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REVIEW ARTICLE

The contemporary plant-soil feedback in legume-cereal intercropping systems: a review of carbon, nutrient, and microbial dynamics

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Abstract

Background Crop diversification practices, such as legume-cereal intercropping, are receiving increasing attention for the large-scale implementation because of crop yield advantages while simultaneously preserving various soil functions. To date, a comprehensive understanding of the soil nutrient and carbon (C) cycling and microbial dynamics underlying the crop yield advantage remains elusive.

Scope This review employs legume-cereal intercropping systems as a model to examine the current knowledge on the modulation of soil nitrogen (N), phosphorus (P), potassium (K), and C biogeochemistry resulting from the co-cultivation of these crops. This analysis emphasizes the functional potential of the soil microbiome and the plant-induced assemblage of microbial communities, highlighting key knowledge gaps. Drawing from this examination, we suggest expanding the traditional Plant-Soil Feedback (PSF) definition to encompass hetero- and conspecific effects occurring within a single growing season. We define this concept as Contemporary Plant-Soil Feedback (CPSF).

Conclusions Our analysis revealed consistent plant-induced changes in the performance and nutrient acquisition of neighboring plants, an effect that would be inadequately classified without this new framework. The examination of the CPSF in legume-cereal intercropping systems demonstrated that yield advantages are supported by more efficient N and C cycling, enhanced P and K availability, and improved maintenance of microbial functionality. This approach offers a novel perspective for investigating plant-soil dynamics in agricultural systems.

Keywords Plant-soil feedback · Multi-cropping systems · Soil nutrient and carbon cycling · Soil microbial assemblages · Soil multifunctionality · Carbon use efficiency

Abbreviations

AMF	Arbuscular mycorrhizal fungi
CPSF	Contemporary plant-soil feedback
CUE	Carbon use efficiency
MBC	Microbial biomass carbon
MBN	Microbial biomass nitrogen
MBP	Microbial biomass phosphorus
PSF	Plant-soil feedback

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RPE Rhizosphere priming effect
SOC Soil organic carbon

Introduction

The challenge of increasing crop yield intensity while sustaining the provision of soil ecosystem services is increasingly important for sustaining the expected increase of the human population (Lehmann et al. 2020). Crop diversification practices, particularly multi-cropping systems, presently have and will have an increasingly relevant role in sustaining the ongoing transition towards more sustainable agricultural systems (Ehrmann and Ritz 2013). Advancements in the knowledge of plant-soil-microbiota interactions are needed to foster an improved comprehension of the shifts in carbon (C) and nutrient cycling, which sustain positive or negative effects on plant performance. Unless this is achieved, efficient management of these systems will not be possible, nor will it be possible to exploit their benefits. In particular, there is a lack of a theory that comprehends all the processes underlying plant-soil interactions occurring during the same cropping season between neighboring plants (Yu et al. 2016; Raseduzzaman and Jensen 2017).

The Plant-Soil Feedback (PSF) has been defined as the plant-mediated alteration of the soil microbiota and soil physicochemical properties, which consequently affect the growth of subsequent plant species during the following growth cycle (Bever 1994; Wang et al. 2021; Koyama et al. 2022; Nannipieri et al. 2023). This definition distinguishes between conspecific and heterospecific effects based on the phylogenetic classification of plants (Bennett and Klironomos 2019). Specifically, heterospecific effects include soil conditioning, which affects plants of different species. Conversely, conspecific effects are those that are exerted by plants on the successors of the same species. However, this definition fails to fully capture the belowground interactions of neighboring plants growing simultaneously, because it describes the effects that occur across different seasons or years. Neighboring plants grow simultaneously, for instance, in natural ecosystems during re-colonization after disturbances or in agroecosystems when annual intercrops are grown at the same time. Therefore, it is necessary to extend the definition of PSF and unravel the underlying mechanisms.

Intercropping is a system in which multiple plant species are co-cultivated so that they are all simultaneously in the vegetative stage for an extended period (Zhang and Li 2003; Duchene et al. 2017). One of the most promising crop combinations investigated is legume-cereal intercropping (Yu et al. 2016; Raseduzzaman and Jensen 2017; Tang et al. 2021). Currently, the preliminary focus on this cropping system is centered on the potential for sustainably enhancing yields by positively influencing soil nutrient cycles, physicochemical soil properties, and the soil microbiota (Zhang and Li 2003; Duchene et al. 2017; Yu et al. 2022). A consistent yield advantage (Yu et al. 2016; Raseduzzaman and Jensen 2017) deriving from this cropping system is attributed to the fundamental principles of ecological biodiversity including physiological, spatial, and temporal complementarity, facilitation, compensation, as well as competition-recovery (Duchene et al. 2017; Xiao et al. 2018; Yu et al. 2022), in fact principles of the PSF. Given the future significance of intercropping in sustaining agricultural systems, it is important to accurately classify the underlying mechanisms that control the soil interactions between two or more plant species.

The objective of this perspective is to identify gaps in the transfer of the PSF theory to interactions between plants growing in the same season in agroecosystems. This study presents compelling evidence that the exclusion of what we define as "contemporary" interactions from the PSF definition would result in a significant omission of its essential components. Therefore, we propose an extended definition of the traditional PSF theory, which we suggest being referred to as the “Contemporary PSF” (CPSF) (Fig. 1). Additionally, we aimed to provide a deeper, mechanistic understanding of the various processes underlying the CPSF in legume-cereal intercropping.

The CPSF can be defined as the set of trade-offs that exist among plant metabolism, soil microbiota, and edaphic properties, which affect the performance of both plants growing in close proximity, whether interspecific or intraspecific. There must be a certain minimum distance between plants to ensure that the exchange of or the competition for resources can occur (Ehrmann and Ritz 2013; Yu et al. 2022; Nannipieri et al. 2023). The same holds true to allow root-secreted functional metabolites to be detected, and to be able to trigger a response, although the distance varies with the mobility of the metabolites under a

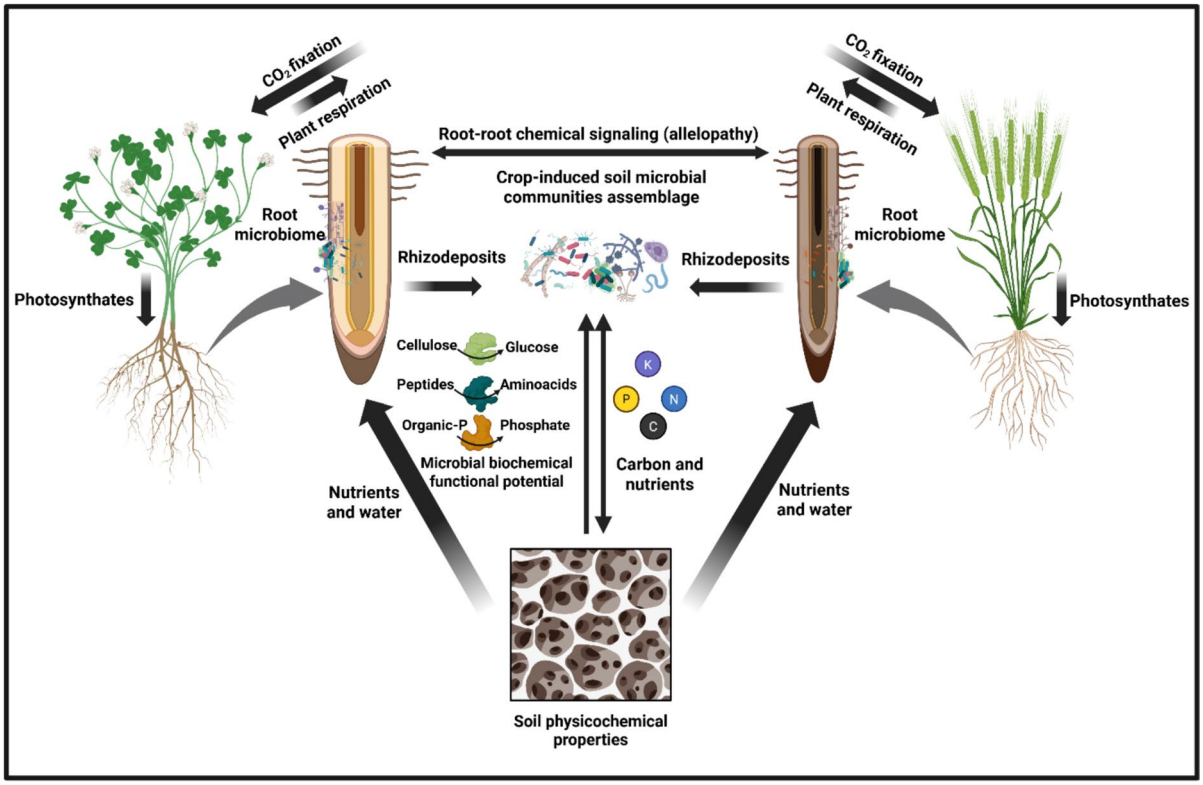

Fig. 1 A conceptual visualization of the scope of the proposed definition of the Contemporary Plant-Soil Feedback. The processes contributing to the CPSF effect comprise the plant-plant communication (allelopathy), the plant-mediated modulation of both bulk and rhizosphere soil microbiota (to different extents, respectively), the role of the root microbiota, the acquisition of nutrients and water from soil, and the effects that the microbiota and plants have on nutrient and C cycling

specific soil environment (Homulle et al. 2022; Yu et al. 2022; Wang et al. 2023a). This definition not only provides a clear chronological classification of the CPSF phenomenon, which only occurs during the plant vegetative stage, but also precludes interspecies interactions among plant families with different pedoclimatic or seasonal requirements that cannot grow simultaneously. Additionally, the spatial classification remains the same as in the traditional PSF definition, as it corresponds to the soil volume that is effectively influenced by the metabolic activities of the plants (Fig. 2). Lastly, it is important to maintain the traditional distinction between intra- and interspecific interactions because the outcome of a modification in the soil environment mediated by a "focal plant" (nutrient sequestration, selection of the rhizosphere microbiota, release of rhizodeposits, secretion of allelopathic compounds, etc.) elicits a response in the "target plant", which depends on the identity of both (Wang et al. 2023a). The outcomes differ from when both plants belong to the same species (Homulle et al. 2022; Yu et al. 2022; Wang et al. 2023a). Thus, the proposed concept of the CPSF addresses a significant gap in our understanding of the PSF in intercropping systems. By extending the traditional PSF definition to encompass simultaneous plant growth and interactions, it provides a more comprehensive framework for studying complex agroecosystems.

Although the differentiation between the traditional PSF and the CPSF mainly resides in the temporal extension of the phenomenon (i.e., across different growing seasons, or within the same season), another very relevant difference is the rhizodeposition pattern. Specifically, it must be considered that, when different plant species grow simultaneously, they release a diverse array of root exudates into the soil. This scenario is only partially captured by the traditional PSF across agronomic seasons, as only some of the

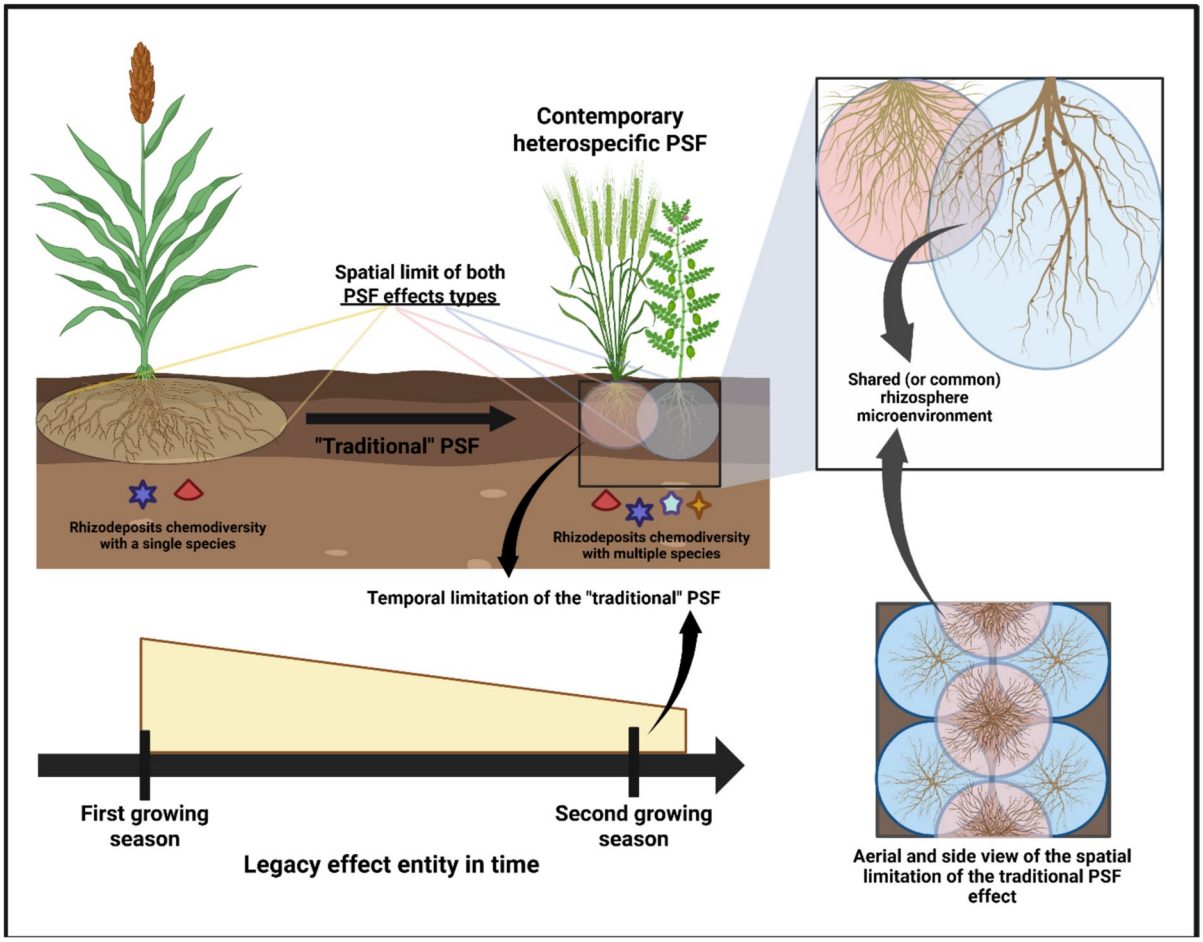

Fig. 2 A representation of the temporal and spatial limitations of the "traditional" and the Contemporary Plant-Soil Feedback (PSF) effect. Although the spatial limitation of the Contemporary Plant-Soil Feedback effect remains the same as the traditional one (i.e. the soil volume substantially influenced actively or passively by one plant), the temporal limitation is different since it comprises the effects mediated on other plants ("target plants") growing at the same time as the "focal plant". Furthermore, it becomes relevant to highlight that a proportion of the soil volume in multispecies systems is contemporarily influenced by more than one species, and it has been indicated here as "shared rhizosphere" or "common rhizosphere" microenvironment

compounds released during the first season remain undegraded by the time the next season arrives (Li et al. 2024). While the impact of the chemical diversity of rhizodeposits on soil microbial community assemblage is only partially understood, recent findings suggest that this research area could be crucial for comprehending the linkage between plant diversity and soil microbial community functioning (Jiang et al. 2024). As a result, the greater is the phylogenetic distance between the intercropped plant species, the more pronounced the differences will be between the rhizosphere microbial communities of the co-culture and sole-cropping systems. Therefore, this spatiotemporal combination of rhizodeposits should be acknowledged as a significant distinction between the traditional and the contemporary effect.

When studying the CPSF, it is essential to consider not only the legacy of rhizodeposits and microbial communities but also the dynamic "coexistence" effect at play. This effect implies that the performance of each crop in multi-cropping systems results from dynamic variations in competition and recovery processes, which are influenced by the phenological stage of each crop and the specific

pedoclimate in which they grow (Ehrmann and Ritz 2013). Disentangling these dynamics can seem overwhelmingly complex, highlighting the growing need for theories and holistic approaches that integrate diverse fields of knowledge. The upcoming sections will delve into the CPSF within the context of legume-cereal intercropping systems, employing this as a model to elucidate the present state of knowledge in this area.

Plant communication strategies

In order to maintain their homeostasis after germination, plants constantly monitor their environment and respond to changes. Plants implement diverse strategies in the soil to communicate with, stimulate, or inhibit specific microbial groups or other plant species (Chaparro et al. 2012; Wang et al. 2023a). These strategies mainly rely on the indirect effects of the nutrient utilization by plants, or on the production, either directly or indirectly, of chemical compounds that affect the growth, spatial distribution and proliferation of sensitive organisms, e.g. allelopathy, and their release into the soil (Fernández-Aparicio et al. 2008; Hooper et al. 2010; Otte et al. 2020). Chemicals are directly released into rhizosphere soil through the process of rhizodeposition. An indirect release occurs when plant residues are degraded or transformed by microorganisms that produce the allelopathic compound as an intermediate or terminal product, and when microbial groups producing allelopathic compounds are selected and actively sustained by plants in their rhizosphere or roots. The role of allelopathic molecules is often overlooked, mainly because of the complex and time-consuming process of identifying the molecules responsible for the communication between a plant species and microbial or plant groups. Although the competition for nutrients has reached a quite advanced understanding, and its role in the CPSF of legume-cereal intercropping systems is well recognized, the same is not true for allelopathy. To the best of our knowledge, this issue has not yet been addressed for this cropping system.

In the following sections, we discuss the effects of legume-cereal co-culture on nutrient acquisition, as well as the effects on the assemblage of soil microbial communities and their functionality related to biogeochemical cycles. The allelopathic mechanisms at the base of the specific effects, when deemed relevant, will only be hypothesized because none of the cited studies addressed them explicitly.

Plant nutrient acquisition advantage

Water and nutrients, particularly nitrogen (N) and phosphorus (P), commonly limit primary production and crop yields. Optimizing nutrient availability in the shared rhizosphere soil is often critical in determining the positive effects of crop diversification on plant nutrition (Jain et al. 2020; Pathan et al. 2020). Nutrient advantages in intercropping systems result from three major factors: (1) resource use complementarity and competition; (2) active resource exchange (facilitation); and (3) enhanced resource mining.

(1) Resource complementarity and competition depend on interspecific niche differentiation, which induces plants to explore other nutrient sources that are less utilized or not utilized by their companion. A classic example is the enhanced investment of resources by legumes to favor the symbiosis with rhizobia when interspecific competition reduces N availability in the soil (Li et al. 2009; Chapagain and Riseman 2015; Zhao et al. 2020, 2022c). A good demonstration can be found in the study by Zhao et al. (2022c) where the authors investigated crop N acquisition in the field using ^{15}N stable isotope probing and found that certain legume-cereal combinations can effectively improve legume N_2 fixation in a sandy loam soil. Specifically, sorghum intercropped with soybean was effective in enhancing N_2 fixation (+ ~ 25%), but not with alfalfa or mung bean, probably due to the different N_2-fixation potential of the various legumes. Another context in which complementarity is pivotal for plant success is the limited availability of soil P. In that case, legumes have the ability to mobilize a P pool that is not available to cereals either by the release of carboxylic acids and phosphatases or through the selection of P-solubilizing bacteria (Li et al. 2007; Tang et al. 2016; Bargaz et al. 2017; Sugihara et al. 2021).

This condition is anyway borderline with active resource sharing, as the alteration of the rhizosphere environment can also be very extensive.

(2) Active resource sharing is the result of diverse phenomena, both microbial- and plant-driven, which to date have been evidenced mainly in the case of N acquisition. Chapagain and Riseman (2015) found that N transfer from some legumes to cereals was consistent (up to 11.9% N compared to the sole cropped cereal). This can lead to an increase in cereal biomass total N, but is associated with a significant reduction in total N content of legume biomass. However, the transfer was inconsistent in pea-barley intercropping (Hauggaard-Nielsen et al. 2001). Wichern et al. (2007) demonstrated that pea rhizodeposits have consistently faster turnover than cereal deposits and can contribute up to 31% to the inorganic N pool in a clayey silt soil. This rapid recycling of legume rhizodeposits is most likely the major driver of facilitation and active resource sharing, although N transfer might occur through both direct and indirect mechanisms. Therefore, cereals may effectively shape the soil microbiota to enhance organic N mineralization, which can facilitate the acquisition of newly fixed N by legumes.

(3) Improved soil resources mining is based on host plant specificity and the selection of beneficial microorganisms, such as mycorrhizal fungi, and physiological traits, such as root morphology. Bargaz et al. (2017) demonstrated that co-cultivation of soybean and wheat effectively prevented the negative effects of P deficiency on shoot biomass P content in both species. The authors suggested that legume root nodules might play an active role in soil P mobilization and its subsequent uptake; however, optimal soil P conditions are necessary for crops to efficiently accumulate N in their biomass. Additionally, some legumes may have a higher susceptibility to arbuscular mycorrhizal fungi (AMF) colonization, which could aid in P, but not in N acquisition. Li et al. (2009) observed higher P uptake in upland rice co-cultivated with mung bean in a neutral P-limited soil under pot conditions (+34% when full root contact was allowed with AMF inoculation). Similar results were obtained by Sugihara et al. (2021) when pigeon pea was intercropped with maize under an intermediate P fertilization level (50 kg P/ha) with full root contact in a severely P-limited soil.

These findings emphasize the significance of nutrient acquisition in the context of the CPSF effect in legume-cereal intercropping systems. Therefore, it is evident that the P and N dynamics in the shared rhizosphere environment of co-cultivated legumes and cereals play a critical role in maximizing plant yield. However, it is important to note that enhanced plant nutrition is the result of improved microbial- and plant-driven alterations in soil nutrient and organic matter turnover.

The state of knowledge on soil nutrient and organic matter cycling

The temporal and spatial availability of soil nutrients is a key factor in determining the plant growth potential (van Groenigen et al. 2015; Homulle et al. 2022; Yu et al. 2022). Moreover, soil organic matter, which is also a critical component of soil fertility, affects plant performance by supporting the metabolic activities of heterotrophic microorganisms and regulating nutrient availability (Chapagain and Riseman 2015; Yang et al. 2021, 2023b). Consequently, the large-scale implementation of mixed cropping systems, which involve plants with different nutrient-acquisition and microbiota-shaping traits, requires a thorough understanding of nutrients and soil organic matter cycling.

Nitrogen

Dynamic changes in the abundance of various organic and inorganic N fractions in soil are an indicator of their availability to plants and microorganisms, as well as the prevalent microbial transformation processes in legume-cereal intercropping systems. Notably, Scalise et al. (2015) discovered that intercropping barley with different legumes in a Mediterranean climate significantly affected N dynamics throughout the growing season. Specifically, the concentration of nitrate (NO_3^-) in the soil was significantly higher when wheat was intercropped with faba bean or pea (up to +~200%), regardless of the sowing ratio employed; however, ammonium (NH_4^+) abundance

did not consistently differ among treatments. This might have been caused by the increased mineralization of N from legume rhizodeposits during the active growth stage, and the prevalent oxidation of NH_4^+ to NO_3^-. In contrast, Yu et al. (2019) found that the concentration of N chemical forms varied inconsistently across the three experimental years, thus showing that higher N availability for the cereal counterpart is not always the case. These differences might be attributed to the diverse pedoclimatic conditions in the two experiments (i.e., a sandy clay loam in a Mediterranean climate and a red soil under a tropical ocean monsoon climate, respectively). Liu and Gong (2022) further demonstrated that all N fractions analyzed in their study (Total N, NH_4^+, NO_3^-, and microbial biomass nitrogen (MBN)) were more actively sustained by intercropping mung bean with millet than in the cereal sole cropping system. Additionally, the authors found that optimal conditions for plant performance and soil N dynamics in the intercrop system could be achieved by applying 120 kg N/ha under field conditions in a semiarid continental monsoon climate. These studies demonstrated that plant-available N forms profit from intercropping cereals and legumes, resulting in fertilizer savings and more closed nutrient cycles (Fig. S1). However, it is essential to address the underlying microbial processes and microscale dynamics in different soil niches that actively influence the N availability for primary production.

An important factor to consider when evaluating soil N conditions is the loss of gaseous N forms, such as nitric oxide (NO), ammonia (NH_3), nitrous oxide (N_2O), and elemental N (N_2). Although many studies have focused on N_2O soil emissions due to their contribution to climate change, it is necessary to understand how plant growth dynamics can be used to manage the various mineral and organic N pools in the soil to reduce gaseous N losses (van Groenigen et al. 2015). This is especially relevant in terms of crop diversification, as legumes can increase soil organic N pools through N-rich rhizodeposition, particularly after maturity (Zhang et al. 2024). For instance, the introduction of soybean to maize under field conditions resulted in a significant reduction in N_2O emissions during the vegetative season (−203 g N_2O-N/ha, −16.2%) (Zhang et al. 2024). This was likely due to the reduced N availability for denitrification, as partly demonstrated by the incorporation of mixed residues of cowpea and maize (Frimpong et al. 2011). Similarly, Castellano-Hinojosa et al. (2022) demonstrated that N_2O emissions were significantly lower when legume species were included in the cover crop mixture than when the mostly-*Poaceae* species mixture was grown without (0.62 vs 1.06 kg N_2O-N/ha per year). In contrast, Pappa et al. (2011) observed contrasting results when intercropping barley with pea or clover in terms of N_2O production, with cumulative emissions being two to four times higher in intercropping than in sole barley (~1 kg N_2O-N/ha vs ~3 kg N_2O-N/ha) in a sandy loam soil, except for co-cultivation with one of the pea varieties. This indicates that soil N_2O emissions can be effectively modulated through legume-cereal intercropping. This, coupled with the knowledge of higher NO_3^- availability for cereals when intercropped with legumes (Scalise et al. 2015; Liu and Gong 2022), implies that cereals use this nutrient more efficiently when they are intercropped than when they are in sole culture, thus contributing to the reduced N_2O production. The variability of these results could be related to the different legume species used and, possibly, to the diverse times required for rhizodeposit mineralization. Further research is needed to shed more light on the underlying biogeochemical mechanisms, including the use of ^{15}N-labelled substrates and constant emission monitoring. Regarding N_2O production from soil under intercropping conditions, it is necessary to investigate the various N_2O production processes in order to implement sustainable practices that minimize N losses.

Phosphorus

Several legume species are widely recognized for their ability to mobilize unavailable forms of soil P (Duchene et al. 2017; Tang et al. 2021; Yu et al. 2022). However, in order to implement this cropping system on a large scale, it is essential to provide a more precise, context-dependent description of the species influence. For instance, Sugihara et al. (2021) intercropped maize with pigeon pea or groundnut by adding 50 kg P/ha to an acidic, continuously maize-cropped soil under pot conditions. While pigeon pea sustained P mobilization from the soil in the maize rhizosphere (up to 100% more plant-available P with full root contact), groundnut competed with the cereal for P resources. The authors hypothesized that AMF and rhizosphere microbial processes may play a role

in P mobilization. Gong et al. (2019) found that intercropping mung bean with millet could significantly enhance millet rhizosphere P availability in an alkaline soil in a semiarid continental monsoon climate under field conditions by up to 21%. In contrast, Tang et al. (2016) observed no evident effect of intercropping faba bean and wheat on the plant-available soil P fraction in a neutral soil with high, low, or no P fertilizer application. In a meta-analysis, Tang et al. (2021) suggested the strong P-mobilizing abilities of faba bean and chickpea, moderate effects of cowpea and no effects of soybean and pea in various intercropping systems. This highlights that different legume species have consistently different genetic potentials for P mobilization from the soil. Furthermore, it is very well known that P uptake by plants is strongly influenced by other edaphic factors, such as pH and texture, possibly leading to different outcomes even when the same species combinations are used in diverse pedoclimates. We conclude that the effects observed in previous studies most likely depend on the combinations of the species that drive plant-induced soil microbiome conditioning. Future investigations should further elucidate the mechanisms responsible for P mobilization in intercropping systems, including the mineralization of organic P, the solubilization of insoluble P by root exudates, and microbial activity.

Potassium and micronutrients

Despite being limiting factors for plant productivity, only a handful of studies exist regarding the effects of intercropping practices on the potassium (K), other macro- and micro-nutrients availability in soil. Gong et al. (2019) investigated the potential of intercropping mung bean with millet to improve rhizosphere K availability for cereals and found that this can be effective when applying 62.25 kg K/ha (+58% in available K). These results suggest that an active transfer of K might occur through the physical interconnection of roots from the different species, since total K was also significantly increased. This indicates a possible improvement in K utilization from fertilizers or an increased availability from soil minerals. In a study on Fe deficiency amelioration in peanut through the intercropping with cereal species, such as oats, barley, and maize, Zuo and Zhang (2008) found that this insufficiency could be effectively avoided. Both effects are likely imputable to the combination of diverse nutrient acquisition strategies by the two plant families and the possible selection of microbial functional groups that mobilize these elements from the soil, resulting in the facilitation of the companion crop. However, the effects of co-culture on the availability of other micronutrients remain poorly studied. Overall, although some results are inconsistent, this area of research remains promising for improving nutrient availability on a large scale.

Soil organic carbon

Increasing plant diversity in agroecosystems has been shown to increase the rhizosphere C input (Gentsch et al. 2020), as well as soil organic carbon (SOC) stocks (Cong et al. 2015). This process may be facilitated by the increased quantity and quality of photosynthates reaching the soil and the enhanced stabilization of organic matter. Introducing legumes into cereal monocultures is expected not only to increase the photosynthetic capacity of plant coverage but also to reduce the C:N ratio of rhizodeposits (Ghosh et al. 2006; Wichern et al. 2007; Regehr et al. 2015). However, the effects of legume-cereal intercropping on SOC stocks varied widely (Fig. S2). After three years of intercropping alfalfa in a monocrop *Poaceae* species pasture (Old World Bluestem, *Bothriochloa bladhii*) in a clay loam soil, changes in SOC and the soil C:N ratio were inconsistent (Bhandari et al. 2020). Similarly, Regehr et al. (2015) found that intercropping soybean with maize did not induce significant increases in SOC stocks or changes in the C:N ratio. Interestingly, Gong et al. (2021) observed significant reductions in mung bean rhizosphere total C when they were intercropped in a loam soil, independent of the N fertilization level (up to −22%). This effect may be due to an enhancement of the rhizosphere priming effect (RPE) induced by more diverse and abundant rhizodeposits during the active growth phase, which could then translate into an enhancement of the SOC status when larger time frames are considered (Yang et al. 2023a). If this hypothesis holds true, legume-cereal intercropping rhizodeposits could favor short-term soil organic matter mineralization in the rhizosphere, thus enhancing nutrient availability to plants. Therefore, different time and spatial frames could explain the variability of the effect.

The RPE pertains to the accelerated (positive priming) or reduced mineralization (negative priming) of organic matter, a process induced by microorganisms activated in the rhizosphere through easily available organic compounds released by living roots, known as rhizodeposits (Kuzyakov 2002). The mechanisms underlying the RPE are contingent upon the factors that limit microbial growth within a specific soil context. It is anticipated that the RPE will exhibit quantitative differences in intercropping systems compared to the sole cropping system, attributable to the increased and diverse rhizodeposition. According to the conceptual framework of the RPE, four primary mechanisms—stoichiometric decomposition, N mining, preferential substrate utilization, soil acidification, and chemical destabilization—could elucidate or predict the rate of the RPE (Kuzyakov 2002; Dijkstra et al. 2013; Favaro et al. 2025). In all these mechanisms, the availability of nutrients and C plays a pivotal role. The N mining mechanism is supposed to have only a marginal role during the growing season, since legumes are expected to provide enough N to soil microorganisms through rhizodeposition, especially N fixation (Wichern et al. 2007). Anyway, during the early phases of the establishment of the symbiosis with rhizobia, legumes and microorganisms might compete for soil mineral N, thus temporarily enhancing the N mining process in N-poor soils. The limitation for some other nutrient, such as P, might induce a similar effect (Xu et al. 2023). The stoichiometric decomposition process is anticipated to occur in scenarios where there is C, but not nutrient limitation for microbial communities. However, the diverse stoichiometry between rhizodeposits and rhizosphere microbial biomass causes nutrient limitation for microbes, which then uptake the limiting nutrients by degrading soil organic matter or newly added organic matter, potentially leading to a positive RPE. Soil acidification and chemical destabilization are expected to be the predominant mechanisms underlying the RPE, as rhizosphere acidification induced by legumes could consistently destabilize SOC, further stimulating the priming effect (Wang et al. 2016). According to the preferential substrate utilization theory, there could be a negative RPE effect. This theory posits that with higher nutrient availability, microbial N/nutrient mining is reduced, prompting microbes to shift from decomposing recalcitrant organic matter to utilizing labile root exudates for their C and energy needs. Consequently, the SOM decomposition could decrease with the input of root exudates. However, other factors, such as initial soil nutrient availability, soil type, soil pH, the C/N ratio of soil organic matter and the functional interactions between the roots and microbes of both plants, could significantly influence the overall RPE throughout the cropping cycle in an intercropping system.

The impact of legume-cereal intercropping on soil-atmosphere gaseous C exchanges is still not sufficiently clear. In particular, cumulative CO_2 emissions were not significantly different between a cover crop mixture mostly composed of *Poaceae* and its intercropping with legume forage species in the interrows of a citrus orchard (Castellano-Hinojosa et al. 2022). A pot study on sugarcane-soybean intercropping indicated no significant differences in soil respiration compared to the respective sole crops (Lian et al. 2019). These results indicate that CO_2 emissions were not stimulated under co-culture, although the C input to the soil via rhizodeposition was supposedly higher, given the additive design used. This might indicate more efficient C utilization for microbial growth compared to the sole cropping system. Net ecosystem productivity can also be consistently higher in intercropping, but crop combinations are pivotal in determining the outcome (Chapagain and Riseman 2015). The results of methane (CH_4) emissions are highly variable, and the intercropping effect might be determined by its interaction with pedoclimatic conditions (Gui et al. 2024). Overall, studies on C exchange rates in the soil-atmosphere system are scarce. However, the few studies available have shown a trend indicating no difference in greenhouse gas emissions between intercropping and monoculture systems. If related to the higher amounts of plant rhizodeposition and residues that reach the soil under intercropping management (Cong et al. 2015), this might actually suggest a net C sequestration. These trends fit well with the higher rhizosphere C input in intercropping systems and the tendency of SOC accumulation and microbial C Use Efficiency (CUE) improvement (Domeignoz-Horta et al. 2024).

Subsoil nitrogen and carbon pools

The extent to which co-cultivation systems can increase the subsoil C and N pools and their retention has not yet been fully elucidated. To address

this question, Yang et al. (2023a) conducted a long-term (11 years) experiment on the effects of maize-pea intercropping on N and C stocks in the soil profile up to a depth of one meter in a sandy loam soil. The results showed that intercropping with reduced N fertilization was more effective in preventing the depletion of soil N stocks than the full N fertilizer dose (300 vs 375 kg N/ha year). Furthermore, SOC stocks significantly increased in the whole profile by up to +22.9%, especially under optimal N fertilization conditions and at depths lower than 20 cm. Promising results were also obtained by Regehr et al. (2015), who reported an increase in gross N immobilization by 16% with maize-soybean intercropping compared to sole cereal in a loam soil, which contributed to the long-term sustainment of soil N stocks. The combination of crop types with different rooting patterns and traits could be the driving factor for explaining these trends (Homulle et al. 2022). However, there is limited knowledge about short-term subsoil C and N dynamics during a single growing season.

Overall, available studies on legume-cereal intercropping systems show that intercropping effectively influences the cycles of soil C and nutrients and, consequently, the nutrient uptake by plants. These systems alter essential plant nutrient cycles and enhance their storage capacity in soil, thereby contributing to the CPSF effect. However, extant research is insufficient to determine whether the positive effects of legume-cereal intercropping on soil edaphic properties are universally applicable across diverse pedoclimatic conditions and fertilization regimes. Despite these data limitations, the findings underscore the significance of soil physicochemical fertility in elucidating the CPSF effect in intercropping systems. Future investigations should encompass a broader range of environmental conditions and agricultural practices to assess the wider applicability and potential benefits of intercropping in enhancing soil fertility and agricultural productivity.

Alterations in diversity, structure, connectivity, and composition of microbial communities

Understanding the response of bulk and rhizosphere soil microbial communities in terms of composition, structure, diversity, and connectivity is essential for monitoring the short- and long-term impacts on the CPSF under crop diversification (Jain et al. 2020). This knowledge can aid in understanding the potential positive changes in soil multifunctionality that may arise from plant diversification (Chen et al. 2020). As a matter of fact, it might be hypothesized that more diverse and interconnected soil communities could harbor a greater functional redundancy that might be expressed even under adverse conditions.

At the microscale level, introducing legumes as a strategy to enhance the diversity of soil niches and microbial communities has shown promising results in certain experiments. For instance, intercropping soybean with sugarcane in a pot experiment resulted in significant increases in the α-diversities of bacterial and fungal rhizosphere communities in both crops as compared to monocultures (Lian et al. 2019). Jiang et al. (2024) demonstrated that rhizodeposit chemodiversity might contribute to the increase in the α-diversity of microbial communities, and a significant correlation with plant nutrient acquisition was observed. This phenomenon was not evident when examining the maize and soybean active rhizosphere bacteriomes, which exhibited a higher degree of specialization compared to sole cropping (Gao et al. 2024). Additionally, the co-culture treatment induced consistent alterations in the community structure, thereby confirming that the changes in the community assemblage were consistent. Similarly, Taschen et al. (2017) observed that the wheat-pea shared active rhizosphere bacterial community was consistently different from the two sole-cropped rhizosphere niches. The authors identified many of the more active species in the intercropping rhizosphere as growth promoting bacteria. However, the outcomes of indoor experiments cannot always be transferred to real-time farm conditions across diverse pedoclimates. Various environmental and edaphic factors can complicate the process of distinguishing crop-induced effects. For example, Yu et al. (2019) found that introducing soybean did not affect maize rhizosphere bacterial diversity under field conditions. Furthermore, in a field experiment Zhao et al. (2022b) discovered that peanut-maize intercropping had a positive impact on fungal richness and diversity in the legume rhizosphere, while it decreased in the cereal one. Liu and Gong (2022), focusing on proso millet-mung bean intercropping, showed strong differences of rhizosphere bacterial and fungal communities to sole cropping of either plant under different N fertilization

rates. In conclusion, more varied rhizodeposition patterns could sustain more diverse bacterial and fungal communities, but additional studies are required to understand the mechanisms driving the variable effects on their assembly under different pedoclimatic conditions.

One important impact of intercropping is the higher interconnectivity and network relations of the microbial communities (Jiang et al. 2024). Peng et al. (2024) discovered that the connectivity between fungal and bacterial communities is greater in millet-peanut intercropping than in either single crop, both in the rhizosphere and bulk soil, under drought stress and non-stress conditions. Notably, AMF play a crucial role in enhancing the stability of soil and root bacteriomes in wheat (Pathan et al. 2023). Thus, AMF host-colonization affinity might be a critical factor to consider when examining the effect of crop diversification on microbial community assemblage. These findings suggest that increasing the number of co-cultivated plant families could have a consistent effect on the stability of the soil bacterial and fungal communities.

The available evidence does not currently allow a clear prediction of how root-root interactions in legume-cereal intercropping systems will impact the composition of bacterial and fungal communities. Studies have shown mixed results on this topic. For instance, Gong et al. (2019) found that a higher availability of easily mineralizable organic compounds derived from legume rhizodeposition in a loam soil favors the proliferation of *Proteobacteria* in the cereal rhizosphere (up to 45% more abundant in relative terms), while the colonization by the order *Rhizobiales* was hindered (−19%). However, Taschen et al. (2017) and Qiao et al. (2024) observed opposite trends when studying the rhizosphere bacteriome of soybean and pea in the presence of maize and wheat intercropping, respectively, in a sandy clay loam and a loamy clay soil. This might be ascribed to the reciprocal influence of legume and cereal rhizodeposits on each other rhizosphere microbiota. The higher microbial availability of more diversified rhizodeposits with a supposedly lower C:N ratio in intercropping appears to stimulate diverse responses on *Actinobacteria* proliferation, since it was favored by the co-culture of pea and wheat (Taschen et al. 2017) and maize and soybean (Fu et al. 2019) but was hampered by proso millet and mung bean (Gong et al. 2019). These effects may be species-specific. In addition, pH may contribute to the impact of intercropping on the soil microbiota. For instance, the root-mediated rhizosphere acidification by legumes might stimulate the growth of *Acidobacteria* groups more efficiently than the sole cereal (Taschen et al. 2017; Gong et al. 2019), although this is not always the case (Fu et al. 2019).

Crop diversification often brings changes in the fungal community composition, but they are generally limited in scope and affect only a small number of taxa. A notable example is the sharp decrease in the relative abundance of *Mortierella* genus observed in the rhizosphere of maize intercropped with peanut in a brown loam soil, as compared to the sole cereal system (−59%) (Zhao et al. 2022b). However, changes at the phylum level were not consistent across different N fertilization levels to allow for clear patterns to emerge in the study conducted by Liu and Gong (2022). This shows that the plant-mediated recruitment of soil fungi might depend on soil N availability, implying a role of fungi for the uptake of this nutrient by plants. In addition, *Glomus_f_Glomeraceae* was found to be the most abundant AMF genus in both maize and soybean rhizospheres and roots in a black soil, and intercropping caused a consistent increase in its abundance in all four niches (soybean root and rhizosphere, maize root and rhizosphere), but the most significant enhancement was observed in the rhizosphere of soybean (+449%) (Zhang et al. 2020). Furthermore, the abundance of *Sordariomycetes* class was the only one that changed consistently in the proso millet rhizosphere when co-cultivated with mung bean (up to +30%) (Gong et al. 2019). However, the direction of these changes was dependent on the co-cultivation pattern. This could imply that the root distribution patterns in soil and the ratio of the different crops might shape the soil fungal community differently. Similarly, Erhunmwunse et al. (2023) found that *Didymellaceae* was the only fungal family consistently more abundant in the rhizoma peanut (*Arachis glabrata*)-bahiagrass (*Paspalum notatum*) bulk soil compared to the forage *Poaceae* sole crop. In summary, the current state of the art does not allow the identification of consistent effects of legumes or cereals on soil fungal community composition under intercropping, nor does it explain the driving factors and mechanisms behind.

Consequently, the investigation of soil microbial communities in legume-cereal intercropping systems has revealed complex interactions and variable outcomes across diverse pedoclimatic conditions. Although some experiments have demonstrated increased microbial diversity and interconnectivity in intercropped systems (Lian et al. 2019; Jiang et al. 2024), field studies have frequently yielded inconsistent results due to the possible confounding effects of numerous environmental and edaphic factors (Yu et al. 2019). The impact of intercropping on bacterial and fungal community composition appears to be context-dependent, with alterations often limited to specific taxa rather than broad phylum-level shifts. Notably, the effects were more pronounced in the bacterial community than in the fungal community. Despite the variability in outcomes, intercropping has demonstrated potential benefits, such as enhanced plant growth promotion (AMF fungi), reduced pathogen pressure (*Mortierella* genus), and improved nutrient mineralization (*Proteobacteria* and *Acidobacteria*). These findings underscore the significance of soil and root microbiome involvement in ecosystem multifunctionality when evaluating the CPSF. Future research should focus on elucidating the mechanisms driving microbial community assembly under diverse pedoclimatic conditions and their role in nutrient and C cycles. This knowledge is crucial for optimizing crop diversification strategies and enhancing sustainable agricultural practices across different environments.

Intercropping effects on microbial functionality related to nutrient and carbon cycles

Soil microbial functionality related to plant nutrients and C cycles is often regarded as a sensitive indicator for evaluating the broader-scale environmental impacts of soil management practices (Pathan et al. 2020). Hence, an understanding of the dynamic temporal changes in N and P cycling occurring under legume-cereal intercropping is needed to suggest optimal management practices, specifically concerning fertilization levels, since optimal doses generally vary in comparison to monocultures (Yu et al. 2016). Furthermore, cropping practices are highly influential towards soil C cycling, which is a key driver of soil biological fertility sustainability (Gentsch et al. 2020). Therefore, optimizing C cycling is vital for maintaining and improving ecosystem functioning.

Nitrogen cycling

Legume-cereal intercropping seems to be more effective in sustaining microbial N cycling compared to the respective sole crops, consistently reducing losses and increasing the temporal availability of N in the rhizosphere. For instance, Qiao et al. (2024) found that intercropping maize with peanut resulted in a 14% increase in N_2 fixation by free-living bacteria and archaea in the peanut rhizosphere. Moreover, the presence of cereal also enhances nodule N_2-fixation potential (Zhao et al. 2020). Additionally, when grasses and forage legumes were intercropped in a citrus orchard, Castellano-Hinojosa et al. (2022) reported higher abundances of *nifH*, *amoA*, *nosZI*, and *nosZII* genes in bulk soil compared to *Poaceae* and *Brassicaceae* mixture, which led to a reduction in the N_2O production potential. Therefore, cereal efficiency in utilizing soil N might underlie the enhanced N_2-fixation, operated by both free-living and symbiotic diazotrophic prokaryotes. However, intercropping soybean with maize (Yu et al. 2019), and *Medicago sativa* with *Dactylis glomerata* (Zhao et al. 2017) did not induce consistent alterations in the microbial N-cycling potential in soil and roots under field conditions or in a rhizobox experiment, respectively. Based on this evidence, it might be speculated that the plant-mediated shaping of the microbiome functional potential in soil might depend on its susceptibility to changes in management, whereas the root microbiome might be more strongly dependent on the plant phylogenetic identity. Zhang et al. (2024) observed that optimizing N dynamics through co-culture led to a 14 and 20% cumulative reduction in N_2O emissions in intercropped maize and soybean strips as compared to the respective sole crops under 80 kg N/ha for maize and 40 kg N/ha for soybean. In addition, soybean increased the N availability of the cereal counterpart by 30 kg N/ha under tested field conditions. The reason for this might be the increased soil N use efficiency of the cereal when intercropped with the legume. Lastly, Chen et al. (2018) observed that only the interaction between N fertilization level and crop type can result in consistent changes in the

nitrification and denitrification potential in the common rhizosphere of intercropped maize and peanut. These studies demonstrate that microbial transformations of N in soil are the basis for the observed advantage in N acquisition by crops, as they underlie the reduction of losses in field conditions. However, the net advantage compared to sole cropping depends on the N fertilizer application rates.

The functional capacity of soil microbial communities in terms of N cycling enzyme activities, typically changes noticeably between the sole and intercropping systems. According to Gong et al. (2019), intercropping with mung beans significantly increased urease activity by approximately 37.5% in the millet rhizosphere compared to the rhizosphere under sole cropping. Similarly, Chen et al. (2018) observed a 24% increase in urease activity in the maize rhizosphere when intercropped with peanut compared to both sole crops with reduced N application by either 30% or 40% compared to the standard commercial dose (200 kg N/ha) in a sandy loam soil. In addition, leucine aminopeptidase activity was significantly stimulated in intercropped broomcorn millet, but not in the mung bean rhizosphere (Gong et al. 2021). Furthermore, peanut-maize intercropping showed the potential to reduce denitrification in terms of nitrate reductase activity, which may impact N losses. This was also associated with reduced protease activity, which partly collides with the hypothesis of a higher RPE due to N mining under intercropping with legumes. The reason might be that the chemical composition of rhizodeposits changes with the plant phenological stages (Sokol et al. 2022), thus regulating the N input to rhizosphere microbial communities and their functional potential. Anyway, only one sampling time was considered in this study. A similar trend in nitrate reductase activity was observed when pea was intercropped with maize in the long term (Yang et al. 2023a). These changes in N-cycling enzyme functional capacity are associated with consistent enhancements in the soil MBN pool in both bulk and rhizosphere soil (Fig. 3) (Wichern et al. 2007; Scalise et al. 2015; Bhandari et al. 2020; Gong et al. 2021; Liu and Gong 2022). Liu and Gong (2022) found that MBN was the most effective N fraction in sustaining the functional potential of soil enzymes. Therefore, co-cultivating legumes and cereals could potentially sustain a more closed soil N cycling, consequently leading to a more efficient utilization by plants and reduced losses. This could occur primarily by enhancing the utilization of organic and inorganic N sources in the rhizosphere of cereals while the legume N_2-fixation potential is directly (symbiotic) and indirectly (non-symbiotic) promoted.

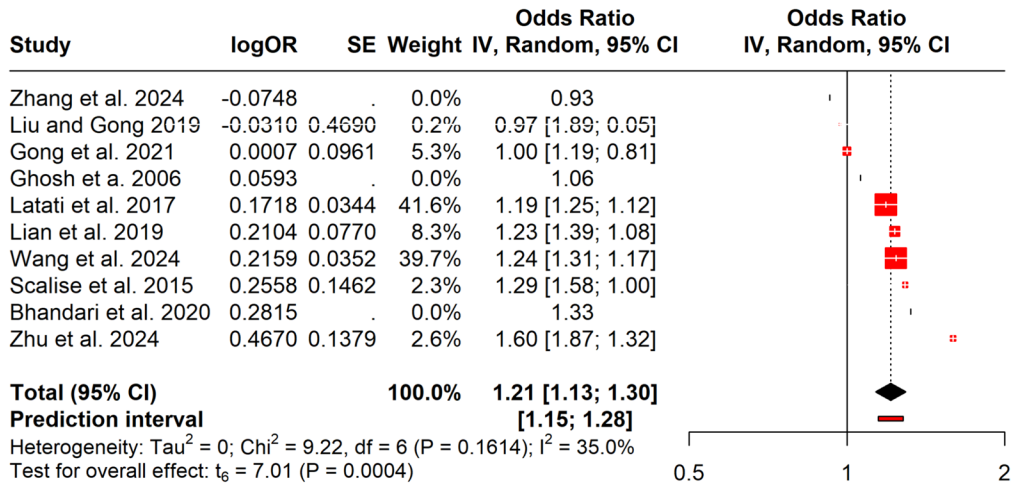

Fig. 3 Forest plot summarizing the effects of intercropping legumes and cereals on the microbial biomass nitrogen (MBN) abundance in soil based on the examined literature. OR indicates the odds ratio, SE represents the standard error, CI represents the confidence interval, and IV indicates the inverse variance

Phosphorus cycling

Although legumes are widely recognized to possess the ability of improving P availability for cereal intercrop partners, the microbial P dynamics underlying this process remain unclear. A study by Wang et al. (2023b) shed some light on this issue by demonstrating that soybean-induced changes in the maize rhizosphere microenvironment resulted in a significant enhancement of the microbial solubilization potential of P resources under optimal P fertilizer application. The bacterial *phoD* gene was identified as a crucial determinant of the P status improvement in maize rhizosphere, and alkaline phosphatase activity was found to be approximately 33% higher in maize rhizosphere when intercropped with soybean compared to sole maize grown in a slightly alkaline soil under field conditions. However, inconsistent differences were observed in the intercropped soybean rhizosphere compared to the respective sole crop. Bargaz et al. (2017) observed a consistent reduction in acid phosphatase activity in the soybean rhizosphere when intercropped with wheat in a rhizobox experiment in a P-poor soil (by up to 30%), but no significant changes were observed in the wheat rhizosphere. Further evidence supporting this phenomenon comes from Tang et al. (2016), who found that legumes can support higher microbial biomass phosphorus (MBP) in P-depleted-soil conditions under faba bean-wheat intercropping (+185%). Competition between microbes and plants for P might explain why this effect was not observed in the plant-available P fraction. Anyway, MBP is considered a soil P pool that is rapidly mineralizable and consequently utilizable by plants over short time spans (Sokol et al. 2022). A similar result was reported by Gong et al. (2021), who found that the millet rhizosphere MBP status was enhanced by introducing mung bean, with minimal negative impacts on microbial P availability in the legume rhizosphere under four different N levels. Additionally, the co-cultivation resulted in a significant reduction in the organic N: organic P mineralization potential in the cereal rhizosphere, as measured in terms of enzymatic activity (Gong et al. 2021). Hence, the legume rhizosphere microenvironment appears to favor optimal conditions for microbial P mobilization, but the potential extent depends on the overall soil P availability. Therefore, rhizosphere microbes play a pivotal role in regulating P availability to plants in the rhizosphere, usually resulting in improved nutrient availability for cereals when intercropped with legumes.

Carbon cycling

Multiple microbial functional traits must be evaluated to improve our understanding of the plant-microbial dynamics underlying changes in the soil C status. For instance, when intercropped, soybean and sugarcane demonstrated significant stimulation capacity of the prokaryotic C fixation and tricarboxylic acid cycle, although lipid metabolism was significantly reduced in both crop rhizospheres, based on phylogenetic identity functional prediction (Lian et al. 2019). Additionally, plant biomass degrading fungi were favored by the co-cultivation in the soybean rhizosphere, further supporting the hypothesis of enhanced biomass nutrient recycling from rhizodeposition. However, mung bean and broomcorn millet rhizosphere β−1,4-glucosidase and β−1,4-N-acetylglucosaminidase activities were not consistently affected by the co-cultivation under three N fertilization levels (Gong et al. 2021). Nevertheless, the potential availability of N and P per unit of C was significantly reduced for soil microbes. Gong et al. (2019) also observed that co-cultivating mung bean with proso millet led to a marked increase in invertase activity in the cereal rhizosphere, but only under specific crop proportions (4:4 and 2:4 proso millet to mung bean ratios). Therefore, these findings imply that the introduction of legumes in cereal sole culture can shape the microbial biochemical potential related to C cycling, possibly resulting in enhanced C acquisition.

Considerable evidence suggests that this might be the case. In fact, the lower C:N ratio in rhizosphere deposits of legumes compared to cereal, along with the higher C inputs may promote C acquisition by microbial communities in intercropping, as the more abundant inputs are not reflected in increased CO_2 emissions (Lian et al. 2019; Castellano-Hinojosa et al. 2022). This is supported by the studies conducted by Latati et al. (2017) and Bhandari et al. (2020), who observed increases in microbial biomass carbon (MBC) between 8 and 41% under intercropping compared to the respective sole crops under different pedoclimatic conditions (a clay soil in a Mediterranean climate, and a sandy soil in a semi-arid climate,

respectively); however, the effect of intercropping on durum wheat rhizosphere MBC were inconsistent when co-cultivated with faba bean (Tang et al. 2016) or even slightly negative under broomcorn millet and mung bean (Gong et al. 2021) under field conditions (Fig. S3). These differences, based on the crop species combination, might be related to the changes in rhizodeposit inputs based on the spatial distribution dynamics of the photosynthetic canopy (Gentsch et al. 2020). Furthermore, microbial necromass C was significantly increased in long-term (11 years) maize intercropping with soybean between 4.9% and 15.3% along with the total SOC pool in a sandy loam soil (Zhu et al. 2024), and it was recognized as a key driver of positive co-occurrence microbial network interactions (Zhao et al. 2023). In addition, fungal necromass C is a fundamental SOC pool to explain the increase in soil C stocks (Zhu et al. 2024). To test the hypothesis that intercropping can improve the C acquisition patterns of soil microbial communities, future studies should evaluate CUE under legume-cereal intercropping in relation to the other soil C fractions by targeting different phenological stages and crop combinations, in order to shed more light on the work done by Domeignoz-Horta et al. (2024). A particular focus should be on dissolved soil organic C abundance, which might be one of the most accessible pools for microbes that could drive the shifts in MBC after short-term changes in cropping practices (Zhu et al. 2024). Overall, more diversified rhizodeposition patterns could be the key variable on which the research attention should focus to favor C acquisition by rhizosphere microbial communities, although the outcomes might be different in soils with contrasting edaphic properties. These changes in the C metabolism of the soil microbes are expected to shape the companion crop performance, due to the concurrent variations of mineral nutrient availability to plants, thus contributing to general CPSF effect.

To summarize, intercropping systems involving legumes and cereals show considerable promise in enhancing soil microbial functions related to microbial nutrient cycling and C transformation processes (Fig. 4, Table S1). This agricultural approach consistently boosts N cycling efficiency, minimizes N losses, and increases N availability in the rhizosphere over time. The system also exhibits the potential for improving P accessibility through microbial-mediated processes, especially in soils where available P is scarce. Intercropping also affects C cycling by modifying the microbial community structure and activities associated with C acquisition and use. The literature suggests that strong synergy exists between the quality and quantity of intercropping residues, rhizodeposition patterns, and rhizosphere microbiome and necromass (Zhao et al. 2023; Zhu et al. 2024; Domeignoz-Horta et al. 2024). These factors might consistently affect microbial CUE, thus affecting SOC stability and abundance. The combined effects on these different biogeochemical processes contribute to enhanced soil fertility and, potentially, more sustainable crop yields. However, the extent and reliability of these advantages fluctuate based on factors, such as crop type, soil conditions, and management strategies. Future studies should concentrate on uncovering the plant-initiated mechanisms driving efficient nutrient acquisition and elucidating their impacts on microbial CUE. These insights will be essential for maximizing the beneficial effects of crop CPSF in intercropping systems, ultimately supporting the sustainable intensification of agricultural production and the improvement of soil health.

The observed effects of improved nutrient acquisition by plants and the consequent increase in crop performance in legume-cereal intercropping are sustained by consistent changes in soil physicochemical properties and the functionality of microbial communities. The improved symbiosis with rhizobia and AMF sustains the N_2 fixation and promotes the transfer to cereals, resulting in reduced losses. Cereals further benefit from the higher P mobilization operated by legumes. The short-term soil organic matter mineralization due to a possibly more consistent priming effect is not associated with higher CO_2 emissions, but with larger microbial and deep-soil C and N pools. Microbial communities under this multicropping system are usually more diverse and interconnected, and their functionality is much higher, resulting in improved N, P and C cycling, and K and micronutrients availability. Therefore, legume-cereal intercropping is expected to be a promising solution to enhance soil multifunctionality while providing higher yields per hectare with reduced inputs. Specifically, the functionality of soil microbial communities is the main mediator of the positive effects imputed to legume-cereal co-culture. The effective management of soil multifunctionality is only possible through the study and the understanding of how

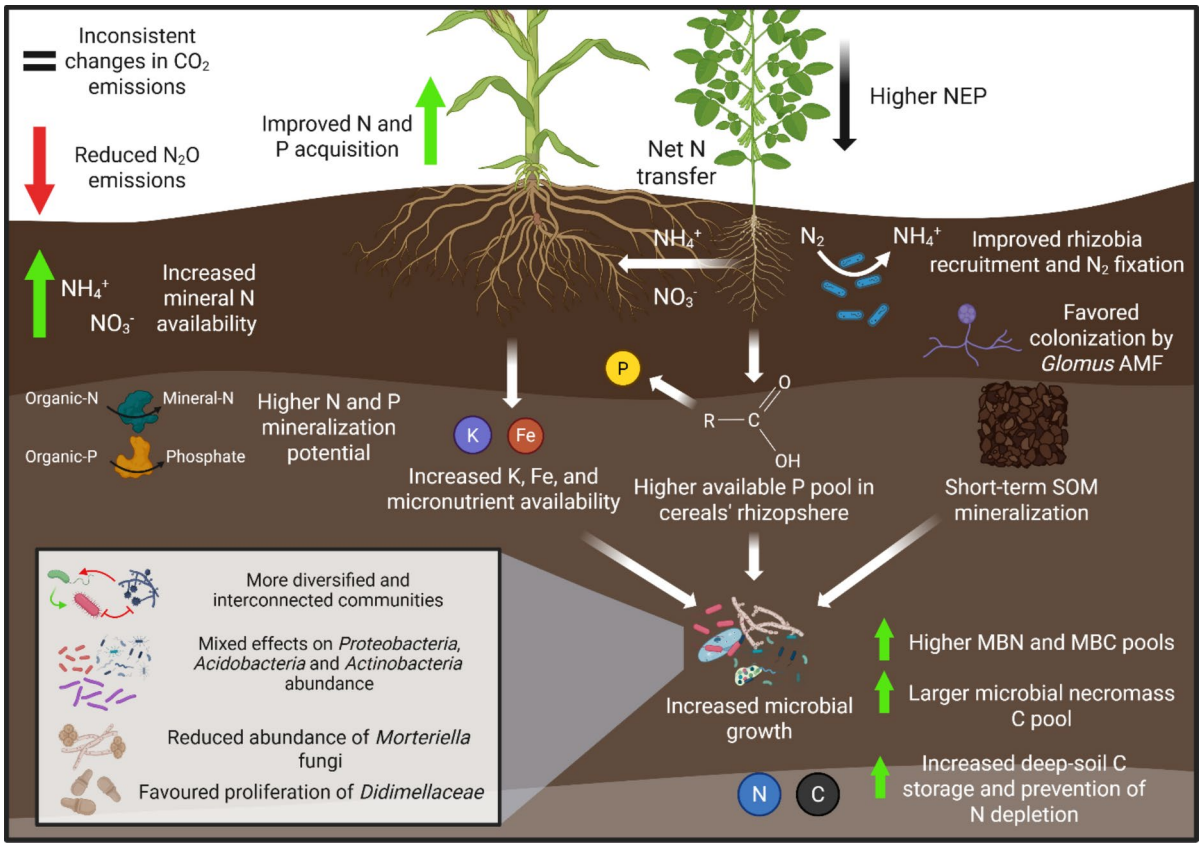

Fig. 4 A summary of the state-of-the-art of legume-cereal intercropping effects on soil biogeochemical cycles of nutrients and carbon, and soil microbial dynamics. The observed effects of improved nutrient acquisition by plants and the consequent increase in crop performance in legume-cereal intercropping are sustained by consistent changes in soil physicochemical properties and the functionality of microbial communities. The improved symbiosis with rhizobia and arbuscular mycorrhiza fungi (AMF) sustains the N_2 fixation and promotes the transfer to cereals, resulting in reduced losses. Cereals further benefit from the higher P mobilization operated by legumes. The short-term soil organic matter (SOM) mineralization due to a possibly more consistent priming effect is not associated with higher CO_2 emissions, but with larger microbial and deep-soil C and N pools. Microbial communities under this multi-cropping system are usually more diverse and interconnected, and their functionality is much higher, resulting in improved N, P, and C cycling, and the increased availability of K, macro-, and micronutrients.

microbial metabolism changes under diverse management strategies in arable soils. The CPSF theory is expected to provide a framework for interpreting the effects of growing different plant species adjacent to one another.

Major knowledge gaps and proposed future research directions

The current understanding of crop diversification-induced CPSF remains incomplete, particularly regarding the long-term effects of legume-cereal intercropping on subsequent crops in terms of soil fertility and health. This is an important area of study, as the question is how the large-scale implementation of these intercropping systems could fit in a crop rotation context. Therefore, finding the optimal crop sequence would be beneficial in maximizing the intercropping-induced changes in soil multifunctionality. For instance, the effects of reducing the total crop residue C:N ratio, and increasing their diversity compared to sole cereal cultivation have only been marginally studied on small scales so far. In particular, it is expected that its implementation in a crop rotation sequence could result in a more efficient

nutrient cycling and a reduction in greenhouse gas emissions when the succeeding crop is cultivated. Research on the influence and utilization of C by soil microbiota may provide a link between the changes in plant community composition and the structure of the soil microbial communities. Furthermore, relating microbial CUE to net ecosystem productivity could help to effectively capture alterations in microbial C cycling and soil C storage potential after short-term management changes in arable soils. Given these considerations, it is necessary to focus future research on optimizing the biochemical functionality of microbial communities to sustain arable soil fertility and health under biodiverse cropping systems.

Some key points of the CPSF still remain unexplored in the context of legume-cereal intercropping systems. The limited availability of data has prevented a comprehensive examination of this topic. Future research should aim to provide a more holistic understanding. To the best of our knowledge, no studies have investigated the effects of legume-cereal intercropping on root-associated microbiome structure, and only very limited knowledge exists on its cycling potential of nutrients and C. It will be even more challenging to understand the soil and root microbiome relationships with rhizodeposition and root metabolites. In addition, the biogeochemical functionality of archaeal communities in arable soils has largely been overlooked. The same is true for the abundance and spread of soil-borne plant pathogens. One of the most pressing knowledge gaps is the need to clarify the relationship between biological and physicochemical soil multifunctionality, crop performance and yield. As a matter of fact, the soil multifunctionality approach could be one of the best strategies to capture the multifaceted CPSF under a complex environment such as field conditions. To address this, multidisciplinary research efforts should be directed towards experimental conditions that realistically simulate the field environment and incorporate a broader range of variables within the CPSF effect.

Conclusions

Overall, the existing literature on soil biogeochemical cycles of nutrients and C, and microbial dynamics under legume-cereal intercropping highlights many advantages over traditional sole cropping systems. These are the more closed N cycling, the improved soil P availability, the higher levels of microbial functionality, and the resulting enhanced nutrient acquisition for plants. However, some of the parameters investigated, such as C cycling and microbial biodiversity and assemblage, showed contrasting responses under diverse pedoclimatic conditions. One of the reasons might be the lack of studies with comparable crop species combinations across different pedoclimatic zones. This highlights the need for further studies to be conducted with diverse legume-cereal combinations across different cropping regions. In doing so, a broader consideration of the provisioning of ecosystem services by soil should be accounted for through the investigation of soil multifunctionality. Therefore, future studies should therefore implement a multidisciplinary approach considering hetero- and conspecific mechanisms of interactions among plants, contributing to what is herewith identified as the CPSF effect. The CPSF in legume-cereal intercropping systems offers a potential for introducing the principles of agroecology to current agricultural practices. We argue that the strong overyielding effect together with the higher resource use efficiency of intercropping systems could be attributed to a positive CPSF. To establish intercropping as a mainstream agricultural practice, we advocate for stronger dissemination activities to farmers, stakeholders, and policy makers to create incentives for greater support through agricultural subsidies.

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Declarations

Competing interests The authors declare that they don't have any competing interests.

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