercropping with legumes is an effective strategy to increase N acquisition in low-N soils. For example, root exudates from maize, such as flavonoids, serve as signaling compounds that promote rhizobial symbiosis with faba bean, increasing nodulation, nodule activity and N_2 fixation [14]. Recent studies have also highlighted the role of rhizosphere bacteria, dependent on maize root exudates, in driving root–root facilitation of N_2 fixation in faba bean [23]. Enhanced N_2 fixation by faba bean increases soil N available to intercropped maize and the resulting acidification of the rhizosphere makes more P available to maize in alkaline soils. The incorporation of legumes into crop rotations can reduce the need for N fertilizers. This is due to the combined effects of legume N_2 fixation and the return and mineralization of N-rich legume residues, which provide additional soil N to subsequent crops [16]. For instance, residues from winter cover crops are incorporated into the soil, enhancing the N-use efficiency and crop yield of subsequent main crops and reducing the environmental degradation caused by overuse of fertilizers. Cover crop residues with low lignin content decompose rapidly, stimulating the turnover of residues through interactions with soil microbial communities [38].

Reducing soil compaction

Soil compaction poses a major challenge to sustainable agriculture, by limiting root extension and impeding roots from penetrating hardened soil and reducing water infiltration. This often leads to an accumulation of ethylene in roots, which acts as a signal, further constraining root growth in crops such as rice [39]. In the context of cascading effects, the root interface is of paramount importance. Improvement of soil physical properties is crucial, as it allows roots to penetrate soil pores and enhances their interactions with microorganisms. Cultivation of crops with robust root-penetrating capabilities can create biopores when their roots decompose, providing a more favorable environment for subsequent crop root growth. Roots tend to grow in these biopores, exploiting the path of least resistance [40].

Crops like chicory (*Cichorium intybus* L.), lucerne (*Medicago sativa* L.), and sunflower (*Helianthus annuus* L.) have thick and deep roots with rapid root growth rates. These crops are used as effective biotillage cover crops [15]. For instance, cultivating deep-rooting chicory and lucerne can leave behind soil pores after harvest, subsequently enhancing soil organic carbon levels. This improvement in soil physical properties benefits the root development and yields of subsequent crops such as wheat and soybean [41]. Radish (*Raphanus sativus* L.), when used in cover crop mixtures, can increase soil organic carbon stocks and promote root growth of neighboring crops, offering a practical solution to mitigate soil compaction [42].

Intercropping also holds the potential to increase rooting depth for efficient exploration of deep soil layers and provide yield advantages compared with sole cropping. In scenarios such as intercropping of sugar beet and chicory, both of which possess robust and extensive tap root systems, the deep roots of sugar beet promote early season nutrient uptake while chicory's deep roots contribute to later season nutrient uptake [43]. Growing an intercrop between the wide-spaced rows of cotton is effective to improve the soil environment; soil porosity is increased when cotton is intercropped with sorghum (*Sorghum bicolor*), sunn hemp (*Crotolaria juncea*), or sesame (*Sesamum indicum*) (53–58%) [44].

Overcoming microbial obstacles

Continuous monoculture practices often result in the accumulation of pathogens, negatively impacting the growth and health of subsequent crops. In this context, interactions at the rhizosphere and microbiome interfaces play crucial roles. To address these soil microbial obstacles, we propose to select species with diverse root exudates that can be intercropped or rotated with species that are compatible with beneficial microbes. Specific crop species or cultivars modulate distinct rhizosphere microorganisms through root exudates, influencing soil microbiome composition and function [45,46]. Crop rotations via the specific effects of different crops growing in the soil successively can suppress diseases through dilution effects or antagonistic interactions between beneficial and pathogenic microbiomes [47–49]. For example, cover crops can alter the composition of root-associated microbiomes, providing protection to subsequent cash-crop seedlings against pathogens [17]. In a 2-year maize–soybean rotation, fungal communities negatively impact maize yield, while bacterial communities contribute to maize recovery in a 4-year crop rotation due to changes in plant pathogen communities [50]. Crops from the Brassicaceae family, such as mustards, release glucosinolates that can suppress soil pathogens. These crops can be strategically selected for crop rotation or cover cropping to reduce pathogen pressure [51]. Some cover crops such as forage oats [*Avena sativa* (L.) Hausskn.] may increase mycorrhizal colonization [52]. Mycorrhizal legacy effects can be harnessed to enhance the functioning of beneficial microbiomes. Plants from preceding crops can influence the assembly of AMF communities in subsequent crops through these legacy effects [53].

Intercropping is also an effective strategy to defend against pathogens by planting crop species known for their defense metabolites [54]. Root exudates of one crop may directly mitigate soil-borne diseases in another. For instance, root exudates of faba bean can alleviate the impact of soil-borne diseases in intercropping. In maize/faba bean intercropping, the relative abundance of rhizobium is increased, while the relative abundance of putative pathogens of intercropped faba bean is reduced compared with that in soils of faba bean monocultures [55]. Additionally, intercropping can trigger allelochemical responses in crops, indirectly reducing diseases in the companion crop. For instance, intercropping of potato onion (*Allium cepa* L. var. *aggregatum*) with tomato (*Solanum lycopersicum* L.) stimulates the root exudation of taxifolin, a flavonoid that recruits specific *Bacillus* sp., inhibiting the growth of the pathogenic fungus *Verticillium dahliae* and inducing systemic resistance in tomato plants [56].

Leveraging cascading effects for sustainable agriculture

We propose a systematic procedural framework to apply the principles of cascading effects to improve sustainable cropping systems, via enhancing crop potential while reducing the need for excessive agricultural inputs (Figure 4). This approach not only enhances the biological capacity of crops but also promotes ecofriendly agricultural practices. To achieve this, we suggest a structured approach comprising three key components.

(i) Diversification with targeted traits of crops through trait-based phenotyping and **plant–soil feedback**. High-throughput phenotyping of crop shoots and roots, such as RhizoTubes [57], facilitates the selection of species combinations based on various traits of crops or

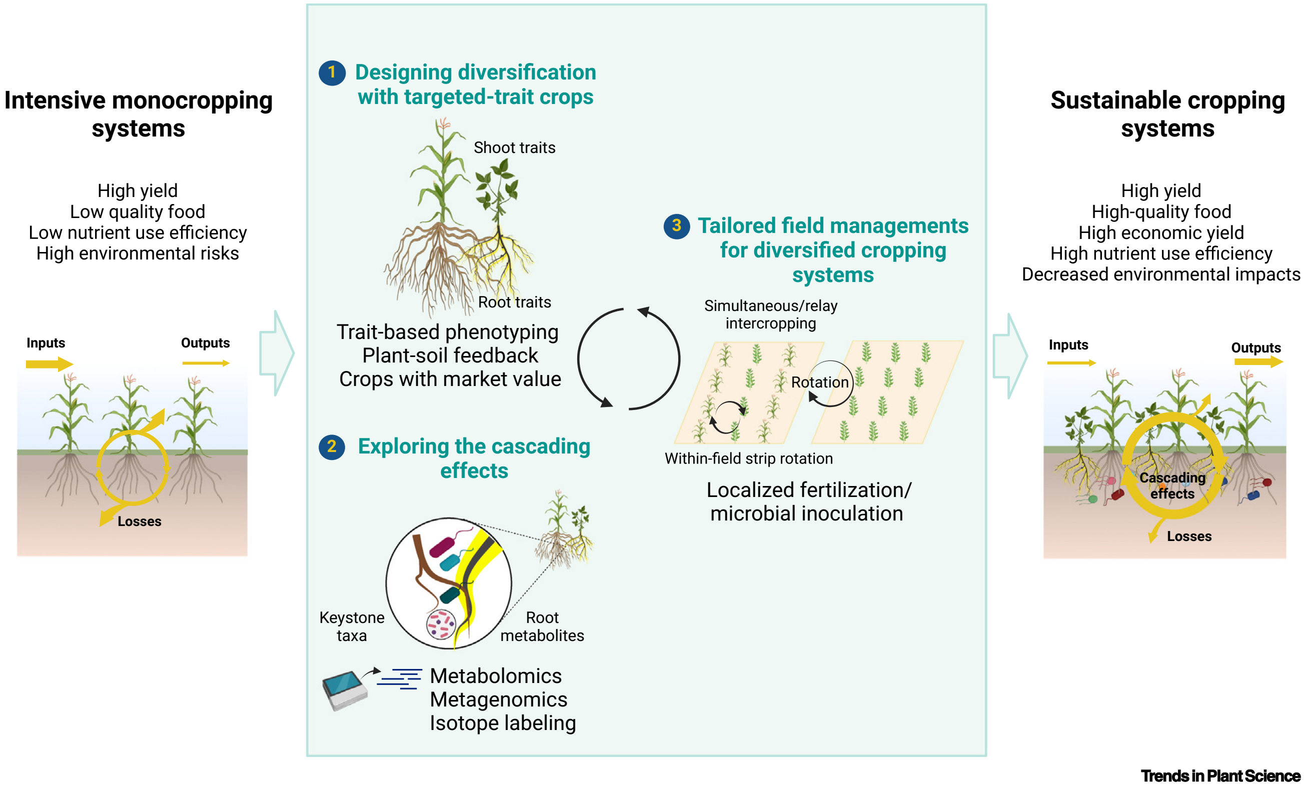

Figure 4. Systematic procedural framework applying cascading effect principles to achieve sustainable cropping systems. Figure created with BioRender.com.

genotypes thereof. These traits encompass root architectural traits (shallow or deep rooted), morphological traits (thin or thick roots), physiological traits (root exudation), and symbiotic traits (association with mycorrhizal fungi and beneficial bacteria). Further, we propose to leverage the concept of plant–soil feedback to design rotation systems [16]. Crop identity, sequence, and management practices, such as tillage intensity and synthetic input application, can be manipulated to create positive plant–soil feedbacks in diversified cropping systems [58–60]. Building a comprehensive database on species- or genotype-specific plant–soil feedbacks in soils conditioned by the same or different species (note that this differs from the classical home/away approach in plant–soil feedback) through experiments and sequencing tools will enable assessment of how crop identity, sequence, and management affect plant–soil feedback [61]. For instance, soil microbial communities are compositionally more similar between closely related plant species, allowing predictions based on species identity and relatedness [62]. This database will contribute to improved crop rotations and enhanced yield and soil health. However, soil microbial effects are spatially and temporally variable, which complicates predictions for the selection of crop species. It is also important to choose market-oriented crop species for diversified cropping systems and to choose commercial varieties widely used in specific regions to screen for resource-efficient varieties for diversified cropping systems. That will help farmers get ready access to the newly designed cropping systems.

(ii) Determining limiting soil factors, such as nutrient deficiency, soil compaction, and microbial obstacles, and quantifying the key interfaces such as root, rhizosphere, and microbiome through stable isotope labeling, such as [^{13}C]DNA stable-isotope probing (SIP) [63]. This technique provides insight into crucial interfaces by highlighting interactions between root systems, the surrounding rhizosphere, and microorganisms. We further need to explore the mechanisms driving plant–soil–microbial cascading effects in crop diversification by identifying keystone microbial species and rhizosphere metabolites using metabolomics and metagenomics. Advanced molecular microbiology methods enable precise characterization of soil microbial communities responsible for cascading effects in crop diversification. Techniques like amplicon sequencing and metagenomics sequencing can help to identify key taxa and metabolites that drive nutrient cycling, disease suppression [50,56], and signaling molecules that stimulate beneficial bacteria [24,64].

(iii) On the basis of newly designed diversified cropping systems, customized field management practices can reinforce the key interface of cascading effects in crop diversification. For instance, the introduction of partial co-growth periods between intercropped species allows temporal complementarity in resource use, reducing competition for nutrients during the same growth period [65]. Within-field strip rotations enhance rhizosphere interactions at the root interface [66]. Tailored field-management practices such as localized fertilization and microbial inoculation in diversified cropping systems are essential for cascading effects to operate effectively. The tailored field management and selected cropping systems that are efficient under specific climate conditions and soil types and with high market value will help to achieve objectives such as reduction of agrochemical inputs and enhanced resource-use efficiency, thereby promoting environmental sustainability while ensuring high-quality food production.

Worldwide adoption of crop diversification remains a huge challenge. For instance, barriers to a transition to intercropping in Europe are related to many factors including the specific crops, cropping methods, and geographical regions, and exist at multiple points along the supply chain [67]. Furthermore, socioeconomic and behavioral drivers impact the adoption of intercropping by farmers [68]. Realizing the sustainable development of intercropping systems requires cooperation between researchers, farmers, extension workers, and industry to produce effective intercropping solutions for practice in various settings.

Concluding remarks and future perspectives

The intricate multi-interface interactions encompassing root–root, root–rhizosphere, rhizosphere–microbiome, and above- and belowground interfaces drive cascading effects, contributing to increased productivity in diversified agroecosystems. Understanding the mechanisms related to the signaling molecules or keystone microbes triggering the complex plant–soil–microbiome interactions would be helpful in further exploring the contributions of plant diversity to plant productivity in agroecosystems. We suggest that implementing principles of cascading effects in agricultural diversification involves the selection of species combinations for intercropping and crop rotations based on specific traits of crops or genotypes thereof to systematically manipulate key interfaces. Moreover, the selection of species combinations and tailored management warrants further studies to alleviate the soil obstacles. By affecting plant–soil–microbiome interactions such as root growth, these cascading effects can be harnessed to enhance crop nutrient acquisition, health, and yield. Breeding genotypes with desirable traits for species combinations that impact the cascading effects in diversified cropping systems needs further research. The systematic approach not only boosts nutrient-use efficiency and crop yield but also reduces inputs and minimizes nutrient loss. However, how to up-scale belowground biotic interactions at the individual plant level to the population/field level where there is inherently greater variation remains a major challenge. Moreover, we suggest that future research is focused on better understanding the barriers and uncertainties for farmers and finding ways to encourage them to adopt crop diversification practices (see Outstanding questions).

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Outstanding questions

What are the signaling molecules or keystone microbes triggering the complex plant–soil–microbiome interactions?

Which species combinations with positive plant–soil–microbe interactions with tailored management (temporal and spatial arrangement, nutrient input) can moderate soil obstacles?

What are the critical root morphological and physiological traits of crop species to target to maximize cascading effects in diversified cropping systems?

How can belowground biotic interactions at the individual plant level be scaled up to the population/field level?

What are the barriers to farmers' adoption of crop diversification?

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Declaration of interests

No interests are declared.

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