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The soil-plant-human gut microbiome axis into perspective

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Microbiomes of soil, plants, and the animal gut are pivotal for key life processes such as nutrient cycling, stress resilience, and immunity. While studies have hinted at a shared microbial reservoir connecting these environments, compelling evidence of a soil-plant-gut microbiome axis is scarce. This perspective explores the potential continuum and diversification of microbes along this axis, highlighting specific microorganisms capable of moving from soil to plants to the human gut. A conceptual framework is proposed to better understand the mechanisms driving interactions among these microbiomes. We also examine how soil, plant, and gut microbiomes may co-evolve and influence one another through reciprocal effects. We consider external environmental factors that could strengthen their interconnections, potentially creating beneficial feedback loops that impact ecosystem and human health.

Transmission of microorganisms from soil to plant to gut

The composition of the human gut microbiome exhibits a discernible geographic pattern¹. This phenomenon is largely influenced by diet and lifestyle, such as food fiber content, urban/rural environments, and exposure to farming². The effects of these external factors on microbiome composition appear to be stronger than host traits such as relatedness and genetics². Consequently, the microbiomes present in the soil and plant environment, in particular the edible plant parts, have recently been proposed as significant drivers of the taxonomic and functional diversity of the human gut microbiome³. Hence, the central aim of this perspective is to critically review if there is such a shared microbial reservoir across soil, plants, and the human gut.

The soil microbiome harbors at least 25% of the Earth's total biodiversity⁴ and acts as a 'microbial seed bank' for the plant microbiome, in particular the roots (i.e., rhizosphere and endosphere)⁵ but also plant seeds and the phyllosphere, i.e., the aboveground plant parts including flowers and fruits^{6,7}. Several examples have shown that fruit and vegetable-associated bacteria can enter the human gut and may contribute to gut microbial diversity⁸. In addition to direct transmission of microbes to the human gut via plant-based products,

the metabolic content of edible plant products can also indirectly regulate the composition of the human gut microbiome⁹. Moreover, incidental or deliberate soil consumption (geophagy) has been proposed to provide health benefits, such as enhanced immunological resilience, through the modulation of the human gut microbiome¹⁰. Hence, the soil microbiome is regarded as a reservoir or 'seed bank' of microorganisms that can enter the human gut directly or indirectly via the plant⁵. But which microorganisms have been reported to transmit from soil to plant to gut? In turn, which members of the human gut microbiome are introduced back into the soil environment and on/in plant tissues through feces and food/water waste¹¹. To gain a deeper understanding of this putative feedback loop, we will also review current knowledge of the reciprocal selection mechanisms and dynamics of the soil-plant-gut microbiome axis.

Mapping the distribution of microbiota across the soil-plant-human gut axis

To determine if there is a microbial reservoir along the soil-plant-human gut axis (Fig. 1), we first classified the microbes in these habitats as either specialists or generalists. Specialists are defined here as microbes confined to specific habitats, while generalists are those

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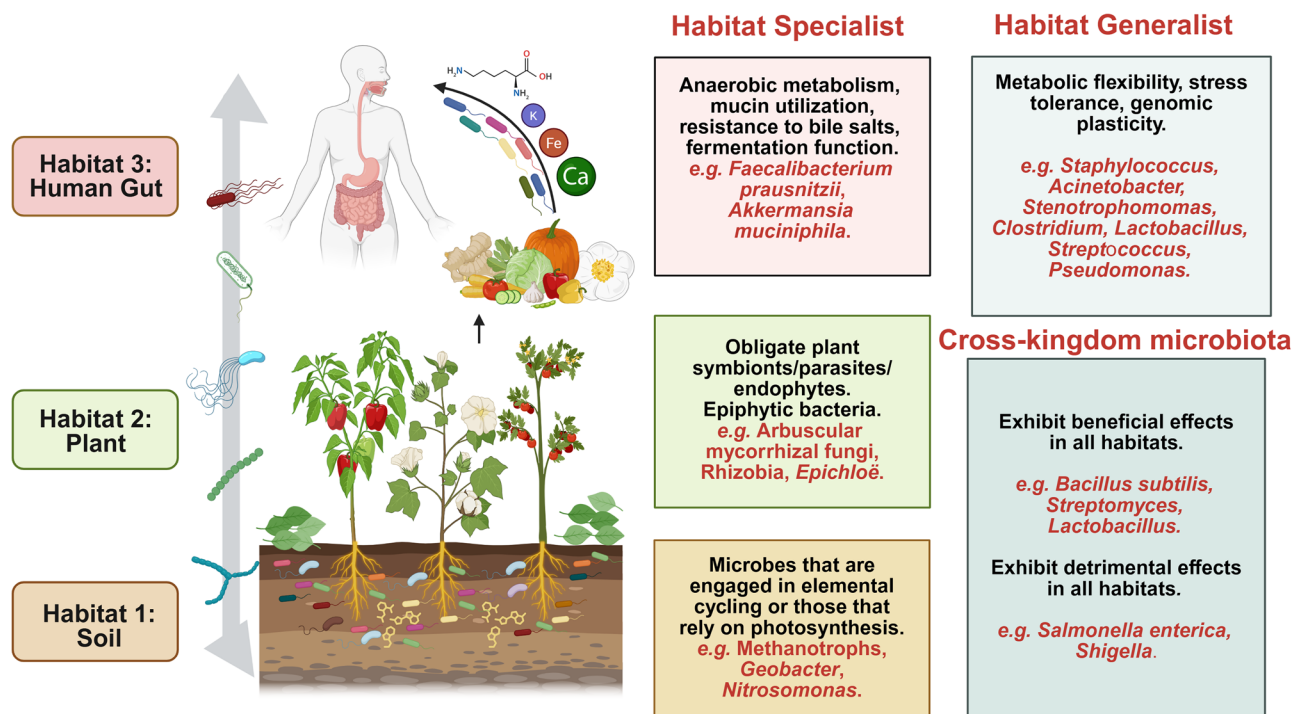


Fig. 1 | Proposed distribution of microbes along the soil-plant-human gut microbiome axis. Soil, plants, and the human gut are each considered distinct habitats. Within each habitat, specific microbial communities known as habitat specialists are identified. Microbes that are distributed across all habitats are

termed here as generalists. Based on their abundance and functions, a group of cross-kingdom microbiota is proposed among the generalist microbes. Created in BioRender. Ma, H. (2025) <https://BioRender.com/b51e6if>.

found across all habitats¹². Being classified as habitat specialists does not preclude their existence in other habitats; rather, they are typically found in much lower abundance outside their primary habitat¹². Among the generalist microbes, we define potential cross-kingdom microbiota as those with a high abundance across all three habitats¹³.

Habitat specialists

Most soil microbes interact with plants, yet certain taxa involved in biogeochemical cycling prefer the soil habitat and typically do not rely on nutrient exchange with hosts as seen in human gut commensals or plant symbionts¹⁴ (Table 1). Therefore, soil habitat specialists are unlikely to traverse along the soil-plant-human gut microbiome axis. For instance, methanotrophs are soil bacteria that utilize methane as their sole source of carbon and energy¹⁵. They are most prevalent in submerged or water-saturated environments, such as wetlands¹⁶, but can also be found in termite guts when inhabiting methane-rich environments¹⁷. Similarly, *Geobacter* plays vital roles in soil elemental cycling and can be found in paddy farmland¹⁸, soils, and marine sediments, where they engage in syntrophic growth with methanogens^{19,20}. *Nitrosomonas*, another example of a soil habitat specialist, is a bacterial genus that contributes to ammonia oxidation in aerated soils²⁰. However, not all microbial genera involved in soil elemental cycling are absent in the human gut. For example, sulfate-reducing *Desulfovibrio* is typically found in soil but also frequently reported in the human gut²¹ and has been associated with gut microbiome dysbiosis²² and colonic diseases²³.

Plant microbiomes typically are formed by recruitment of a subset of the soil microbiome via the spatiotemporal release of exudates from plant seeds, roots, and leaves. Among these are microbial taxa that exhibit an intimate association with plants, here defined as plant habitat specialists. For instance, arbuscular mycorrhizal fungi (AMF) are obligate biotrophs reliant on plants for carbon supply to complete their life cycle²⁴. This symbiotic relationship enhances plant nutrient

acquisition (e.g., phosphate and nitrates) from the soil and can also boost disease resistance in plant hosts²⁵. Similarly, N₂-fixing rhizobia manifest their symbiosis through the formation of nodules, serving as miniature factories for nitrogen supply to the host plants, predominantly legumes^{26,27}. Similarly, *Epichloë*, a genus of filamentous fungal endophytes, has co-evolved with cool-season grasses, forming long-term symbiotic associations²⁸. Soil-borne plant pathogens can also be regarded as plant habitat specialists, proliferating upon encountering suitable hosts and entering back into dormancy in soil in the absence of their hosts²⁹. Establishment of these associations involves intricate chemical communication between the plant and the soil microbiome via specific constituents in plant exudates. For example, phenolic acids such as salicylic acid, vanillic acid, can attract saprotrophic fungi like *Fusarium* species³⁰, while strigolactones play a crucial role in the establishment of symbiotic relationships between plants and AMF³¹.

The composition of the human gut microbiome is continuously influenced by microbes entering via plant-based food and the environment. Unlike soil and plants, microbes considered as human gut habitat specialists typically possess anaerobic metabolism and adaptability to varying pH levels. The duodenum has a more acidic environment compared to the jejunum and ileum, while the large intestine maintains a relatively neutral pH³². Additionally, human gut habitat specialists should have the ability to utilize mucin, as the gut mucosa forms a protective barrier for epithelial cells and serves as an ecological niche for specific non-harmful members of the gut microbiome^{2,33}. For example, *Akkermansia muciniphila* is well known for its mucin-degrading capabilities, which not only enable it to thrive in the gut environment but also to contribute to its role in maintaining gut barrier integrity and metabolic health³³. *A. muciniphila* is highly abundant in the human gut^{34,35}, and has been shown to diminish obesity, type 2 and type 1 diabetes mellitus, hepatic steatosis, intestinal inflammation, and various cancers in mice³⁶. Furthermore, bile salts

Table 1 | Examples of putative habitat specialists and generalists along the soil-plant-gut axis

Taxonomic information of the microbial genus and species	Specialists/Generalist / cross-kingdom microbiota	Description of the habitat and functional traits of the specialist or generalist	References
Methanotrophs	Specialist	Soil: methane utilization	15–17
<i>Geobacter</i>	Specialist	Soil: soil elemental cycling	18–20
<i>Nitrosomonas</i>	Specialist	Soil: ammonia oxidation	20
<i>Desulfovibrio</i>	Specialist that may colonize the human gut	Soil: sulfate-reduction	21–23
Arbuscular mycorrhizal fungi	Specialist	Plant: symbionts	24,25,31
N ₂ -fixing rhizobia	Specialist	Plant: symbionts	26,27
<i>Epichloë</i>	Specialist	Plant: endophyte	28
Soil-borne plant pathogens	Specialist	Plant: parasites	29,30
<i>Akkermansia muciniphila</i>	Specialist	Human gut: mucin degrader, maintain gut barrier integrity, anti-inflammatory	33–36
<i>Faecalibacterium prausnitzii</i>	Specialist	Human gut: butyrate producer, anti-inflammatory	34,35,41,42
<i>Christensenella minuta</i> <i>Anaerobutyricum soehngenii</i> <i>Oxalobacter formigenes</i>	Specialist	Human gut: commensals	36
<i>Clostridium</i> spp.	Generalist	Soil and plant: biological nitrogen fixation, phosphate solubilization Human gut: fermentation of carbohydrates	45–47
<i>Clostridium butyricum</i>	Generalist	Soil and plant: nitrogen fixation Human gut: butyrate-producer	46,48–50
<i>Clostridium difficile</i> , <i>Clostridium perfringens</i>	Generalist	Soil and plant: unknown functions Human gut: toxin producer	47,51
<i>Acinetobacter</i> spp. (<i>Acinetobacter baumannii</i> , <i>Acinetobacter calcoaceticus</i> , <i>Acinetobacter aeruginosa</i>)	Generalist	Soil: phenol and dibutyl phthalate degradation Plant: phosphate solubilization Human gut: opportunistic pathogens, antibiotic resistance	52–61
<i>Staphylococcus</i> , <i>Streptococcus</i>	Generalist	Soil and plant: unknown functions Human gut: opportunistic pathogen	35,62–66
<i>Stenotrophomonas</i>	Generalist	Soil: nutrient cycling Plant: producing plant growth hormones and chitinases Human gut: opportunistic pathogen	49,67–69
<i>Helicobacter pylori</i>	Generalist	Soil and plant: unknown functions Human gut: pathogen, antibiotic resistance	93–99
<i>Pseudomonas</i> spp.	Generalist	Soil and plant: unknown functions Human gut: opportunistic pathogens, antibiotic resistance	49,100–105
<i>Ruminococcus</i>	Generalist	Soil and plant: unknown functions Human gut: commensals	70–72
<i>Bacillus subtilis</i>	Cross-kingdom microbiota: all beneficial	Soil and plant: growth promotion Human gut: anticancer, antioxidant, vitamin production	73–76
<i>Lactobacillus</i>	Cross-kingdom microbiota: all beneficial	Soil: degrade polluting metals Plant: growth promotion and biocontrol Human gut: probiotic	38,49,77–82
<i>Streptomyces</i>	Cross-kingdom microbiota: all beneficial	Soil: unknown function Plant: growth promotion, biocontrol Human gut: probiotic	83,84
<i>Lactococcus</i>	Cross-kingdom microbiota: all beneficial	Soil: unknown function Plant: growth promotion Human gut: commensal	49,80,85
<i>Salmonella enterica</i>	Cross-kingdom microbiota: all harmful	Soil: unknown function Plant: causes disease symptoms Human gut: pathogen	56,86–88
<i>Shigella</i>	Cross-kingdom microbiota: all harmful	Soil: unknown function Plant: causes disease symptoms Human gut: pathogen	56,89

can be abundant in the small intestine, significantly influencing microbial colonization of the human gut³⁷. For instance, the enzymatic preferences of bile salt hydrolases significantly affect the fitness of *Lactobacillus* and their colonization in humans³⁸. Fermentation by gut microbes is crucial for converting luminal compounds into secondary

metabolites and is considered an indicator of a healthy gut microbiome^{39,40}. For example, *Faecalibacterium prausnitzii*, a major butyrate producer, contributes to gut health by fermenting fibers and producing short-chain fatty acids that have anti-inflammatory effects, which help suppress conditions like irritable bowel syndrome, obesity,

and celiac disease⁴¹. In this context, *F. prausnitzii* has been proposed as a biomarker for a healthy gut^{34,35,42}. Other beneficial gut habitat specialists include *Christensenella minuta*, *Anaerobutyricum soehngenii*, and *Oxalobacter formigenes*³⁶.

Habitat generalists

Habitat generalists should preferably possess specific features such as metabolic flexibility, stress tolerance, and genome plasticity, allowing them to adapt to the different environments^{43,44}. For instance, *Clostridium* spp. encompasses many habitat generalists such as *C. cadaveris* and *C. senegalense*, characterized by its metabolic flexibility, can thrive in diverse environments (Table 1)⁴⁵. In soil and plants, *Clostridium* species can exhibit beneficial functions such as biological nitrogen fixation and phosphate solubilization⁴⁶. In the human gut, *Clostridium* can ferment carbohydrates to produce short-chain fatty acids, promoting gut health⁴⁷. *C. butyricum*, a human gut symbiont known for its butyrate-producing and anti-cancer properties^{48,49}, has also been isolated from soil⁵⁰. However, certain *Clostridium* strains, including *Clostridium difficile* and *Clostridium perfringens*, produce toxins with neurotoxic, hemolytic, and enterotoxigenic properties⁴⁷. They were also isolated from the soil and therefore, their transmission along the soil-plant-gut axis warrants attention⁵¹. Similarly, *Acinetobacter* exhibits diverse metabolic functions such as phenol and dibutyl phthalate degradation in soil, as well as phosphate solubilization for plants^{52–54}. *Acinetobacter* species also reside in the human gut, influencing gut epithelium modulation^{55,56}. Several *Acinetobacter* species, including *A. baumannii* and *A. calcoaceticus*, can be found in soil and water, but are also opportunistic human pathogens^{57,58}. Their persistence in these different environments poses a threat to human health and may be attributed to several traits, including their high level of resistance to desiccation⁵⁹, horizontal gene transfer⁶⁰, and lipopolysaccharides (LPS) in their outer membrane⁶¹. Similarly, *Staphylococcus* and *Streptococcus* have been identified as opportunistic human pathogens³⁵, but have also been detected in plant rhizospheres^{62–65} and soil environments⁶⁶. Also, *Stenotrophomonas* can be considered a habitat generalist, as it inhabits both the plant rhizosphere and endosphere, where it acts as a beneficial microbe by inducing plant growth hormones and chitinases⁶⁷. In soil, *Stenotrophomonas* plays a role in nutrient cycling, particularly in nitrogen and sulfur⁶⁷. In humans, *Stenotrophomonas* can colonize the gut^{49,68} and act as a pathogen to immunocompromised and debilitated individuals, leading to severe inflammation and infection⁶⁹. Its persistence in diverse environments is attributed to its metabolic versatility, ability to form biofilms, production of extracellular enzymes, and resistance to multiple stress conditions⁶⁹. Also, *Pseudomonas* and *Helicobacter* can be considered as habitat generalists. Except for potential pathogenic species, other human gut commensals such as *Ruminococcus*, which has been identified as one of the most abundant taxa in the human gut by several global studies^{70,71}, have also been reported in the rhizosphere of Antarctic vascular plants⁷². Therefore, the reservoir of microbial genera along the soil-plant-gut axis may be larger than we currently know. Considering that several competitive traits and their corresponding genes are distinctly different among species of a given genus and even among strains of a given species, comparative meta-analyses will be needed to align so-called metagenome assembled genomes (MAGs) of microbiome members along the axis to further delineate and validate the taxonomic identity and frequency of habitat generalists and cross-kingdom microbiota across these different habitats beyond the genus and species level.

Putative cross-kingdom microbiota along the soil-plant-human gut axis

The core (cross-kingdom) microbiota is traditionally defined by its taxonomic composition, but also its functional roles in relation to the host should be considered⁷³. For instance, *Bacillus subtilis*, known for

its considerable genome diversity, thrives in various environments (Table 1)⁷⁴. Capable of forming dormant endospores in response to nutrient deprivation and environmental stresses, *B. subtilis* acts as an important plant growth-promoting rhizobacterium, conferring biotic and abiotic stress tolerance to plants through induced systemic resistance, biofilm formation, and lipopeptide production^{73,75}. Moreover, *B. subtilis* is widely employed in bioremediation⁷⁵, but is also extensively studied in humans for the production of vitamins and metabolites with anticancer and antioxidant properties, potentially influencing human longevity and reducing the risk of Parkinson's disease⁷⁶. Also, *Lactobacillus* represents a group of bacteria with beneficial functions for humans, plants, and soil environments. In the human gut, *Lactobacillus* acts as a probiotic for immune regulation, inhibiting the colonization of enteric pathogens through the production of metabolites such as organic acids, hydrogen peroxide, nitric oxide, short-chain fatty acids, and bacteriocins⁷⁷. The robust metabolic capabilities of *Lactobacillus* also contribute to its anti-inflammatory properties⁷⁸. A recent meta-analysis integrating 168,000 human gut samples globally, reported that *Lactobacillus* is one of the most abundant gut microbiota, representing a key taxon contributing to the variability observed in gut samples from Europe and North America⁴⁹. For plants, *Lactobacillus* has shown growth-promoting effects and has been used as a biocontrol strains in several studies^{79,80}. In soil environments, *Lactobacillus* has demonstrated the ability to remediate polluting metals⁸¹. The generalist nature of *Lactobacillus* may be attributed to its comprehensive genetic catalog for carbohydrate and protein modification, production of host interaction factors and bacteriocins, and stress response mechanisms⁸². Another noteworthy genus is *Streptomyces*, soil-dwelling bacteria renowned for their antibiotic production, plant growth-promoting, and biocontrol traits⁸³. While less prevalent in the human gut, *Streptomyces* are gaining attention as potential probiotics due to their detoxification of mycotoxins, production of extracellular polymeric substances with anticancer properties, and synthesis of anti-inflammatory polyketides⁸⁴. Other microbes, such as *Lactococcus*, are also identified as abundant gut commensals globally⁴⁹ and have been used as probiotics for treating IBD and Type 2 diabetes⁸⁵, but also exhibit plant growth-promoting effects attributed to the production of organic acids and siderophores⁸⁰.

In contrast to these 'beneficial cross-kingdom microbiota', the pathogen *Salmonella enterica* manifests in various disease syndromes, with food contamination as the primary mode of transmission^{56,86}. Studies have shown that *Salmonella* attaches to and colonizes plants but can even infect them, with the rate of infection contingent upon the activation of the plant immune system, sometimes resulting in plant leaf chlorosis and wilting⁸⁷. Additionally, soil may serve as a reservoir for *Salmonella* species, as *S. enterica* has been found in a sandy loamy soil⁸⁸. Other human pathogenic bacteria, such as the enteric pathogen *Shigella*, have been found to colonize the leaves and roots of *Arabidopsis* through the adoption of type III effectors^{56,89}. However, the effects of *Shigella* on plants and its survival in soil still require further investigation. Thus, it is imperative to further explore the vast reservoir of beneficial and deleterious cross-kingdom microbial taxa along the soil-plant-human gut axis at genus and preferably at species and strain levels. In this context, identification of the extensive intraspecific diversity of microbial genera is essential to better define their specialist or generalist behavior across the soil-plant-human gut microbiome axis and to identify specific genes or gene clusters associated with that lifestyle⁹⁰.

Feedback loop and co-evolution between soil, plant and human gut microbiomes

Species originating from distinct lineages can undergo reciprocal evolutionary changes over time, leading to the establishment of interdependent ecological relationships that significantly influence

their phenotypes⁹¹. Co-evolution is defined as the process whereby a change in a trait of individuals within one population occurs in response to a trait exhibited by individuals in a second population⁹². In the context of the soil-plant-human microbiome axis, the soil acts as a reservoir for various bacterial taxa such as *Helicobacter pylori*, which can transfer to the human gut through food contamination or wastewater used for irrigation^{93,94}. Nucleotide sequences of *H. pylori* in the environment show 96%–100% homology with those in the human gut⁹⁵. The bacterium's highly plastic genome, marked by intraspecific recombination, enhances its colonization ability in the human gut, even under antibiotic pressure^{96,97}. In *H. pylori*, distinct resistance profiles, encompassing single and multidrug resistance, were identified⁹⁸. Antimicrobial resistance genes induced by medical therapeutics may be reintroduced back into the soil microbiome and impose a subsequent selection pressure on soil-borne *H. pylori*, which in turn may augment the risk of new infections in humans⁹⁹. A second example of a bacterium that may exert a reciprocal influence along the soil-plant-human gut microbiome axis includes *Pseudomonas*. The persistence of *Pseudomonas* in various habitats may be attributed to its versatile metabolic ability to utilize a wide range of organic and inorganic compounds as energy sources^{49,100,101}, its ability to form protective biofilms to survive environmental stresses¹⁰², and the presence of multidrug efflux pumps, which contribute to its antibiotic resistance¹⁰³. The combination of its genomic plasticity, environmental exposure, and biofilm formation makes horizontal gene transfer particularly prominent in *Pseudomonas*, enabling it to easily acquire foreign genes and disseminate antibiotic resistance genes, toxins, and other advantageous traits¹⁰⁴, eventually mediating functional changes in the different microbiomes along the axis¹⁰⁵.

To date, several mechanisms have been proposed that drive these reciprocal effects and co-evolution among soil, plant, and human gut microbiomes. These include molecular mimicry, horizontal gene transfer, cross-feeding, and host selection (Table 2). These mechanisms will be discussed in more detail below.

Molecular mimicry

Molecular mimicry is characterized by analogous structural features shared by molecules originating from distinct genes or their corresponding protein products¹⁰⁶. Microorganisms in one microbiome can produce molecules that exhibit structural similarity to essential signaling molecules in the other microbiome (Table 2). This resemblance may give rise to selection pressures between the interconnected microbiomes. For example, lipopolysaccharides (LPS) in the outer membrane of soil-borne Gram-negative bacteria have long been used as markers of soil microbial community structure¹⁰⁷. Its structural features also resemble those of host-derived molecules that trigger pattern recognition receptors, such as Toll-like receptors (TLRs) in

plants and humans¹⁰⁸. In the human gut, this activation subsequently initiates inflammatory responses that not only contribute to tissue immunity but also facilitates coordination with the adaptive immune system¹⁰⁹. This structural similarity can result in LPS acting as a pathogen-associated molecular pattern (PAMP), eliciting an immune response that spans plant and human systems¹¹⁰. Another example is peptidoglycan in the bacterial cell wall that is a direct target for innate immune receptors and modulates the accessibility of other PAMPs to additional innate immune receptors¹¹¹. It has been suggested that this peptidoglycan-mediated host immunity is evolutionary conserved¹¹². Application of eight common clinical antibiotics to soil resulted in significant alterations in gene expression, including the biosynthesis of peptidoglycan¹¹³. Hypothetically, these alterations in turn may affect human immunity via exposure to qualitative and quantitative changes in these cellular structures of soil microorganisms when transmitted to the human gut microbiome. Although most examples described so far relate to molecules of pathogenic bacteria, there are a few examples of beneficial molecular mimicry. One such as example is the soil-dwelling butyrate producer *Kineothrix alysoides*, whose abundance in the gut increased significantly following exposure to high-biodiversity soil¹¹⁰. Butyrate enhances human health by modulating energy metabolism, improving insulin sensitivity, regulating lipid metabolism, and reducing inflammation, primarily through activation of G-protein coupled receptors (GPRs) and epigenetic regulation of gene expression¹¹⁴. Hence, human immune responses may be modulated via the plant¹¹⁵ and food microbiome¹¹⁶, while human activities can affect the biosynthesis and dynamics of these molecules within the soil environment.

Horizontal gene transfer

Horizontal gene transfer is an extensively studied mechanism of interaction between the soil microbiome and the human gut microbiome^{115,117}. Horizontal gene transfer represents mechanisms through which microorganisms acquire foreign DNA from other (micro)organisms. The main mechanisms of horizontal gene transfer within natural microbial communities include transformation, conjugation, transduction, and outer membrane vesicles¹¹⁸. The acquired DNA may confer traits that broaden the ecological niche of a microorganism, alter its interactions with the host or confer a competitive advantage over other microorganisms¹¹⁸. One well-studied example in the context of the soil-plant-human gut microbiome axis is the transfer of antibiotic resistance genes introduced into the soil environment through manure, biosolids, and wastewater derived from human and animal waste¹¹⁹, and even microplastics¹²⁰. Consequently, antibiotic-resistant bacteria and antibiotic resistance genes present in the soil microbiome can transfer to clinically relevant microbial pathogens or to the human gut microbiota through various routes such as the food

Table 2 | Examples of mechanisms governing reciprocal effects along the soil-plant-gut microbiome axis

Scale	Mechanisms	Processes and definition	Examples
Molecule	Molecular mimicry	Production of molecules by microbiota in one microbiome that resemble key signaling molecules in another microbiome.	Lipopolysaccharides (LPS), Peptidoglycan, Butyrate
Gene	Horizontal gene transfer	Acquisition of new genes and traits in one microbiome from the other.	Antibiotic resistance genes, exopolysaccharide (EPS) genes
Species	Arms Race	The antagonistic interactions between soil, plant, and human gut microbiomes resist mutual colonization.	Colonization resistance
	Cross-feeding	Reciprocal metabolic adaptations and interactions that benefit microbiomes along the soil-plant-gut axis.	Cross-feeding
Host	Host selection	Plants play a crucial role in recruiting specific microbial taxa from soil through host-selective effects. This, in turn, influences the microbiome composition along the soil-plant-gut axis.	Plant domestication
		Enterotypes reflect the interaction between the host's genetics, immune system, and dietary factors, all of which shape the gut microbiome and influence transmission of and colonization by soil and plant microbes.	Enterotypes

chain, drinking water, or environmental exposure^{117,121,122}. During these processes, plant selection of their microbiome and the merger with the manure microbiome, known as community coalescence, have been identified as two critical factors determining the transmission of antibiotic-resistant genes^{123,124}. Accordingly, studies have shown that individuals exposed to specific farms exhibit gut microbiomes with antibiotic resistance gene patterns similar to those found in the environmental samples from the respective farms¹²⁵. For instance, about 27% of microbes transmitted from environmental soil and dust in swine farms to the human gut harbored at least one antibiotic resistance gene¹²⁵. This mechanism has the potential to induce significant and rapid co-evolutionary changes across broader phylogenetic lineages of microorganisms, irrespective of their relatedness, extending beyond the confines of solely vertical transmission between the parent and its offspring¹²⁶. Another group of genes that could be transferred between the soil and human gut microbiomes is the EPS biosynthetic genes. In soil microbes, these genes support various functions, including symbiosis with plants and biofilm formation¹²⁷. In the human gut, EPS biosynthesis by commensal bacteria benefits the host through immune modulation, reduced gastrointestinal stress, and pathogen inhibition¹²⁸. Horizontal gene transfer of EPS production genes has been found in various environments, such as food systems¹²⁹ and bacterial biofilm matrices¹³⁰. Therefore, it can be hypothesized that the exchange of EPS biosynthesis genes may occur between soil microbes and human gut microbes, likely leading to beneficial reciprocal effects in both habitats along the axis.

Colonization resistance

The concept of the ‘Arms Race’, commonly applied to the co-evolution between hosts and parasites, describes the reciprocal selection that drives adaptation and counter-adaptation of the interacting partners¹³¹. Colonization resistance refers to the phenomenon where commensal microorganisms of a host act as a protective barrier against the invasion, colonization, and proliferation of both pathogens and indigenous pathobionts¹³² (Table 2). This concept has also been employed more broadly to characterize how the resident microbiota hinders the colonization of introduced microorganisms¹³³. In the human gut, colonization resistance becomes evident when antibiotics are used, as several pathogens and invading microbes can only effectively colonize and proliferate in this vacuum¹³⁴. The mechanisms underlying colonization resistance operate through both direct and indirect means. Indirect mechanisms encompass nutrient competition¹³⁵, and antagonism by gut microbes producing antimicrobial peptides, short-chain fatty acids or secondary bile acids¹³³. Direct mechanisms of colonization resistance include the mucosal barrier¹³⁶, oxygen limitation in the gut¹³², and host antimicrobial peptides and cytokines¹³². Similarly, colonization resistance in soil can be observed when introduced beneficial microbial strains fail to persist and express specific activities in situ despite demonstrating significant effects under controlled conditions in the lab or greenhouse¹³⁷. Also, the invasiveness of the human-associated bacterium *Escherichia coli* O157:H7 in soil was inversely related to the diversity of resident soil microbial communities¹³⁸. However, microbial invaders can also establish and induce changes in soil bacterial diversity^{139,140}. The variability in the outcome of microbial invasions may be contingent with the taxonomic and functional diversity of the resident microbiome (soil, plant or human). For example, colonization resistance of the human gut is observed under homeostasis, whereas dysbiosis of the gut microbiome compromises colonization resistance¹³².

Cross feeding

The fourth mechanism underlying reciprocal effects between soil, plant, and human gut microbiomes involves cross-feeding (Table 2). The cooperative exchange of metabolites as energy and nutrient source among different microbial species or strains¹⁴¹ is largely

determined by metabolic dissimilarity and complementarity^{142,143}. Although direct cross-feeding interactions between microbiota along the soil-plant-gut axis have not been widely demonstrated and experimentally validated, shared metabolic functions across these microbiomes suggest potential indirect influences. Bacteria in particular, frequently engage in obligate metabolic mutualisms with other (micro)organisms to expand their ecological niche¹⁴⁴. In the human gut, plant fibers containing cellulose and hemicellulose are challenging to digest, necessitating the presence of a diverse array of degrading enzymes such as glycoside hydrolases and polysaccharide lyases. These enzymes are not produced, or are produced only in limited quantities, by mammals themselves¹⁴⁵. Interestingly, glycoside hydrolases have been found in soil, plant and human gut microbiomes, with the bacteria producing these enzymes exhibiting conserved functions across these microbiomes¹⁴⁶. Soil microorganisms are also capable of producing vitamins, including cobalamin¹⁴⁷. Cobalamin (vitamin B₁₂), is crucial in the human gut and many organisms reliant on cobalamin acquisition depend on other species for its provision¹⁴⁸. Butyrate-producing bacteria in the gut, which have various beneficial effects on human health, require cobalamin for their growth¹⁴⁹. While the human gut does not/seldomly directly feed on soil microbes, the plant microbiome may act as an intermediary by hosting microbes that synthesize or modify essential metabolites¹⁵⁰. Through the consumption of plant-based foods, these metabolites, including fibers and vitamins synthesized by soil bacteria, reach the human gut, where gut microbiota further metabolize them¹⁵⁰. This interplay along the soil-plant-human gut microbiome highlights the potential for cooperative interactions and the exchange of essential resources, without the need for direct transmission of the involved microorganisms along the axis.

Host selection

Soil type can be a factor influencing the assembly of the plant microbiome; however, its impact is context-dependent. In natural ecosystems, the effects of soil type may be less pronounced compared to agricultural settings¹⁵¹. However, within each soil environmental context, the local proliferation of microbes is influenced by plants, as they actively recruit microbes from the soil into the rhizosphere through selection by root exudation composition, root architecture, and plant litter decomposition¹⁵². This subsequently leads to plant species-specific microbiomes, which in turn may influence human gut microbiomes. One illustrative example is the process of plant domestication, where humans transformed wild plant species into highly productive crops for human consumption. These cultivated varieties exhibit traits such as larger fruit size, higher growth rates, and altered chemistry¹⁵³. Consequently, when compared to their wild relatives, crops exhibit a reduced specific root length, higher root density, altered root exudation, and root-associated microbiomes¹⁵⁴. This was further exemplified by microbiome studies of recombinant inbred line populations of a cross between wild relatives and their domesticated crop cultivar that exhibit changes in microbiome compositions associated with specific quantitative trait loci in crop genomes¹⁵⁵. To what extent these changes in plant chemistry and microbiome composition affect the human gut microbiome is an emerging topic of research¹⁵⁶. A recent study revealed an association between the presence of metabolic pathways in various fruits and vegetables and homeostasis of the human gut microbiome¹⁵⁷. This association includes pathways related to the synthesis of glutamate and biotin, as well as numerous carbohydrate-active enzymes^{156,157}.

Microbes, derived from plants (or the diet), along with other host factors such as immune condition and genetic makeup, contribute to the formation of specific enterotypes in the human gut^{158,159}. For example, enterotypes are characterized as *Bacteroides*, *Prevotella*, and *Ruminococcus* types, based on the dominant species¹⁶⁰. This leads to functional differentiation among these enterotypes, such as the *Bacteroides* enterotype, which ferments carbohydrates and possesses a

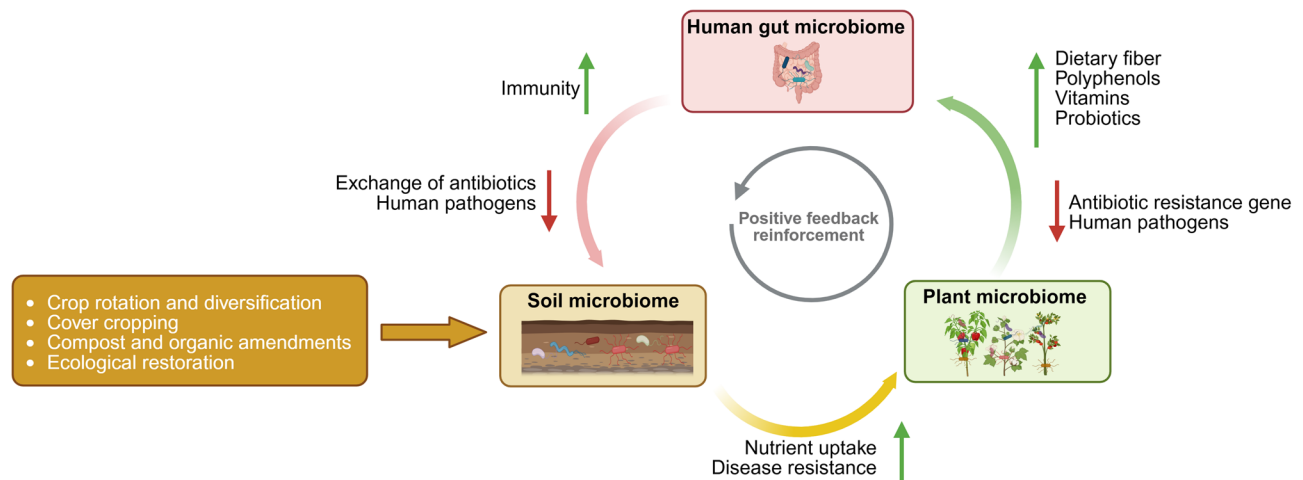


Fig. 2 | Potential future steps to create positive feedback loops along the soil-plant-human gut axis. External drivers, such as crop rotation, diversification, cover cropping, organic compost, and ecological restoration, have been proposed to enhance soil biodiversity and health. A healthy soil ecosystem promotes nutrient uptake and enhances plant disease resistance by fostering the enrichment of beneficial microbes in the plant rhizosphere, phyllosphere and spermosphere. This, in turn, contributes to a robust plant microbiome capable of producing nutrient-rich food, including dietary fiber, polyphenols, and vitamins. The enhanced plant microbiome also has the potential to support microorganisms with probiotic

effects while reducing the frequency of human pathogens and antibiotic resistance genes when transferred to the human gut. Furthermore, the soil microbiome can directly interact with the human microbiome. Moreover, a healthy human gut microbiome plays a role in decreasing the frequency of (opportunistic) human pathogens and antibiotic resistance genes reintroduced into the soil through fecal and waste matter, thus completing a positive feedback loop that benefits both soil and human health. Created in BioRender. Ma, H. (2025) <https://BioRender.com/b51e6if>.

broad saccharolytic potential¹⁶¹. The *Prevotella* enterotype primarily degrades mucin glycoproteins, while the *Ruminococcus* enterotype is involved in binding mucins, transporting them, and degrading sugars in the gut¹⁶¹. Conversely, the specificity of enterotypes also influences the future colonization of other microbes, as they are linked to the dysbiosis status of the gut microbiome¹⁶² or the disease status of the human host¹⁶³. This makes it both an important outcome and a deterministic factor in the human host's selection of their gut microbiome.

Outlook: creating a positive feedback loop in the soil-plant-human gut axis

The reciprocal influences as well as the distribution and proliferation of microbes along the soil-plant-gut axis are subject to various environmental factors. These factors may range from unpredictable climate change events to physiochemical changes in specific micro-habitats. Therefore, managing potential external drivers to create a positive feedback loop along the axis is essential for achieving better “One Health” outcomes.

A healthy plant microbiome can positively influence the human gut microbiome primarily through two mechanisms (Fig. 2). First, the plant phyllosphere and other edible plant parts can transmit soil microorganisms to the human gut. With increased soil microbial diversity, the potential negative impact on the gut microbiome through the plant microbiome may decrease. For instance, enhanced soil microbial diversity correlates with a decreased abundance of antibiotic-resistant genes in the soil^{164–166} and increased antagonistic effects against human pathogens¹⁶⁷. Additionally, plant extracts, including phenolic compounds, chlorophyll, and carotenoids, can act as prebiotics for beneficial microbes already present in the human gut¹⁶⁸. Secondly, an improved soil microbiome can sustain plants producing food with higher nutrient contents, such as vitamins, polyphenols, and dietary fiber¹⁶⁹. For example, biofertilizers have been found to increase the dietary fiber content of onions¹⁷⁰ and corn¹⁷¹, the vitamin content of tomatoes¹⁷², and the polyphenol content of eggplants¹⁷³. Subsequently, this higher dietary fiber content enhances the production of short-chain fatty acids by gut bacteria, indirectly

contributing to improvement in human health by reducing inflammation, preventing cancer, and supplying energy¹⁷⁴. Furthermore, the polyphenols in food promote beneficial strains in the gut, such as *A. muciniphila*¹⁷⁵ and enhance antimicrobial activities against pathogens¹⁷⁶.

In addition to using plants as a mediator, numerous studies have demonstrated a positive link between soil biodiversity and human health, often referred to as ‘natural immunity’^{177,178}. Particularly in early life, exposure of humans to the natural soil environment aids in the development of a diverse molecular memory, facilitating rapid recognition of harmful organisms¹⁷⁹. Furthermore, exposure to the natural environment can introduce beneficial gut microbiota, including butyrate-producing bacteria¹⁸⁰ and beneficial fungi¹⁸¹. These microbial components acquired by the gut contribute to activation of the innate immune system. For instance, feeding a soil slurry to mice has been shown to alleviate inflammation¹⁷⁸, while exposing inbred laboratory mice to the outdoor environment reduces pathogen infections, increases circulating granulocytes, and promotes differentiation of T cell populations via the colonization of intestinal fungi¹⁸¹. Moreover, higher environmental biodiversity has been associated with an increased proportion of regulatory T cells and elevated plasma TGF- β 1 levels in children¹⁸². Therefore, exposure to the natural environment can serve as a prophylactic measure in preventing immune-mediated diseases (Fig. 2). In return, a healthy gut microbiome may reduce the presence of antibiotic-resistant genes and human pathogens that could be reintroduced back to the soil environment through feces and waste. Thus, while exposure to the natural environment carries the risk of closer contact with potential human pathogens, a healthy soil microbiome could diminish these chances. In this way, the positive loop along the soil-plant-human gut axis can be reinforced.

Conclusions

The importance of including the soil and plant microbiomes in human health is increasingly recognized³. In this perspective, we have provided several examples of microorganisms that can transmit from soil or plants to the human gut and exert specific influences. Typical examples highlighted and detailed in the sections above include

Bacillus, *Pseudomonas* and *Clostridium* species. The question if there are unifying beneficial or detrimental functions in these distinct ecosystems was more difficult to address and the available data and results are still largely circumstantial and hypothetical. To this end, we propose to integrate co-evolutionary concepts, where the soil, plant, and human gut microbiomes may influence each other's evolutionary trajectories over time, providing a better understanding of the exchange and interactions between the soil microbiome and human gut microbiome. Also identifying habitat specialists, habitat generalists, and potential cross-kingdom microbiota along the soil-plant-human gut microbiome axis at the species and preferably strain level could provide us with a deeper understanding of the microbial fluxes along the axis. In this context, large-scale genomic identification of the extensive intraspecific diversity of microbial genera is essential to identify their life-style associated genes⁹⁰ and monitor their population dynamics and distribution across the soil-plant-human gut microbiome axis.

Data availability

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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Author contributions

All authors contributed to the manuscript's conception. H.M. led the writing, with valuable revisions and input from J.M.R. and D.C.

Competing interests

The authors declare no competing interests.

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