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Soil microbiome interventions for carbon sequestration and climate mitigation

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ABSTRACT Mitigating climate change in soil ecosystems involves complex plant and microbial processes regulating carbon pools and flows. Here, we advocate for the use of soil microbiome interventions to help increase soil carbon stocks and curb greenhouse gas emissions from managed soils. Direct interventions include the introduction of microbial strains, consortia, phage, and soil transplants, whereas indirect interventions include managing soil conditions or additives to modulate community composition or its activities. Approaches to increase soil carbon stocks using microbially catalyzed processes include increasing carbon inputs from plants, promoting soil organic matter (SOM) formation, and reducing SOM turnover and production of diverse greenhouse gases. Marginal or degraded soils may provide the greatest opportunities for enhancing global soil carbon stocks. Among the many knowledge gaps in this field, crucial gaps include the processes influencing the transformation of plant-derived soil carbon inputs into SOM and the identity of the microbes and microbial activities impacting this transformation. As a critical step forward, we encourage broadening the current widespread screening of potentially beneficial soil microorganisms to encompass functions relevant to stimulating soil carbon stocks. Moreover, in developing these interventions, we must consider the potential ecological ramifications and uncertainties, such as incurred by the widespread introduction of homogenous inoculants and consortia, and the need for site-specificity given the extreme variation among soil habitats. Incentivization and implementation at large spatial scales could effectively harness increases in soil carbon stocks, helping to mitigate the impacts of climate change.

KEYWORDS microbial communities, climate change, soil organic matter, inoculants, soil health, plant growth promotion, soil carbon stocks, soil transplants

Climate change poses one of the greatest challenges of the 21st century, demanding innovative and effective solutions across all sectors of society. Among the various strategies, soil microbiome interventions have emerged as a potential strategy to mitigate the impacts of climate change (1, 2). The soil microbiome—the ensemble of bacteria, fungi, archaea, protists, and viruses, and their activities within a soil habitat—plays a pivotal role in the health, structure, and fertility of the soil (3–7). Soil microorganisms are potent actors in climate-relevant processes via their influence on soil carbon turnover and sequestration, along with their consumption and production of greenhouse gasses (GHGs) (Fig. 1). Leveraging soil microbial activities to increase soil carbon stocks may thus be a promising strategy, but it is not one without challenges. Processes in the soil microbiome have complex biogeochemical feedbacks (8), which are dependent on geography and history (9), and are inherently linked with plant biodiversity (10). Soil microbiome interventions may be particularly relevant in disturbed sites

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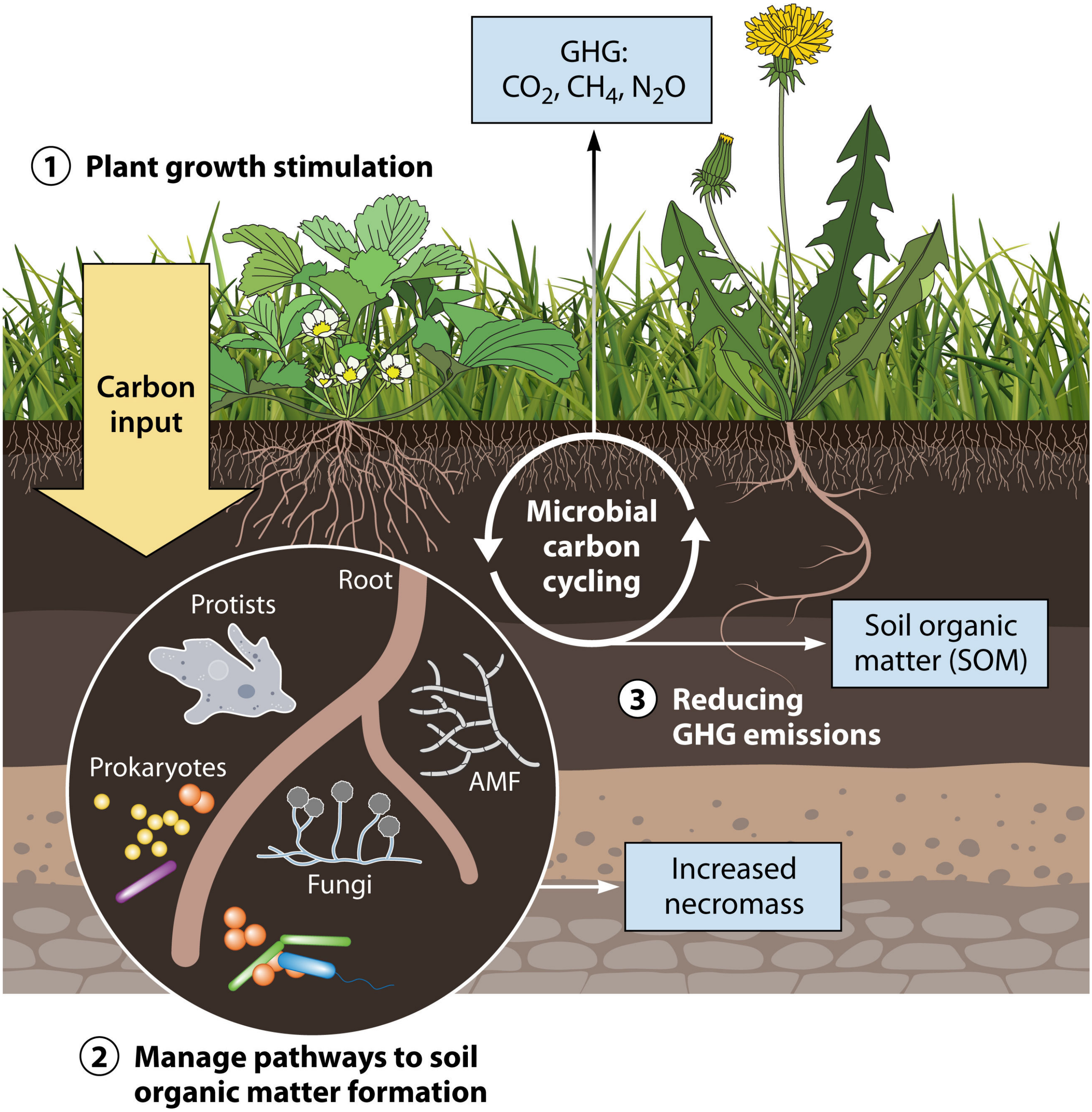


FIG 1 Soil climate-relevant processes and leverage possibilities for microbiome interventions. Most of the carbon input into soils comes from plant-fixed carbon with augmentation by autotrophic microorganisms. Carbon use efficiency determines how much of the carbon inflow is either converted by microbial activity to microbial biomass and longer term sequestered carbon, or recycled back to the atmosphere in the form of respiration products (CO_2, CH_4, and N_2O—as being a product from organic carbon respiration under anoxic conditions; GHG, greenhouse gases). Three possible areas for soil microbiome intervention: (1) plant growth stimulation (more primary carbon input), (2) manage pathways for soil organic matter (SOM) transformations and increase necromass formation—leading to longer SOM residence times (AMF, arbuscular mycorrhizal fungi), and (3) reduction of greenhouse gas emissions: CO_2, CH_4, and N_2O.

(11) because they may help replenish soil organic matter (SOM) and reverse the effects of soil degradation (12). Promoting soil microbiome stewardship has the potential to simultaneously increase soil health, plant productivity and augment soil carbon stocks (2). However, if we are to leverage microbial processes to boost soil carbon sequestration

or curb GHG emissions, we need to accurately identify what is possible in any given context, what time-scales are relevant for successful interventions, what fundamental and practical constraints exist, and where the greatest uncertainties lie.

TARGETS FOR SOIL CARBON MANAGEMENT

Near-term approaches are urgently needed to prevent further increases in, and eventually reduce, atmospheric GHG levels and minimize undesirable scenarios predicted by climate models. Global soils hold significant potential to mitigate part of the GHG off-set in the atmosphere. The soil off-set was estimated at 13.5 ± 2.9 Pg of the 36.3 Pg global CO_2 emissions from fossil fuels and industry in 2023 (for comparison, 10.3 ± 1.5 Pg is being captured by the global ocean; http://globalcarbonatlas.org). Compared with the global SOM pool of ca. 1,500 Pg C (in the top 1 m, 130 million km^2 soil), this seems a small proportion, but standing SOM stocks are outcomes of multiple processes of (slow) accrual, turnover and loss, and vary greatly with geography (13, 14). Relatively straightforward and rapidly implementable improvements in soil management practices, such as reduced tillage, use of cover crops, and erosion control, could help to replenish soil carbon stocks by 2–5 Pg (13). Since many soils have lost part of their SOM as a result of poor management, as much as 1.8 PgC in additional C removal may be achieved annually over the next 20 years with continued SOM sequestration (14, 15). Soil microbiome interventions have the potential to enhance this contribution even further by altering microbially catalyzed processes to achieve net increases in organic carbon stocks in soils (16).

The general concepts of the soil carbon cycle and sinks are well understood (Fig. 1). However, there are many unresolved intricacies and feedbacks (17) that limit our capacity to rationally design interventions that involve the soil microbiome. First, important questions remain about the processes that impact the proportion of plant-derived carbon inputs that are converted to SOM versus the amount that is transformed into CO_2, CH_4, or other volatile C-compounds that can escape back into the atmosphere (18–20). Second, the precise roles of individual microbial species and guilds and their activities and products during the turnover and formation of SOM remain unclear (21–23). Third, SOM itself is an extremely complex mixture of organic compounds that can be protected from microbial decomposition through various chemical, physical, and biological processes with distinct efficacies and vulnerabilities (24, 25). Below, we discuss some of these knowledge gaps, the potential for addressing them to enable microbiome interventions, and how these interventions might be designed based on prior experience and insights from other microbiome-related fields. Ultimately, enhancing soil carbon stocks through microbiome interventions needs to be part of a broader climate strategy that includes both reducing GHG emissions and adopting carbon capture technologies, some of which may again involve the soil as a vault for carbon burial (26).

AREAS OF INTERVENTION FOR SHIFTING THE SOIL CARBON BALANCE

Given the current understanding of the soil carbon cycle, microbially catalyzed processes could be altered to a net increase in carbon stocks or reduction of GHG emissions in three ways (Fig. 1): (i) utilize microbes to increase carbon inputs from plants, (ii) promote microbially mediated pathways that enhance the formation of SOM and reduce its turnover, and (iii) reduce microbial production of GHGs that are more powerful than CO_2, primarily methane and nitrous oxide (N_2O).

Increase the carbon inputs from plants

The major source for carbon input into the soil is through biological carbon fixation mediated by plants (8), and further by autotrophic (or mixotrophic) soil bacteria (27). Plant inputs consist of litter from above-ground tissues (stem and leaves), decaying roots, and mucilage, exudates, and root-associated microbial products collectively referred to as rhizodeposits. In recent years, rhizodeposits have received significant attention because they were identified as greater contributors to carbon inputs in many soils than above-ground tissues (28). Rhizodeposits provide a major conduit of carbon into deeper soils and include sugars, amino acids, and various other organic acids from root exudates. These serve as crucial energy and carbon sources to support catabolic and anabolic processes of soil microorganisms and shape both root-associated bacterial and fungal communities (29, 30). Exudates promote growth of microbial biomass, the dead remains of which can contribute to SOM formation and thereby increase soil carbon stocks (31). However, root carbon inputs in general, and exudates in particular, can undermine carbon stocks by stimulating microbial activity and associated SOM decomposition (the so-called "priming" effect), returning carbon to the atmosphere in form of CO_2, CH_4, or other volatile C compounds (32).

Microbiome interventions to increase plant inputs could be integrated with existing agronomic approaches, including cover crops and crop rotations to increase carbon stocks in deep soil, and crop breeding for increased root-to-shoot biomass, rooting depth (33), or root surface area (34). For example, recent plant breeding advances show that it is possible to stimulate the production of compounds like suberin, which generally have long residence times in the soil (35), suggesting the possibility of intentionally modulating root compounds to alter the composition of root-associated microorganisms. A direct microbiome intervention would be the application of microbial inoculants to stimulate plant growth or combat disease. For example, arbuscular mycorrhizal fungi (AMF) inoculants can promote plant root growth and increase soil carbon stocks (36, 37). Similarly, bacterial inoculants can enhance plant-derived carbon inputs into the soil and can do this without counter-productive increases in microbial respiration (38). Strain inoculation can also affect the C:N ratio in plant tissue (38), or influence soil nitrogen transformations, with potential secondary effects on soil carbon metabolism (39). Moreover, the application of plant growth-promoting microorganisms has also been shown to change the composition and the quantity of root exudates (40–42).

Many aspects of microbial metabolism of root exudates remain poorly understood. Elucidating the mechanisms by which plant growth-promoting microorganisms influence both root exudation and the metabolic activities of the soil microbial community is challenging due to the confounding impacts of plant root exudation and microbial metabolism on the exudate metabolome and to technical limitations in quantitative exudate chemistry (43). Additional unresolved questions include which microbial species are most relevant to the formation and decomposition of SOM, and how these species impact plant carbon inputs and alter rhizodeposition. Also, how do changes in C:N availability influence microbial decomposition rates and thus litter persistence in the soil, and how this is depending on the type of plant cover (44). If and how microbial metabolism of root exudates impacts soil carbon stocks in the long term remain largely unknown.

Managing pathways to soil organic matter (SOM) turnover

A variety of processes contributes to long-term storage of the carbon contained in SOM. Recent models of the soil carbon cycle suggest that microbial carbon use efficiency (CUE, the ratio between biomass carbon gain and carbon loss by respiration) is a critical variable, with higher microbial CUE positively correlating with higher SOM levels (23). CUE is thus linked to SOM accumulation and designing interventions that favor microbial biomass growth rather than microbial respiration (i.e., increase the CUE) could thus represent a viable path for increasing soil carbon stocks. An example would be to reduce accessibility to external electron acceptors, favoring slow-growing bacteria or fermentative pathways. SOM is, however, complex and composed of different operational or functional pools: dissolved organic matter (DOM), particulate organic matter (POM), or mineral-associated organic matter (MAOM) (45). DOM contains soluble and relatively low-molecular-weight compounds that are in principle accessible for microbial uptake and metabolism. POM consists of plant and microbial tissues (e.g., cell walls and membranes) that have been fragmented and can be either free or trapped in soil aggregates and tend to have residence times of years to decades (46). MAOM consists of microbially transformed plant litter (19), dead microbial cells (necromass), or microbial breakdown products that are chemically bound to soil minerals (19, 47). These chemical associations render carbon compounds contained within MAOM inaccessible to microbes and their enzymes, resulting in residence times of hundreds to thousands of years (48–50). Other studies propose that decomposition rates should be considered from a spatiotemporal perspective, as they are influencedd by the probability of contact between microbes or their excreted enzymes and SOM (or MAOM), the chemical compound diversity and the metabolic investments by microbes (51).

In addition to promoting microbial biomass in soil through microbial growth, recent attention has focused on promoting the accumulation of microbial necromass, as this can contribute to persistent SOM (21, 52, 53). Microbial necromass includes dead cell residues, extracellular polymeric substances, and other microbial exo-metabolites (54). Microbial necromass may become inaccessible for metabolic transformation or respiration by other microorganisms because the cells are trapped inside soil pores or bound to mineral surfaces (55). Indeed, most microbial necromass appears to be found in MAOM (19), and this necromass is known to be a quantitatively important contributor to persistent SOM (24). Distinct cell death pathways may be responsible for differences in the composition and reactivity of the microbial necromass (21). For example, senescence, predation, and environmental stress lead to distinct chemical transformations that increase the cell wall-to-cytosol ratios, reduce nutrient contents, and deplete easily degradable compounds. These transformations result in microbial necromass that does not merely reflect the composition of living microbial biomass but represents a chemically altered state that contributes differently to SOM persistence (21). On the other hand, we know too little about actual growth, activity, and death of microbes in soils (56). Soil microorganisms are characterized by both rapid opportunistic as well as slow growers. High death rates, predation, infection, and persistence are all parts of evolved ecological strategies of individual microbial species and viruses/phages (57, 58). To turn necromass formation into a precision microbial intervention tool, we need to obtain a much clearer understanding of the intricacies of natural growth and death cycles in complex communities, and how these may be influenced by climate change (59).

Another approach that can enhance SOM formation is to encourage the production of microbial exopolysaccharides. These are important both as sequestered carbon and in the context of soil aggregation (7), as they help form micro-aggregates that more stably retain sequestered carbon (25). Microbial exopolymers are also important in the development of desert soil biocrusts (60), which stabilize soils and reduce erosion. AMF inoculants are of interest as they excrete glomalin, a protein known to promote MAOM and aggregate formation (61, 62). However, recent evaluations of AMF inoculants highlight the need for quality standards in the inoculant industry to fully realize the benefits provided by these microbes (63). Composting (64) could also be envisioned as process to control the conditions that favor biomass or necromass accumulation, and potentially enrich for refractory SOM while reducing GHG emissions. Compost material can subsequently be used to enrich soils for SOM, which is particularly beneficial for degraded soils (65).

Reduce pathways of microbial turnover that lead to GHG emissions

Microbial respiration is a general process leading to turnover of soil carbon to microbial biomass, byproducts, and gaseous end-products. A portion of the carbon input into soil is therefore released in the form of respiratory end-products, such as CO_2 or methane (CH_4). In addition, anaerobic carbon respiration leads to the formation of nitrous oxide (N_2O) when nitrate or nitrite is used as a final electron acceptor. Given that N_2O and CH_4 are GHGs even more potent than CO_2, though more short-lived, soil microbiome interventions targeting climate change mitigation should also aim to minimize their emissions. Depending on the context, this might be achieved by directly targeting microbial denitrification as well as methane oxidation and formation pathways, although few studies have attempted this. Sites with high CH_4 emissions may benefit from strategies that favor methanotrophic bacteria, which consume CH_4, or by outcompeting methanogenic archaea for substrate. As an example, drawing inspiration from natural processes observed in stratified lakes, inoculating with “cable” bacteria in rice-paddy soil microcosms stimulated the activity of sulfate-reducing bacteria, which effectively competed with methanogens for hydrogen and acetate, thereby reducing CH_4 emissions (66). Recently, successfully tested ideas to reduce N_2O emissions consisted of increasing the transformation rates of N_2O to N_2 by introducing specific nitrous oxide reducers into the soil, or by stimulating expression of the key catalytic enzyme, nitrous oxide reductase (NosZ), in resident denitrifiers (67–69). Because the activity of NosZ reductases in denitrifying bacteria often hinges on the availability of key nutrients, such as copper and vitamin B12 (70), the enhancement of these nutrients in targeted soils could be transformative components of bio-stimulation and bioinoculant interventions.

SOIL MICROBIOME INTERVENTIONS AND THEIR CHALLENGES

The processes and mechanisms listed above could potentially be deployable for redirecting soil microbial and ecological processes to a net increase in carbon stocks. However, how might this be achieved through soil microbiome management? Microbiome interventions in general have been defined as any method used to manage, alter, restore, rehabilitate, or engineer microbial community composition and its functional activity, promoting its stewardship (12, 71). These can take the form of direct interventions, such as introducing, inhibiting, or removing specific bacterial strains or consortia (72), applying phage (73), or introducing diverse taxa through soil transplants (74). They can also take the form of indirect interventions, such as managing the boundary conditions of the soil habitat to favor or suppress specific microbial-catalyzed processes. In the context of soil carbon management, microbiome interventions can be envisioned in each of the three domains defined above (Fig. 1), to enhance the ability of the soil to capture and store carbon and influence the microbial processes that regulate GHG emissions. The choice for where and how to intervene will depend on the soil and environmental context and the state or composition of the resident soil microbiota. Although few soil microbiome interventions have been specifically targeting soil carbon management to date (72), we can draw valuable insights from previous experiences and challenges encountered in other environmental, agricultural and human health contexts.

Microbial inoculants have long been used in agriculture and soil management. In the context of soil microbiome interventions, the use of inoculants can be described as the functional equivalent of human or animal probiotics (75). The intent of inoculants has been to enhance beneficial microbial-driven processes, such as nitrogen-fixation and plant growth promotion for crop production (76–79), grassland management (80), reforestation (81), xenobiotic compound degradation (82, 83), and inhibition of plant pests (84) and pathogens (85). The direct application of nitrogen-fixing rhizobia to leguminous plants has been practiced for more than 100 years (86), and since then, a wide range of microbial species have been deployed as soil inoculants (87). Mycorrhizal fungal inoculants are also widely used as biofertilizers and for restoring degraded or nutrient-poor soils (88). Meta-analyses of microbial inoculant studies indicate an overall positive effect on crop yields, with alleviation of abiotic stress, the use of native strains, and higher initial nutrient levels as the main contributing factors (89, 90). Still, the efficacy of many inoculants is highly variable (63, 90, 91), and we are only beginning to understand the ecological processes underlying the outcomes of these interventions (83).

One of the major general challenges in reshaping the soil microbiota is its enormous biomass and its high functional and taxonomic diversity (24). This complexity ensures a high level of functional redundancy, which results in the occupation of most nutritional and spatial niches in typical soil habitats (3, 92). Consequently, newly introduced microbial inoculants often fail to proliferate and persist, or to trigger microbiome responses (76, 83). The challenge to establishing an inoculant within a soil microbiome mirrors that for microbes consumed as probiotics in the human and animal intestinal tract, highlighting a phenomenon known as colonization resistance (93, 94). Moreover, recent studies have indicated that soil bacterial inoculants may leak metabolites during growth that inadvertently facilitate the proliferation of native soil microorganisms, thus disfavoring the inoculant via increased competitive pressure (83). Inoculants therefore must be carefully selected by evaluating both their proliferation potential and their interaction with, and potential impact on, the growth of other soil microbes. Also, selective carbon or nutrient niches could be engineered for inoculants to proliferate, persist and/or carry out their intended functions (72, 83, 95, 96).

Soil inoculants may not need to permanently establish in a community to provide benefits. Their transient presence or renewed introduction may be sufficient to affect an intended functionality, as observed with host-associated probiotics (75). For example, the presence of an inoculant on a seed during germination may be sufficient to allow root colonization and induce sustained plant growth benefits (97), alleviate environmental stress on plants, and improve plant nutrient quality (89). The biological significance of microbes to seed germination, seed health, and subsequent plant growth, coupled with the ease of introducing inoculants via seeds, has made seed coatings a common delivery mechanism for inoculants (98). On the other hand, even transiently present microbial inoculants can cause sustained shifts in the resident microbiota composition (99, 100), alter the complexity and network stability of the soil microbiome (90), and decrease nutritional niche breadth (101).

Rather than inoculants comprising individual or mixtures of cultured isolates, inoculants can take the form of microbiome transplants. Transplants have received heightened interest in soils as well as in host-associated microbiomes. Transplants may allow a poorly performing community to be seeded with a more diverse or better-performing community, which may recolonize and effectively "reset" the microbiome in the system (74). This approach parallels that of gut microbiome interventions in which fecal transplants from healthy donors are used to reset dysbiotic intestinal communities in patients suffering from recurrent infection with *Clostridiodes difficile* and/or from prolonged use of antibiotics (102, 103). One important difference, though, is that the colonization by fecal transplants is facilitated by emptying the intestine of most of its microbial content, whereas this cannot be done in the case of soils and soil transplants. Nevertheless, soil transplants, with or without isolation or enrichment for microbes with target functions, could potentially reset dysfunctional soil microbiomes or reconstruct microbiomes in soils with extremely impoverished microbiota (74, 104). Carefully controlled experiments will be essential to better understand the ecological processes driving the outcomes of soil transplants. This understanding will be critical for predicting their potential to restore degraded sites, given that such predictions are challenged by the extreme variability in soil habitats and the complexity of soil biological and chemical conditions.

OPPORTUNITIES TO LEVERAGE EXISTING MICROBIOME INTERVENTIONS TO ENHANCE SOIL CARBON STORAGE

How do we transform conceptual but sparse information on soil microbiome interventions into practical methods for significantly increasing soil carbon stocks at the global scale? At present, microbial inoculants or transplants are primarily used to promote plant productivity in croplands, grasslands, and forests, regenerate impoverished soils, and restore soil ecosystems. However, the impact of such interventions on soil carbon stocks is rarely monitored or even considered. We recommend refining these inoculants and transplant applications to simultaneously address the three broad microbial processes controlling soil carbon stocks (Fig. 1).

The same microbial inoculants used to promote plant productivity could indirectly stimulate soil carbon stocks by providing greater carbon inputs (101). Microbial inoculants, including AMF, can significantly improve plant growth in large-scale agriculture applications (36, 37, 105). A wealth of knowledge and experience has accumulated regarding the use of microbial inoculants to enhance plant productivity. For example, the optimal timing of inoculation for colonization success and functional outcomes, the influence of abiotic factors on inoculant physiology in the soil, and the effects of seasonal variation and agricultural practices have been characterized for many inoculants (106). Whereas many commercially available microbial inoculants contain generalist species found in most soil types (107), inoculant functions may be optimized with a better understanding of site- and plant host-specific effects (108, 109). Knowledge of the resident microbial community and expected microbe–microbe interactions might help guide appropriate introduced inoculant mixtures to avoid unproductive competition (83). Soil management practices may further help to overcome potential negative effects of abiotic factors, such as non-optimal pH, low moisture content, toxic compounds, or nutrient imbalances on inoculant effectiveness and long-term inoculant survival (110, 111).

The greatest opportunity for enhancing soil carbon stocks may be realized in marginal or degraded soils. The application of AMF is widely known to improve plant water and nutrient uptake in marginal soils, leading to increased biomass production and higher SOM content (36, 37, 112). However, soils can also be inoculated with diverse, native soil communities, such as via soil transplants, spores recovered from soils, or soil microorganisms that are recovered and regrown (113). Such native soil community-based inoculants were shown to increase ecosystem recovery by an average of 64% across the globe, translating directly to increases in primary production and soil carbon stocks (114). Using native species or transplants from nearby local environments for microbial inoculations may help to avoid the possibly damaging impacts of invasive species, maximize the beneficial impacts on ecological recovery, and translate to particularly effective microbiome interventions (101). Such procedures should be carefully considered, however, in order to minimize damage to the local environment from which the source soils are collected. Moreover, although regulations for the release of native species vary among countries, best practices and a unified, science-based and flexible framework for microbiome stewardship, as recently proposed for soil interventions such as transplants (12), are critical to minimize these risks.

UNKNOWN ECOLOGICAL RAMIFICATIONS OF MICROBIOME INTERVENTIONS

The use of microbiome interventions holds promise despite possibilities that many inoculants may fail to establish, survive, or function effectively following introduction into a new environment (83, 115). Similarly, although microbial inoculants and transplants may offer the greatest benefits to plant growth, soil health, and soil carbon storage in marginal or degraded soils, their successful establishment may be particularly precarious in these soils because of low fertility, poor physical structure, or extreme pH (116, 117) and may require simultaneous optimization of soil conditions, such as through amendments and other management tools. Successful inoculant deployment in any soil may be further altered by unpredictable weather events or the effects of land management practices, such as the application of pesticides and fertilizers, tillage and cover crops, or poor and poorly documented product viability (63). Collectively, these are manageable risks that can be studied in specific experimental setups, customized and tested at the pilot scale, and therefore optimized. However, the ecological ramifications of the targeted as well as widespread introduction of microbes into soils are largely unknown. Here, we highlight two such concerns.

First, introduced strains that overcome the challenge of competing with native microorganisms and establish in a soil may have negative impacts (118). These impacts include triggering the growth, activity, or altered behavior of native pathogens or parasites, or presenting an invasion threat due to unintended traits or functions (105). Over time, microbiome interventions could create new selective pressures that drive species evolution and ecological succession, potentially offsetting the intended benefits of the original inoculum or inducing the loss of beneficial ecosystem services (118). For example, a widespread introduction of a single synthetic consortium could lead to a regional loss of diversity, critical functional redundancies, and potential community resilience. Increasing our understanding of when a native microbial community is likely to be outcompeted or displaced by an introduced synthetic consortium is critical for anticipating, predicting, and ideally mitigating any potential long-term negative impacts of these microbiome interventions. These impacts may also be minimized by using restoration-based interventions that prioritize native microbial species or transplants (12).

Second, interventions in soil microbial processes may have unforeseen adverse effects due to our limited understanding of the mechanisms and pathways that govern and influence SOM turnover (Fig. 1). For example, we have only recently gained insights into a major microbial component of SOM with the finding that, in many soils, a significant proportion—up to 60%—of the cellular biomass is inactive or dead, particularly among fast-growing organisms (119, 120). How the complex slow dynamics of SOM formation are related to the diverse ecological strategies of individual microbial species in soils and to the feedbacks of predators on communities is currently unclear (57). Thus, interrupting these life-death cycles by inoculating fast-growing strains or stimulating necromass formation may have unpredictable impacts on microbial food webs in the soil and the residence time of the produced SOM. Again, studies exploring the potential impacts of inoculants and inoculant traits, such as changes in growth rates and CUE, on the soil metabolic interaction network and SOM formation are critical.

KEY RESEARCH QUESTIONS MOVING FORWARD

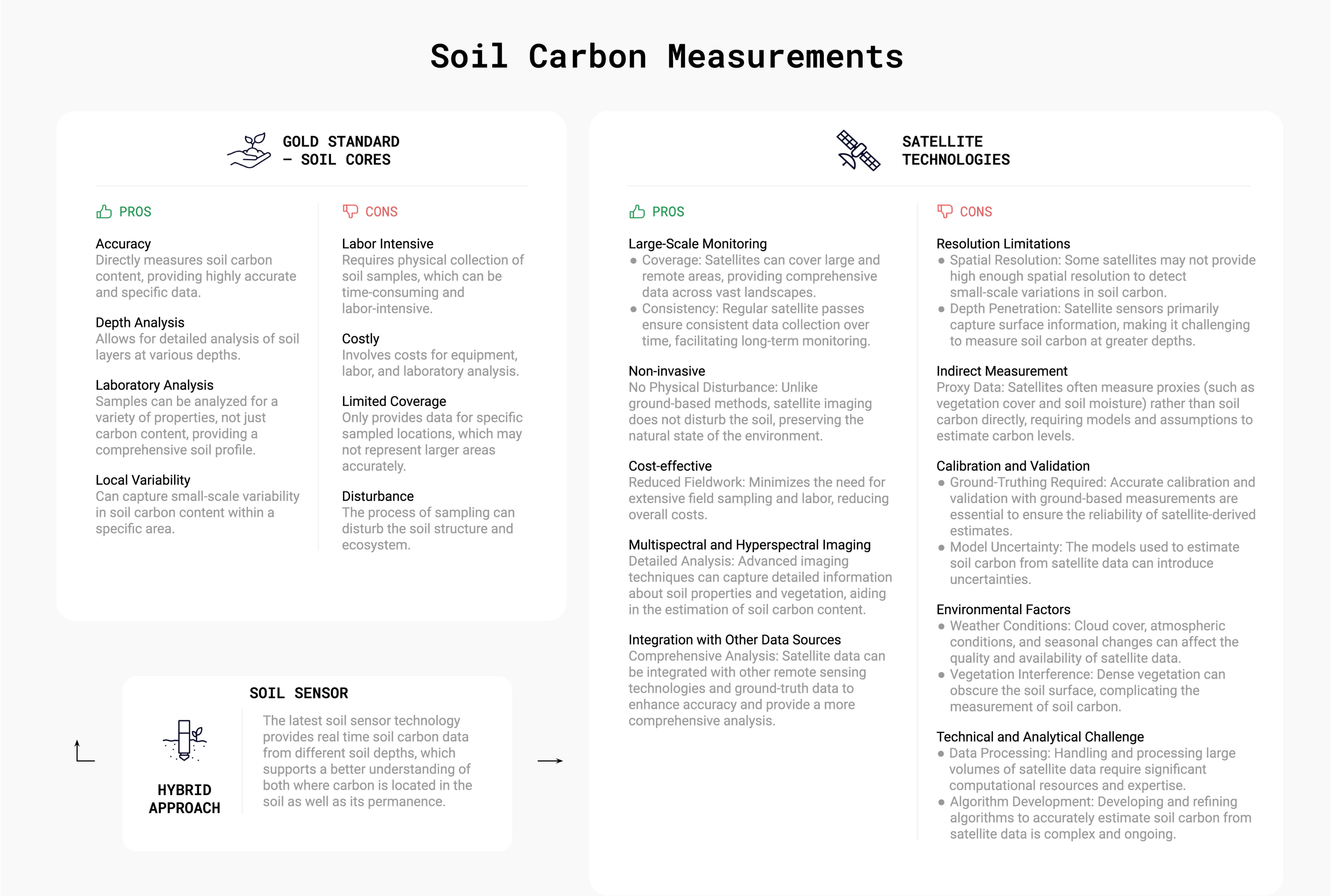
Addressing the knowledge gaps in soil microbiome interventions requires a multi-tiered approach that spans microscale laboratory settings to large-scale field studies. At the smallest scale, *in vitro* experiments offer controlled conditions to investigate the basic physiological and genetic responses of soil microbes when interacting with other microbes, plants, higher taxa in the soil, and varying abiotic soil conditions. These experiments are crucial for understanding the fundamental interactions that may influence microbial inoculant activities and their impact on SOM without the complexity of simultaneous exposure to a full range of uncontrolled environmental factors. Laboratory microcosm studies should also address the spatial distribution of inoculants in soils and in association with soil minerals, as the emergent habitat characteristics will dictate community assembly, establishment and interactions with plants, other soil microorganisms, and minerals, and ultimately, influence SOM formation and turnover (121). Some control may be exerted on inoculant distribution by recruitment to seeds and plant root exudates, or by interactions with other microbes, such as along fungi (122).

Experiments that scale up to greenhouse trials enable exploitation of a semi-controlled environment where edaphic factors such as moisture, temperature, nutrient levels and inoculant carrier can be manipulated, with control over the presence of extreme environmental variables. These studies can help refine our understanding of how inoculants interact with plants, other microbes, and soil characteristics under more realistic conditions. Ultimately, the effectiveness and practicality of microbiome interventions must be validated in field pilot trials that expose the inoculants to the full spectrum of environmental variability and land management practices. Field trials will be crucial to assess inoculant colonization and long-term survival, depth and spatial distribution, effects on resident soil microbiota composition, and the ecological impact of inoculants across different climatic and soil conditions, representing a key risk assessment step for microbiome stewardship (12). They can also provide data on how microbiome interventions affect carbon stocks on a landscape scale. In parallel to medical cohort studies where thousands of individuals need to be sampled longitudinally to find statistically meaningful correlations between gut or stool microbiome changes and treatments, such field studies will involve extensive spatial and temporal sampling, high levels of replication, characterization of intrinsic soil properties, and ideally, a standardized approach to facilitate subsequent meta-analysis. Realistically, the diversity of plant species (e.g., crops, trees, forage grasses) and the soils and climates they grow in are vast compared with a medical cohort, further illustrating the need for studies to identify controlling variables that predict the success of specific interventions at different sites. Thus, the research community should prioritize studies that offer the greatest simultaneous societal benefits, including plant health and productivity, soil carbon stock accrual, climate change mitigation, and sustainable ecosystem health.

Novel strategies to optimize inoculant survival and persistence may also be necessary. For example, a more detailed understanding of soil–microbe–plant interactions would facilitate the use of plants to create selective nutrient niches for inoculant growth (76). In addition, priming the soil system with nutrients or other organisms can alter nutrient niches and enhance the likelihood of colonization by introduced inoculants (123, 124). Inoculation strategies may also need to be tailored to specific soil conditions, which may include optimizing inoculation timing, selecting microbial strains suited to specific environmental conditions, and integrating microbial inoculants with sustainable land management practices. Deepening our knowledge on microbial physiology and metabolism during growth and non-growth stages will ultimately enable better design and formulation of microbial consortia for soil application. Finally, administering multiple inoculant doses, selecting for niche-specific carriers (pre- and symbiotics), and generating slow-release microbial formulations may help compensate for the inability of some inoculants to survive or proliferate in high numbers in the soil.

Knowledge of the biotic and abiotic conditions of the target introduction sites should be exploited to identify the optimal microbiome intervention strategy. In addition to characterizing the existing soil biodiversity and the nutritional, chemical, and physical specificities of that soil, the potential for net carbon storage at the site should be evaluated. This involves characterizing soil carbon pools, as well as the composition and functional potential of the soil microbiota at the start and during interventions (125–127). For example, a productive, stable agricultural soil ecosystem is typically rich in organic matter at different decay stages and maintains both taxonomically and functionally diverse microorganisms (5), whereas impoverished soils may lack these, and these contrasting situations may require different inoculation strategies. Interventions in productive systems may be limited to the addition of single inoculants or synthetic consortia targeting very specific underlying processes, such as curbing GHG production or reducing SOM turnover. In contrast, the absence of a functioning soil microbiome in impoverished soils may be a key limiting factor for their ecological recovery (114). Here, the use of soil microbiome transplants in conjunction with native pioneer plant colonizers could be a first step to rebuild soil SOM and, eventually, foster better plant productivity (128, 129).

Crucial for any intervention in soil carbon processes are reliable soil carbon measurements on a wider scale and over time (Fig. 2). Currently, this is typically done through destructive sampling, requiring time-consuming and expensive protocols in specialized laboratories (130). Consequently, these measurements lack the scalability required for both detailed local studies across various spatial and temporal scales and for extensive global studies, although international efforts are underway to increase the scale at which soils and predicted soil carbon are mapped (e.g., https://esdac.jrc.ec.europa.eu/projects/lucas). The success of microbiome interventions as a strategy requires that we have the measurement tools needed to demonstrate durable SOM formation in real-world field conditions, thus highlighting the need to develop reliable, high throughput measurement approaches. Similarly, the success of interventions requires the application of emission measurements to ensure that any increases in soil carbon stocks are not offset by enhanced emissions of other GHGs. Finally, computational models are essential to integrate data from diverse experimental setups to predict the outcomes of microbiome interventions under different scenarios. They are also needed to help in designing optimized soil management strategies to maximize carbon sequestration.



Soil Carbon Measurements

GOLD STANDARD – SOIL CORES

PROS

Accuracy
Directly measures soil carbon content, providing highly accurate and specific data.

Depth Analysis
Allows for detailed analysis of soil layers at various depths.

Laboratory Analysis
Samples can be analyzed for a variety of properties, not just carbon content, providing a comprehensive soil profile.

Local Variability
Can capture small-scale variability in soil carbon content within a specific area.

CONS

Labor Intensive
Requires physical collection of soil samples, which can be time-consuming and labor-intensive.

Costly
Involves costs for equipment, labor, and laboratory analysis.

Limited Coverage
Only provides data for specific sampled locations, which may not represent larger areas accurately.

Disturbance
The process of sampling can disturb the soil structure and ecosystem.

SATELLITE TECHNOLOGIES

PROS

Large-Scale Monitoring
- Coverage: Satellites can cover large and remote areas, providing comprehensive data across vast landscapes.
- Consistency: Regular satellite passes ensure consistent data collection over time, facilitating long-term monitoring.

Non-invasive
No Physical Disturbance: Unlike ground-based methods, satellite imaging does not disturb the soil, preserving the natural state of the environment.

Cost-effective
Reduced Fieldwork: Minimizes the need for extensive field sampling and labor, reducing overall costs.

Multispectral and Hyperspectral Imaging
Detailed Analysis: Advanced imaging techniques can capture detailed information about soil properties and vegetation, aiding in the estimation of soil carbon content.

Integration with Other Data Sources
Comprehensive Analysis: Satellite data can be integrated with other remote sensing technologies and ground-truth data to enhance accuracy and provide a more comprehensive analysis.

CONS

Resolution Limitations
- Spatial Resolution: Some satellites may not provide high enough spatial resolution to detect small-scale variations in soil carbon.
- Depth Penetration: Satellite sensors primarily capture surface information, making it challenging to measure soil carbon at greater depths.

Indirect Measurement
Proxy Data: Satellites often measure proxies (such as vegetation cover and soil moisture) rather than soil carbon directly, requiring models and assumptions to estimate carbon levels.

Calibration and Validation
- Ground-Truthing Required: Accurate calibration and validation with ground-based measurements are essential to ensure the reliability of satellite-derived estimates.
- Model Uncertainty: The models used to estimate soil carbon from satellite data can introduce uncertainties.

Environmental Factors
- Weather Conditions: Cloud cover, atmospheric conditions, and seasonal changes can affect the quality and availability of satellite data.
- Vegetation Interference: Dense vegetation can obscure the soil surface, complicating the measurement of soil carbon.

Technical and Analytical Challenge
- Data Processing: Handling and processing large volumes of satellite data require significant computational resources and expertise.
- Algorithm Development: Developing and refining algorithms to accurately estimate soil carbon from satellite data is complex and ongoing.

SOIL SENSOR

HYBRID APPROACH

The latest soil sensor technology provides real time soil carbon data from different soil depths, which supports a better understanding of both where carbon is located in the soil as well as its permanence.

FIG 2 How to measure soil carbon stocks. Existing technologies to measure soil carbon stocks on a larger scale and over time have proven to be inaccurate and quite limited, as described in the pros and cons sections in the figure. A hybrid measurement approach that includes highly sensitive soil sensor technologies could open new opportunities to model soil carbon distribution and permanence with greater accuracy. The development of high-quality measurement and modeling approaches are essential to improving the precision and reliability of soil carbon models, ultimately leading to better-informed decisions for soil management and carbon sequestration efforts. For soil carbon measurements, the gold standard involves collecting soil cores and obtaining soil organic carbon (SOC) values via dry combustion (e.g., reference 131). However, this process is laborious and expensive, making it impractical for large-scale and seasonal monitoring. Alternatively, soil carbon can be measured using satellite technologies and machine learning approaches (e.g., reference 132), which can collect large amounts of data from remote and inaccessible locations with lower investments compared with conventional methods. However, satellite imaging has its limitations. Accurate measurements require the top layer of soil to be dry and free of vegetation, and the atmosphere needs to be cloud-free. Satellites primarily capture information from the Earth's surface or near-surface layers, making it difficult to measure carbon content below the surface accurately. New inventions are emerging, such as high-resolution soil carbon sensor technologies that can measure different carbon pools (SIC, SOC, SOM, TC, and carbonous soil minerals) as well as other key soil metrics, such as salinity, nitrate, ammonia, pH, bulk density, moisture in near real-time (133–135). Local sensors may thus be able to provide valuable time-series data, allowing for more precise modeling when combined with low spatial resolution satellite technologies.

CONCLUSIONS

The loss of soil carbon from farming since the dawn of human cultivation is one of the many factors contributing to the rise in global GHGs (136). Reversing these losses is an important strategy to mitigate the effects of climate change. Given the urgency of this problem to society, we cannot afford to wait for a comprehensive understanding before acting. Here, we advocate for an expansion of the controlled use of soil microbiome interventions to achieve net soil carbon stock accrual without increasing emissions of other non-CO_2 GHGs, while simultaneously permitting gains in crop production or soil/plant health.

Many knowledge gaps regarding soil microbiome interventions remain. Filling these gaps is particularly challenging due to the diversity of crops, soil types, soil degradation levels, climate zones, and land management practices used throughout the world; thus, an effective one-size-fits-all approach is unlikely. Even within a single soil site, the complexities of plant type, soil depth, and water application can impact soil microorganisms and their functions (137). Hence, microbiome intervention strategies must be tailored to the specific ecological and climatic conditions of each land management setting and rigorously evaluated for their impacts on soil carbon stocks. On the other hand, developing good practices and appropriate policies for minimizing risks and damage to natural soils by soil microbiome interventions is also needed.

Because we cannot afford to wait for a comprehensive understanding due to the urgency of climate change, we must address key uncertainties (inoculation success, ecological risks, net soil carbon stock gain) while simultaneously and iteratively designing, evaluating, and optimizing microbiome interventions. Furthermore, these interventions must be incentivized and adopted at a global scale if soil carbon stock increases are to help off-set the atmospheric carbon surplus. Thus, we must strive to balance the need for specificity in strategies tailored to specific ecological and climatic conditions with the global scale of the change needed. This can be done by leveraging diverse experimental designs and systems to identify patterns in the soil–plant–climate conditions that are most amenable to manipulating soil functions with specific types of microbial inoculants and interventions. Ultimately, the deployment of these microbiome interventions should therefore adopt a hybrid framework including a core of common therapies that should be tested and applied in a customized and decentralized way to address the different environmental conditions across different sites. Here, we have identified challenges, opportunities and key knowledge gaps to inform future research priorities. Our aim is to advance the effective integration of soil carbon sequestration processes into emerging microbiome intervention technologies, thereby exploiting the vital role of soils in addressing global carbon cycle imbalances while ensuring sustainable food security.

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The authors are members of the Soil Microbiome Consortium for Climate Mitigation ("Soil Stars"), a group of scientists united to building a knowledgebase to develop and promote microbial solutions and communication strategies that can be deployed to solve complex problems at the nexus of agriculture, environmental sustainability, and climate resilience. Our work emphasizes the development of practical, scalable solutions that can be implemented globally to enhance soil health, optimize agricultural productivity, and reduce carbon footprints. This article was written on the basis of a 2024 discussion workshop, with authorship based on the voluntary participation of anyone in the consortium. More information on the Soil Microbiome Consortium for Climate Mitigation can be found at https://thesoilstars.com/.

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ADDITIONAL FILES

The following material is available online.

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PEER REVIEW HISTORY (review-history.pdf). An accounting of the reviewer comments and feedback.

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