

Peer-to-Peer Review

Does Soil Contribute to the Human Gut Microbiome?

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Abstract

- Soil and the human gut contain approximately the same number of active microorganisms, while human gut microbiome diversity is only 10% that of soil biodiversity and has decreased dramatically with the modern lifestyle.
- From hunter-gatherers to an urbanized society, the human gut has lost alpha diversity. Interestingly, beta diversity has increased, meaning that people in urban areas have more differentiated individual microbiomes.
- On top of little contact with soil and feces, hygienic measures, antibiotics and a low fiber diet of processed food have led to a loss of beneficial microbes. At the same time, loss of soil biodiversity is observed in many rural areas. These developments concur with an increase in lifestyle diseases related to the human intestinal microbiome.

Abstract

In order to correct the damages in the microbiomes (soil, human), the authors consider the human intestinal microbiome as well as the soil/root microbiome as 'superorganisms' which, by close contact, replenish each other with inoculants, genes and growth-sustaining molecules.

Introduction

- From early childhood, we are in contact with soil; we taste it, we inhale it, and we drink water which has passed through soil. Moreover, we ingest plants grown on soils together with soil microbiota. Since pre-history, humans have also willingly consumed soils as a supplement to their otherwise nutrient-poor local diet, a habitude called “geophagy”.
- The intestinal environment is subject to a constant influx of microbial colonizers [4] The microbial community of the gut is very dynamic and consists of autochthonous and allochthonous members (that are absorbed by food and water, as well as by direct contact with the environment/soil in which they live
- In view of the functional similarities between the intestinal microbial community and the soil microbial ecosystem, a relationship between both appears possible.
- As human activities are changing the distribution and abundance of soil microorganisms, e.g., by agricultural land use [9], the resultant changes in microbial ecosystems may not only affect biogeochemical cycles but also human health.

2. The Complex Relationship between the Soil Microbiome and the Human Intestinal Microbiome

- The Human Microbiome Project has developed into a major field of biomedical research focussing mainly on the intestinal microbial community that plays a major role in human health and diseases
- The intestinal microbial community represents an ecosystem of a trillion microbial cells with an aggregate 9.9 million microbial genes across the fecal microbiome
- The greatest number of cells within the human gut is found in the colon which supports a diverse and dense population of microbes, dominated by anaerobes that utilize carbohydrates

- With respect to the numerous and diverse functions of the intestinal microbiome in human health, it is evident that it is also involved in numerous gastrointestinal (GI) and non-gastrointestinal diseases, such as obesity/metabolic syndrome, atherosclerosis/cardiovascular diseases, neurologic/psychiatric diseases and others
- All in all, it can be stated that, in recent years, the intestinal human microbiome has become one of the most dynamic areas of biomedical research and holds an enormous potential for interventions, regarding human health and disease
- major advances in recent years provide increasing individual diagnostics, preventive as well as therapeutic options for patients with inherited or acquired malignant or non-malignant diseases
- Soils existed globally a long time before mammals and hominids came into existence and are by far the most extensive natural microbial gene reservoir on earth
- the question arises as to whether the soil microbiome as an exogenous parameter affects the development of the human intestinal microbiome.

- Since 2010, the Earth Microbiome Project has focused on this gene reservoir. It is a major collaborative effort to characterize microbial life on this planet by using DNA sequencing and mass spectrometry of crowd-sourced samples to understand patterns in microbial ecology across the microbiomes and habitats of the earth
- On a per gram basis, the intestine, specifically the colon, has the highest concentration of cells of all biomes listed in Table 1 [17,18]. Considering the diversity of these habitats, the estimated number of species on a per gram basis suggests that soils harbor the most diverse populations of any environment with several thousand species (Table 1) [17]. Compared to soil, the number of species in human feces is approximately a factor of 10 lower (Table 1). However, in soils, a large proportion of cells (~80%) is inactive compared to the human gut, where only approximately ~20% of cells are dormant [19].

3. The Human Intestinal Microbiome – Its Development and Evolution

- The microbial diversity in the human gut is a coevolution between microbial communities and their hosts
- Human-associated intestinal microbial communities are more similar to one another than to those of other mammalian species
- When mammals have been classified as herbivores, omnivores and carnivores, their microbiota are clustered into groups that meet these categories
- Interestingly, the gut microbiomes of several mammalian lineages have diverged at roughly the same rate over the past 75 million years

- Contrary to expectations, the number of dietary transitions within a lineage does not influence rates of microbiome divergence but instead, some of the most dramatic changes are associated with the loss of bacterial taxa, such as those accompanying the transition from terrestrial to marine life and hence the loss of contact with soil
- Another dramatic and fairly recent change has been an acceleration of divergence between humans and other primates due to the massive loss of bacteria in the human lineage [33].
- Nutrition/diet was of paramount importance for the clustering pattern in primates
- Human gut communities seem to be comparable to those of other omnivores viewed as unspecialized frugivores, whose flexible diet includes seeds and meat depending on availability
- While most insects contain only dozens of microbial species in their guts, mammalian guts contain thousands of species

- The microbial population of the human gut derived from the ancestors, individually from the mother through vertical transmission during gestation, during birth, and after birth through contact with maternal body sites, with the greatest contribution of the maternal gut
- Within the first three years of life, the gut bacterial phylogenetic composition evolves to an adult-like community
- This process is affected mainly by the way of birth (vaginal versus Caesarian section) and baby feeding (breastfeeding versus infant formula).
- With increasing age, the gut microbiota develop similar to other family members—due to shared households, the environment seems to be a stronger predictor than host genetics
- The ‘grandmother hypothesis’, which is supported by isotope studies [37], older women foraging for tubers was essential for the nourishment of children, which induced greater reproductive fitness [37]. It implicates the ingestion of soil and possible positive consequences thereof [37].

- An important role of underground roots, bulbs and tubers as reported in the diet of early Homo species can still be observed in a Tanzanian population of traditional foragers inhabiting arid savannah woodlands [37].
- The gut community composition must be predominantly shaped by non-genetic factors [40] related to the environment, including lifestyle and diet.
- The GI microbiota can even influence host genes, thereby regulating energy expenditure and storage
- The highest diversity of bacteria and genetic functions ever reported in a human group was found in a remote secluded population of hunter-gatherers in the Amazon jungle
- A study analysed the composition of the gut microbiome from different regions, with lowest bacterial diversity in the urban US citizens compared to rural Amerindian and Malawian populations
- They conclude that short-term as well as long-term changes of the microbiome do occur on an individual level as well as on a community level and contact with soil plays a role in both scales.

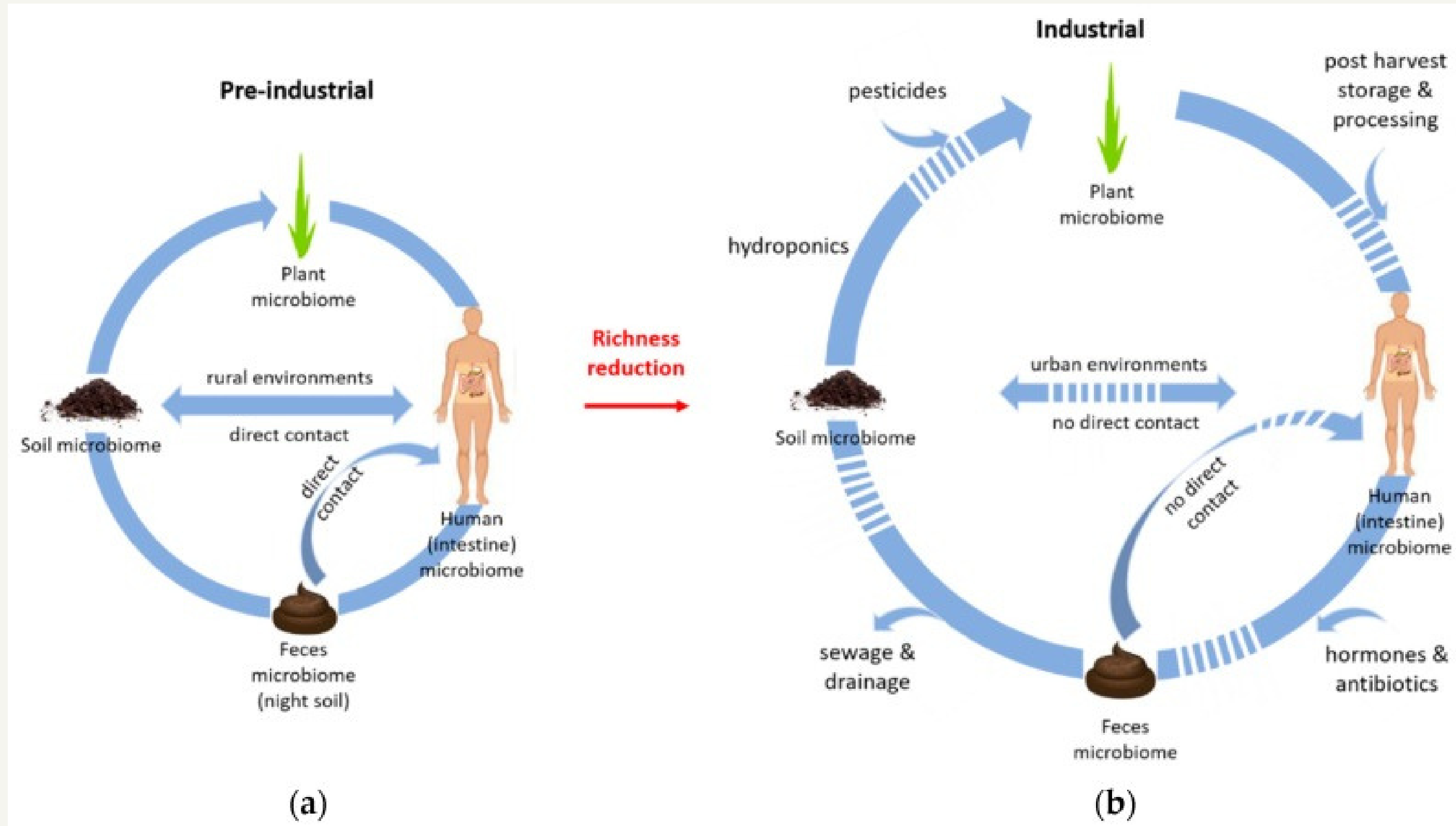
4. Human Intestinal Microbiome and the Environment–Lifestyle

- The loss of contact with outdoor-associated natural beneficial microbiota indirectly affects the human gut microbiome and may have negative consequences on human health
- Research documents that children encountering early contact with environments that are less hygienic such as outdoor settings and farms are less susceptible to develop autoimmune diseases.
- This is supported by the 'hygiene hypotheses', which suggest that environments with rich microbial diversity protect against allergies and autoimmune disorders.
- Nevertheless, it is important to note that modern hygiene, antibiotics, and modern agricultural practices have contributed tremendously to a major reduction in human disease burdens and mortality.

- There is further evidence that soil biodiversity is interrelated with the gut microbiome.
- The gut microbial diversity in mice was increased by exposure to soil microbes [48]. Gut microbial diversity could increase in mice that are in contact with non-sterile soil on a normal diet, while it was unaffected by sterile soil
- Microbes in the soil can change the community composition, and seemed to affect it to a similar degree as diet
- The health of mammals is largely affected by domestication. horses, and most zoo animals.
- A recent study of the gut microbiome of terrestrially living baboons showed that soil is the most dominant predictor for shaping the gut microbiota with a 15 times stronger effect than host genetics [7].
- While the vegetation was not strongly determining the gut microbiota, the fact that the diet of the omnivorous baboons is in close contact with soil supports the potential transmission of soil microbiota for gut colonization

- Rural environments that are rich in microbiota, such as traditional farms, have been shown to have health benefits in humans
- In particular, manual agriculture with close contact to soil, practiced by Amish communities, in a microbial rich rural environment has shown significant beneficial effects on immune functions compared to rural Hutterites who practice mechanized agriculture
- In pre-industrial times, small structured farms dominated and a large part of the population was working in the agricultural sector, pastoralists or hunter gatherers, and so their lifestyle was in close direct contact with nature (i.e., soil, plants
- changes in human life style can ablate the protective health impact due to changes in diet, living conditions and environmental biodiversity

Fig1. The microbiota in our environment influence the human intestine microbiome, via direct contact with soil and feces as well as via food



- Increasing global population and the need for housing and food have intensified agricultural practices and urbanization. Growing industrialization of agriculture results in reduced soil biodiversity
- Already over 50% of the world's population lives in cities, which is expected to increase to approximately two-thirds by 2050 [52]. The ongoing global urbanization has led to a loss of contact with the natural environment by separation from the outdoors [53].
- The reduced contact with microbes in the living environment, but also increased sanitation and use of antibiotics pesticides and hormones [43] depleted the richness of gut microbiota
- The lifestyle of hunter-gatherers, which is close to our ancestors, showed the highest richness of the gut microbiome
- A diet that is high in fibers and complex carbohydrates, which is typical for rural African populations, may preserve gut microbiome richness unlike the consumption of highly processed food that is common in urban areas of industrial western countries

- the richness of gut bacterial species in adults is higher in rural societies as compared to urban communities [41,54,55], while lower beta diversity (variation between individuals) was observed in rural populations
- both environmental exposure and horizontal microbial dispersal are likely to drive the gut microbiome in rural populations, while the urban lifestyle results in the dispersal limitation of microbes.
- This low dispersal can explain the high inter-individual variation of the human gut microbiome of urban citizens (beta diversity).
- Limited dispersal combined with sanitation, medication and dietary changes reduces the successful colonization and hence gut microbiome richness
- Thus, fecal contamination of water resources poses a significant risk for human health by spreading infectious diseases from fecal pathogens [57]. Sanitation practices such as water treatment as well as microbial hazard and risk analyses of drinking water resources are state of the art for developed Western countries and reduce the risk for infections with intestinal pathogens.

- the importance of soil microbiota for human health, increasing the degradation of harmful pollutants, thus reducing the impact of poor anthropogenic sanitation.
- soil has a unique function to provide clean drinking water - enhanced by the soil biodiversity too, likely due to their involvement in, improving soil structure and water infiltration, and hence percolation through the profile
- Soil and animal feces may be important for the evolution of the human gut microbiome considering that, after weaning, infants crawl on the ground and explore the environment with their mouth
- A rich environment during this phase is important to human health for immunomodulatory development in early life.
- Access to more biodiverse areas in urban environments, such as green spaces and parks, is related to health benefits regardless of socioeconomic status [63], which can be associated with the exposure to rich environmental microbiota
- To resume: Soil is therefore a key primary source of a healthy intestinal microbiome of humans.

5. Human Intestinal Microbiome and Diet/Nutrition

- Besides the urban lifestyle and loss of contact with nature, our diet has also changed within the last decennia.
- In addition to more processed nutrition, the intake of more energy-rich food, abundant in sugars and fat, decreases the biodiversity of the intestine [65].
- Often, this results in a vicious cycle as the promoted microbes in the gastrointestinal tract are under selective pressure to manipulate host eating behavior and may generate cravings for unhealthy foods that suppress their microbial competitors
- Medication, in particular the intake of specific drugs, mainly drives the gut microbiome of Western populations

- Increased medical antibiotic intake as well as increased meat consumption has led to an increasing number of antibiotic-resistant bacteria and genes and has caused serious environmental problems
- the gut is the preferred habitat for antibiotic resistance bacterial proliferation due to high population densities [21].
- Among antibiotic resistance areas, hot spots are municipal wastewater systems that show high loads of bacteria [67].
- In this context, the consumption of genetically modified plants should also be considered with caution, because the modified genes could be transferred via bacteria into the rhizosphere or the intestine
- diet is relevant for shaping the human gut microbiome is further supported by the study of Martinez et al. [54] which suggests that a diet rich in plant derived carbohydrates and fibers is a stronger predictor for gut microbial diversity patterns in the less developed areas of Papua New Guinea than antibiotics, although this is a locally common medication

- The gut microbiome of hunter-gatherers with no access to medication [55] showed significant differences in phylum- or genus-level abundance between males and females, indicating a traditional separation of work and diet between genders
- women are more likely to stay in one place with the family having a diet rich in tubers and fibers, while hunting was conducted by men
- Bifidobacteria are a vital component of gut microbiome of the Western civilization due to dietary preferences, such as dairy and meat consumption
- The microbiomes of non-Westernized populations resemble those of vegetarians and vegans
- Specific types of food result in predictable shifts in intestinal microbiota, and hence the human intestinal microbiome can be directly affected by the diet
- Human diet has changed in the industrial age from a mainly seasonal and locally produced large variety of crop species to few high-yielding varieties.
- Together with increasing monoculture cropping, the use of pesticides (Figure 1) further reduces soil biodiversity.

- As soil microbes colonize the plants, soil biodiversity and plant microbiome diversity may be different before and after harvest
- post-harvesting operations before consumption include: cleaning, milling, separating, mixing, drying/hydrating, heating, dispersing, packaging, storage, distribution, transport and others
- sustaining soil biodiversity, in particular symbiotic microbes, could reduce food preservation measures.
- Beside the reduction of pest risks, root symbionts can increase the nutritional quality of food/crop, including vitamins, mineral content (macro- and microelements), and antioxidants, together with other secondary plant metabolites that are beneficial for human health
- This underlines that a healthy diet and lifestyle are coupled via the consumption of food from farms which use soil management practices fostering soil biodiversity.

- Modern changes in farming and nutrition also include plant breeding efforts, e.g., to reduce the bitterness of Brassicaceae, such as broccoli, cauliflower, and cabbage. The bitterness is due to glucosinolates, which help the plant to resist pathogens and is assumed to be an anti-cancer metabolite. Hence, the digestive function of glucosinolates is mostly depleted in the human gut
- As with bitter plant species, the consumption of fresh fruit that are almost un-processed is beneficial for human health specifically as soil biodiversity stimulates the secondary metabolite production
- the effects on secondary metabolites via high or low soil biodiversity are lost during processing
- In contrast to traditional smallholder farming, large scale farms, rather common in many industrialized countries, perform intensive farming practices, such as monoculture cropping of few plant species for optimizing yields.

- This has reduced the variety of food for humans and additionally increased the potential threats through contaminants due to the use of agrochemicals.
- A recent meta-study of agricultural soils has shown that organic farming is a means to enhance soil microbial abundance and activity

6. Soil Microbiome as a Functional Ecosystem – Potential Links to the Gut Microbiome

- Globally, soils are highly diverse, as are their microbes. There are only a few species that can be found in all soils, while there are numerous rare species that only occur in particular soils or geographical areas
- [global soil biodiversity atlas and homepage](#) was elaborated by several research groups
- Thus, it has become possible to compare the geographical data of soil microbiomes with human gut microbiomes

- While there is still a lack of data for comparing the gut and soil microbiome over large geographical areas and a number of critical methodological issues, there seem to be fundamental differences between the two habitats.
- One major difference is that soil is a medium limited in carbon and energy and microbes maintain a starving-survival lifestyle [77], whereas, in the human intestine, carbon and energy are abundant.
- The situation is different in the rhizosphere, where a constant proliferation of C-rich root exudates exists, providing nutrients and energy. The microbial community of the rhizosphere is related to the root endophyte community as well as the bulk soil community
- Internal and external symbionts at plant roots differ, with the former like bacteria in animal guts while the latter more akin to those colonizing the skin
- There are many functional similarities between the plant rhizosphere and the human gut microbiome:

(i) The gut and rhizosphere are open systems with large surface areas overpopulated with microbes.

(ii) The gut and rhizosphere are characterized by a gradient of oxygen, water and pH, resulting in a diversity of niches.

(iii) The gut and rhizosphere microbiome structures are shaped according to host genotype and age. Both provide protection against pathogens and modulate the immune system

- These cross-kingdom similarities in microbiome ecology lead to the discussion of similar strategies for the biocontrol of pathogens in plants and in humans
- One commonly observed phenomenon is that the survival rates of invaders are inversely related to the diversity of the native microbiome.
- These findings point toward the paramount importance of sustaining rich diversity in soils/rhizospheres in the first place in order to avoid the necessity for biotechnological interventions at a later stage (e.g., introduction of probiotics or symbionts)

- The rhizosphere microbiome is related to soil type, moisture, age, plant genotype and root lysates and exudates [5]. Similar to the human gut, the rhizosphere offers a vast surface (via root hairs, or microvilli [5]) and hence multiple microenvironments to be colonized by a large number of species.
- These microenvironments are reduced if there is extensive soil tillage or in hydroponic cultivation.
- Bulk soil generally shows a more stable population of slower growing microbiota, such as Acidobacteria, Chloroflexi, Verrucomicrobia, and Planctomycetes, which have been previously described as soil oligotrophs

(Oligotrophs are characterized by slow growth, low rates of metabolism, and generally low population density)

- The application of excessive doses of mineral fertilizers reduces survival conditions for soil oligotrophs

- Besides improper land management, land use change has serious effects on microbial communities.
- In particular, soil sealing and soil erosion lead to the loss of large areas of soils together with their typical indigenous microbial populations, a loss which cannot be reverted
- Also biofilms can be found in both the human GI tract/gut [89,90] and the rhizosphere [91,92]. The gut and soil rhizosphere are nutrient-rich environments and follow circadian cycles, such as the fixation of nitrogen in rice roots, which is higher during daytime than in the dark, as well as the hormone melatonin in the human GI tract, which controls the biological clock
- The gut as well as the rhizosphere microbiome can be considered as “superorganisms” - important for the health and performance of the host.
- (i) the gut microbiota are important for producing essential amino acids and vitamins such as B12 and K, and (ii) the root microbiota for producing hormones that are promoting plant health by improved nutrient acquisition, resistance to abiotic (i.e., drought) and biotic (i.e., pathogens) stress, and by sustaining growth

- The deficiency of some micronutrients in humans, derived from nutrient-depleted soils, can have substantial effects as co-factors in metabolism, modulating enzyme activities, or functioning as coenzymes
- Any reduction of aboveground and belowground soil biodiversity threatens soil ecosystem functions
- losses in soil biodiversity are due to direct anthropogenic activities.
- Indirect anthropogenic effects due to climate change will increasingly impact soil functioning through stressing soil organisms and affecting biodiversity, as indicated by soil warming experiments
- mechanization of agriculture in combination with the use of agrochemicals such as mineral fertilizers and pesticides, reduce soil biodiversity.
- the use of antibiotics and hormones have substantial effect on the gut microbiome of the Western population was recently proven

7. Summary

- Recent research data indicate that the modern lifestyle/environment is the most active driver in shaping the human intestinal microbiome despite the confounding influence of dietary habits, culture, and host genetics.
- Furthermore, specific ways of agricultural practices, especially soil management, may improve the current food quality.
- recent findings suggest the investigation of the soil and root microbiota in more detail may identify effects on human health, possibly, among others, by adopting a lifestyle of former generations

- This lifestyle, such as the reduced consumption of livestock and dairy products and the intake of a higher diversity of nutritional fibers and bitter substances may have beneficial effects on our health.
- The intake of mostly unprocessed organically grown regional products is one way towards this goal.
- Further, wild relatives of the currently used high-yielding crop varieties could increase aboveground and belowground biodiversity, and hence provide benefits to soil and human health, e.g., through reintroducing lost beneficial microbes.
- A rich soil microbiome would also have several advantages for the terrestrial ecosystem through increased nutrient use efficiency and uptake, which may improve plant yields as well as plant resistance and resilience against global climatic change and biotic stressors.

8. Conclusion

- The soil contributes to the human gut microbiome—it was essential in the evolution of the human gut microbiome and it is a major inoculant and provider of beneficial gut microorganisms.
- In recent decades, however, contact with soil has largely been reduced, which together with a modern lifestyle and nutrition has led to the depletion of the gut microbiome with adverse effects to human health. Therefore, we suggest increasing research on the geographical and functional relationships to identify the causes and effects between soils and gut microbiota in order to benefit human health and the environment.



Thank you!



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