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How hydrogen sulfide deposition from oil exploitation may affect bacterial communities and the health of forest soils in Congolese coastal plains?

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The hydrogen sulfide (H₂S) deposition from oil exploitation occurring since 1969 may potentially affect bacterial communities in acacia and eucalyptus plantations of the Congolese coastal plains. These plantations have been implemented on previous native savannas to use the unsuitable soils for agriculture, provide pulp wood and fuel wood energy, and preserve the natural forests. Increased carbon (C) and nitrogen (N) stocks in stands containing acacia relative to baseline (eucalyptus) stocks have been reported. Phosphorus availability also improved in coarse particulate organic matter (4,000-250 µm) in afforested stands as compared to natural savannas. Investigation of the abundance of bacterial phyla by metabarcoding of the 16S rRNA bacterial gene in different stands of monocultures and mixed-species stands reveals the prevalence of Actinobacteria in all stands. This phylum is generally associated with the presence of sulfur in industrial areas and has a crucial role in organic matter decomposition. This may be linked to improved soil attributes (C, N, and P) and related to oil exploitation in addition to natural processes. This review shows, therefore, how potentially human activities may impact bacterial community composition, which may further change other soil attributes. It also acknowledges that the sustainability of forest plantations on inherently nutrient-poor soils strongly relies on interactions between soil functions, the environment, and human activities driven by soil organisms.

KEYWORDS

human activities, forest plantations, soil bacterial communities, C sequestration, soil attributes (C,N,P, S)

Introduction

Taking into consideration the potential risk of the endangered savanna ecosystems (1, 2), infertile soils unsuitable for agriculture beneath the tropical savannas in the Congolese coastal plains have been used for fast-growing plantations such as eucalyptus since the 1950s (3, 4). Soils are Arenosols, the most represented soil type in Africa (22%) (https://esdac.jrc.ec.europa. eu/content/soil-map-soil-atlas-africa). They span over 6 million hectares, from the Democratic Republic of the Congo (DRC) through the Republic of the Congo (RoC) to Gabon (5–7) in Central Africa, which is home to the second largest rainforest ecosystem in the world (https://www.onegreenplanet.org/animalsandnature/the-worlds-second-largest-rainforest-congo/). These soils are sandy (>90% of sand) with an inherently nutrient-poor status, i.e., very low soil organic matter (SOM) content (<1% of SOM) (8).

Afforestation or reforestation is a significant forest management practice worldwide (9, 10) to sequester carbon (C) in both soil and biomass, with a potential impact on mitigating climate change, furnishing wood, and restoring land degradation (11-14). Furthermore, afforestation also aims to preserve natural forests and ensure other soil and ecosystem services (10; https://www.conserve-energy-future.com/ importance-advantages-afforestation.php). Forest plantations established in the Congolese coastal plains help build healthier soil and enable economic and environmental benefits such as nontimber products, production of pulp (for the industry), and fuel wood energy (for the local population). In fact, 94% of the population relies on them for their energy needs, both on their own and in the neighboring countries of the Congo Basin (11). In addition, when well managed, these forest plantations enhance soil health and ecosystem biodiversity (6, 7, 15).

To improve soil fertility and sustain diminishing forest productivity after the first rotation, since nutrients are exported through wood harvest and poorly replaced with fertilizers (16), nitrogen-fixing trees (NFTs) such as acacias have been introduced in the eucalyptus plantations in the 1990s (17, 18). These mixed-species (acacias and eucalyptus) plantations improved soil health, i.e., soil fertility through increased N status (19-22) and enhanced phosphorus cycling in both forest floor and soil (23-25). However, the decline in available P in stands containing acacia (26) due to symbiotic N₂ fixation (27) was reported. These plantations may also have the potential to enhance soil sulfur concentrations, which appear to be two to three higher than commonly observed (28), since although considered an essential plant nutrient, soil S concentration is only about 10% of that of the total N (29). Benefits have also been reported through C sequestration in soil (6, 19) and increased stand wood biomass, i.e., forest productivity (21, 30), that boost the potential to mitigate climate change through increased C stocks (6, 14, 31).

Soil habitat, i.e., its diversity, regulates the conservation and productivity of ecosystems (32). Important functions, such as decomposition of organic residues, nutrient cycling, bioturbation, suppression of soil-borne diseases and pests, and other environmental services (watershed protection, preservation of soil structure, mitigation of greenhouse gas emissions), strongly rely on soil biota (33). Afforestation and the introduction of nitrogen-fixing trees in forest plantations change soil biota, e.g., may lead to shifts in the composition and structure of faunal, microbial, bacterial, and fungal communities (34-38). Peerawat et al. (39) reported that the bacterial and macrofaunal diversity are more resistant to land-use conversion than the fungal diversity. Soil moisture favors positive correlations between mesofaunal abundance and diversity, and it drives ecological interactions between soil mesofauna and microorganisms in acacia plantations in Brazil (40). In addition, Zagatto et al. (41) reported that Acacia mangium litter has exclusive orders in the groups Symphyla, Protura, and Pseudoscorpionida, which are considered indicators of environmental quality. Acacia litter is most favorable to mesofauna compared to eucalyptus due to its high nutritional quality and above-average biomass, which induces high fauna density and diversity.

Anthropogenic activities and biogeochemical processes are obviously linked and act on both terrestrial and aquatic ecosystems and the environment with an undeniable impact on the well-being of living organisms, i.e., plants, animals, and humans (42-45). Hydrogen sulfide (H₂S) is naturally present in the atmosphere at low concentrations (0.02 μ l L⁻¹) (46–48). Nevertheless, this threshold level may be surpassed in areas with volcanic activity and polluted industrial or livestock production (46, 49), such as the Congolese coastal plains in the Republic of the Congo. Regions harboring higher concentrations of H₂S have higher microbial species diversity with the dominance of the Actinobacteria phylum (49), while sulfur stimulates growth and enhances the biomass of Actinobacteria, a gram-positive bacteria (42). Actinobacteria harbor a high ability to decompose a broad range of hydrocarbons, pesticides, and feather waste (50). Increased C and N stocks at 7 years of the first rotation of forest plantations (stands containing acacia, 19, 22) and phosphorus availability (afforested stands, 23) may be related to prevalence of Actinobacteria determined using metabarcoding of the 16S rRNA bacterial gene (31). Besides, H₂S resulting from natural processes and enabling the presence of Actinobacteria (48), the prevalence of Actinobaceria may result from human activities (31, 49) and potentially benefit to soil attributes such as C and P dynamics. Sustaining these ecosystems strongly depends, therefore, on interactions between bacterial communities related to other soil functions, the environment, and human activities.

Up to date, few studies to evaluate microbial communities (bacterial or fungal and macrofauna) and soil biodiversity status have been conducted in the forest plantations of the Congolese coastal plains. Enhanced activity of edaphic macroarthropod communities, i.e., the dominance of cockroaches in acacia litter as opposed to ants in eucalyptus, has been reported in the forest plantations of the Congolese coastal plains (17). Albeit there is no difference in Actinobacteria, the prevalent phylum among stands, both its prevalence and strong correlation to sulfur (S) have been noticed at all levels of the taxonomy using metabarcoding of the 16S rRNA bacterial gene. In addition, a shift in the bacterial community composition was evidenced by the dominance of Proteobacteria in eucalyptus monoculture against Firmicutes in stands containing acacia (51). Therefore, further studies are needed to confirm this trend. The current review paper aims to strengthen and confirm our knowledge on (1) how, in addition to natural processes, human activities (H₂S deposition from oil exploitation) can modify soil bacterial community composition and soil health; and (2) how the prevalence of Actinobacteria phyla can benefit soil attributes and boost SOM dynamics and soil health through C sequestration and/or land restoration.

Human activities such as oil exploitation leading to H₂S emissions may modify soil bacterial community composition and soil health

Studies reporting the improvement in soil health of sandy soils in forest and agroforestry systems to fight hunger and desertification, boost forest conservation, and ecosystem biodiversity, and mitigation to climate change have been performed in Central Africa (6, 7, 19, 52, 53). Changes occurring in soil processes and functions are driven by soil organisms (54). The role of soil biota in driving and enhancing nutrient dynamics and cycling to improve soil health is crucial, as its interaction with the environment and human activities to ensure soil functions (31, 40, 41, 54). Along with changes in soil organic matter quantity and quality, enhanced activity of edaphic macroarthropod communities through the dominance of ants in eucalyptus against cockroaches in acacia litter has been reported in mixed-species forest plantations of the Congolese coastal plains (17). More than two decades later, bacterial community composition reported Actinobacteria as the dominant phylum in all stands, with Firmicutes as the second prevalent phylum in stands containing acacia and Proteobacteria in monoculture of eucalyptus (51). Anthropogenic activities affect the environment, i.e., both terrestrial and/or marine ecosystems, and may impact the soil microbiome, e.g., its richness and/or diversity and soil health (36, 40, 41, 43, 55, 56). This can be illustrated by the conceptual scheme demonstrating how human activities, the environment, and biogeochemical processes are linked to human well-being through soil health and contribute to four out of the 17

sustainable development goals (SDGs) (Sustainable Development Goals: 17 Goals to Transform our World | United Nations, Figure 1). The figure shows how activities such as oil exploitation, mining, building, and land-use change (e.g., conversion of forest to croplands) may endanger soil health and delay the achievement of these targeted SDGs of the United Nations. Human well-being is linked to SDG 3, i.e., "Good health and well-being," while food security as the first challenge in Figure 1 is linked to SDG 2 "Zero hunger." The second challenge, i.e., mitigating climate change, is linked to SDG 13, "Climate action." Soil sustainable management and co-benefits as a third challenge are linked to SDGs 2 and 15, "No hunger," and "Life on land," respectively. The latter SDG, i.e., SGD 15, "Life on land," is also linked to the fourth challenge, which is the conservation of biodiversity (Figure 1).

To highlight and better understand these interactions, some examples from different countries have been reported in Table 1. In the heaps of limestone mines in North-West Russia, highthroughput sequencing of soils revealed significant differences in *Proteobacteria*, *Chloroflexi*, *Acidobacteria*, and *Actinobacteria* phyla (44, Table 1). The authors noted that *Actinobacteria* was the only phylum presenting the most profound increase of

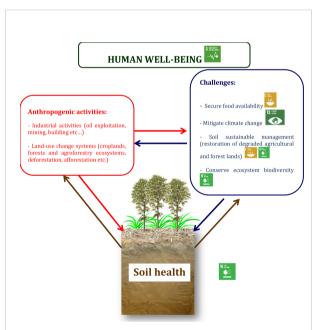


FIGURE 1

Human activities, the environment, and biogeochemical processes are linked to its well-being. Human well-being and challenges are linked to four out of 17 sustainable development goals (SDG) of the United Nations (Sustainable Development Goals: 17 Goals to Transform our WorldUnited Nations): SDG 2: end hunger, achieve food security, improve nutrition, and promote sustainable agriculture; SDG 3: ensure healthy lives and promote well-being for all at all ages; SDG 13: take urgent action to combat climate change and its impacts; and SDG 15: protect, restore, and promote sustainable use of terrestrial ecosystems; sustainably manage forests; combat desertification; halt and reverse land degradation; and halt biodiversity loss.

Location	Type of activities	Soil type	Soil microbiome	C sequestration	Land restoration	References
Worldwide	Natural	-	Actinobacteria high guanine and cytosine content in DNA)	Important in decomposing organic material and C cycle	Vital in organic matter turnover (nutrient replenishment)	Anandan et al. (50)
Russia (North- West)	Anthropogenic (mines of limestones, phosphorites, and shales)	Rhendzic leptosols Embryonic podzols	Proteobacteria, Chloroflexi, Acidobacteria, and Actinobacteria (intensive increased of OTUs)		2, 26, and 70 years of self- restoration	Abakumov et al. (44)
China (Chongqing, Changshu, and Yingtan)	Agricultural sites (rice fields)	-	Proteobacteria, Firmicutes, Bacteroides, and Actinobacteria	Boosted by Actinobacteria		Bao et al. (57)
Congolese coastal plains (Central Africa)	Acacia and eucalyptus plantations	Arenosols	Prevalence of <i>Actinobacteria</i> in all stands: <i>Proteobacteria</i> (eucalyptus) and <i>Firmicutes</i> (stands containing acacia)	Increased C stocks (stands containing acacia)		Koutika et al. (19, 51) and Koutika (6)
South-eastern Brazil (Sao Paulo State)	Mixed-species plantations of acacia and eucalyptus	Ferralsols	Dominance of <i>Proteobacteria</i> and <i>Acidobacteria</i> (0 and 300 cm) Increased soil microbial richness	Accumulation of C and N in soil organic fractions (eucalyptus and acacia stands)		Pereira et al. (36, 37)
Northeast China	Experimental site of continuous rice cropping	Haplic Phaeozems	Prevalence of: Proteobacteria, Bacteroidetes, Firmicutes, Acidobacteria, and Verrucomicrobia	Increased soil total organic C contents and active soil organic carbon (SOC) fractions	Relative enhancement of abundances of microbes involved in the carbon cycle	Yan et al. (43)

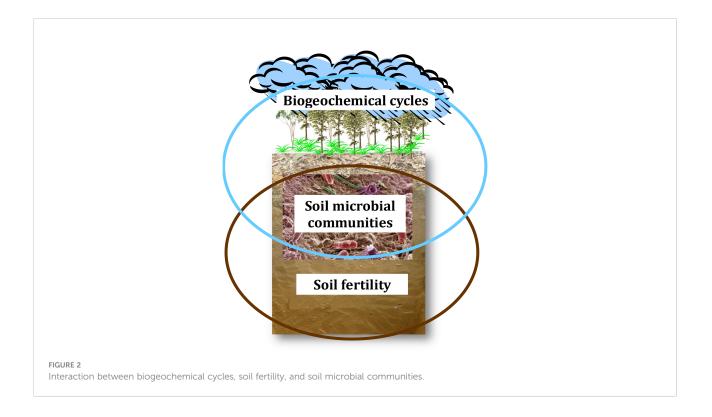
TABLE 1 Effects of different activities on soil microbiome, soil C sequestration, and land restoration worldwide.

operational taxonomic units (OTUs) (up to eight times more in 200 years of soil). H₂S may become a threat to the surrounding environment and public health, as it may be a source of odors (46, 47). To acknowledge the sulfur bioconversion process in landfill covers and to establish techniques to manage odor pollution, Xia et al. (47) reported both Comamonas and Acinetobacter (Proteobacteria phylum) as genera that have a crucial role in metabolizing H₂S in the waste biocover soil. The authors also argued that the decline in the pH values occurring in landfill covers is potentially a result of adsorption, absorption, and biotransformation of H₂S. In the forest plantations of the Congolese coastal plains, the H₂S, which probably is partially derived from oil exploration (occurring since 1969), may have enhance the prevalence of Actinobacteria phylum sensitive to S concentrations (49, 51). No difference has been noticed regarding the Actinobacteria, which harbors prevalence in all studied stands, i.e., in the monoculture acacia and eucalyptus and mixed-species stands (50% acacia and 50% eucalyptus) (51). This may have further boosted its growth and biomass, as commonly found in industrial areas (49), and enhanced organic material dynamics since Actinobacteria play a key role in decomposing organic materials (50). Increased C stocks reported in stands containing acacia (19, 22) or an increase in available phosphorus in afforested soils (23) reported in mixedspecies forest plantations in coastal plains may, therefore, be linked to the prevalence of Actinobacteria phyla in the bacterial community composition of these soils (51).

Other human activities, such as land-use changes, i.e., the establishment of cropping, forest and agroforestry systems, the indirect impact of human activities leading to climate change or land degradation may also change the soil microbiome and soil health (54). It has been reported that the dominant groups of bacterial communities in acid soils are commonly Acidobacteria and Proteobacteria (49, 58). An investigation of the bacterial community structure of monoculture acacia and eucalyptus forest plantations along a depth profile (0 to 800 cm) revealed the dominance of Proteobacteria and Acidobacteria (recurrent in samples between 0 and 300 cm) with the prevalence of Firmicutes and Proteobacteria in pure eucalyptus (36). Nonetheless, acid and sandy soils (pH <4.5 and >90% sand) harboring the bacterial community composition dominated by Actinobacteria, followed by Proteobacteria, Firmicutes, and Acidobacteria contained higher C and N stocks in stands containing acacia relative to eucalyptus in the Congolese coastal plains (19, 51). As oligotrophic bacteria, even in the nondominant phylum, Actinobacteria play an ecophysiological role in carbon cycling, mainly in less-fertile soils due to their relatively larger proportion of genes implicated in plant residue decomposition and crucial involvement in interspecies interactions (57). In a continuous rice cropping system in Northeast China, Yan et al. (43) outlined the dominance of Proteobacteria, Bacteroidetes, Firmicutes, Acidobacteria, and Verrucomicrobia based on their relative abundances, along with an enhanced soil microbial richness; however, the authors found no difference in soil microbial diversity. Hence, the response to the first question is given: it shows how human activities (industrial, agricultural) do change the soil bacterial communities in various ecosystems and do impact soil health and benefits and human well-being through four out of the 17 SDGs of the United Nations (Sustainable Development Goals: 17 Goals to Transform our World | United Nations, Figure 1 and Table 1).

Prevalence of *Actinobacteria* phyla may benefit soil attributes and boost SOM dynamics and soil health through C sequestration and/or land restoration

Industrial processes such as the combustion of biomass and fossil fuels, along with livestock production, generate atmospheric H_2S in addition to natural sources (46). Investigation revealed the dominance of the *Actinobacteria* phylum in regions with high concentrations of H_2S exhibiting to what extent the sulfur cycle is influenced by the dynamic environmental conditions (49). The *Actinobacteria* phylum is among the most widely distributed bacterial phyla in soils that harbor a vast capacity to degenerate plant residues *in vitro* (50, 57, 59). As a matter of fact, *Actinobacteria* play an essential part in organic matter turnover, the carbon cycle, and humus formation by decomposing organic materials such as cellulose and chitin and filling up the supply of nutrients in the soil (50). In addition, Actinobacteria fix nitrogen, involving an enhanced N availability during microbial-driven plant residue decomposition (60) and the production of antibiotics (57). Both characteristics lead to strengthening their ability to procure carbon sources, preserving them from environmental perturbations (57, 59, 60), potentially enhancing C sequestration and having an impact on both mitigating climate change and restoring degraded lands. Microbial community composition is linked not only to biogeochemical nutrient cycles of N, C, S, C/ N, and available P and soil fertility (Figure 2) but also to soil functions, i.e., C sequestration, N, S, O, and P cycles and availability as well as to land reclamation (Table 1). Figure 2 schematizes the fundamental role of soil organisms (e.g., soil microbial communities) within biogeochemical cycles and soil fertility to enable the regulation, conservation, and efficiency of ecosystems (32). Soil organisms are the key parameter in the physical, chemical, and biological improvement of soil fertility, enabling soil functions such as C accumulation or N mineralization. Phylum composition and abundance of the rhizomicrobial communities (Pinus tabuliformis Carr. Forests) were investigated using high-throughput DNA sequencing in North China (55). The authors reported an enhanced Actinobacteria, Proteobacteria, and Firmicutes abundance, even though the Proteobacteria were recognized as keystone organisms for root-driven C accumulation in primary succession and Basidiomycota as the core for root-driven C accumulation in climax communities (55).



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Furthermore, changes due to human activities, such as afforestation, through improved soil health, i.e., enhanced soil attributes (C, N, P, S), may be linked to bacterial community composition (prevalence of Actinobacteria phylum) in the Congolese coastal plains. Increased C stocks, i.e., 0.8 t ha⁻¹ in acacia monoculture stands (100%) and 1.9 t ha⁻¹ in the mixedspecies (50% acacia and acacia 50% eucalyptus) stands relative to the eucalyptus monoculture (100%) down to 25 cm at the end of the first 7-year rotation were reported (6, 19). Higher N stocks in stands containing acacia, i.e., 1.25 ± 0.02 t ha⁻¹ (acacia monoculture) and 1.28 \pm 0.03 t ha⁻¹ (mixed acacia-eucalyptus) relative to 1.19 \pm 0.02 t ha⁻¹ (eucalyptus monoculture) stands were also outlined in the same depth (19). In addition, it has also been reported that during the first 2 years of the second rotation, the stands containing acacia harbored higher values of the cumulative net N stocks, i.e., 343 ± 21 kg ha⁻¹ (acacia) and 287 \pm 17 kg ha⁻¹ (acacia–eucalyptus) compared to 189 \pm 12 kg ha⁻¹ (eucalyptus) (22). This improvement in N status is also revealed through the N concentration in coarse particulate organic matter (POM, 4,000-250 µm), which was 30% higher in acacia (100%) than in eucalyptus (100%) stands at year 2 of the second 7-year rotation at 0-5 cm depth (20). Besides the increase in C and N concentrations in stands containing acacia compared to eucalyptus, available phosphorus (P) was lower in stands containing acacia relative to eucalyptus, while the contrary tendency was observed for S (28). Higher S concentrations were reported in stands containing acacia harboring the higher C stocks relative to eucalyptus monoculture (6, 28). Even though P is needed for the symbiotic atmospheric N₂ fixation for the nitrogen-fixing species (27), and a decline in available P was reported in stands containing acacia (26), all afforested stands contained more available P than natural savannas (23). This highlights the targeted ecosystem's potential for mitigating climate change (C sequestration), contributing to both food security through improved soil fertility (mainly N), sustainable soil management (land restoration), and human welfare, i.e., and four (2, 3, 13, and 15) of the seventeen SDGs of the United Nations (6, 14, 28, 31, 37). Different studies published worldwide confirmed the strong reliance of forest plantation ecosystems, especially those on inherently nutrient-poor soils, such as those of the Congolese coastal plains and the entire Congo Basin (6, 11, 31), on the link between soil functioning (C sequestration, nutrient cycling, etc.), the environment, and human activities driven by soil organisms.

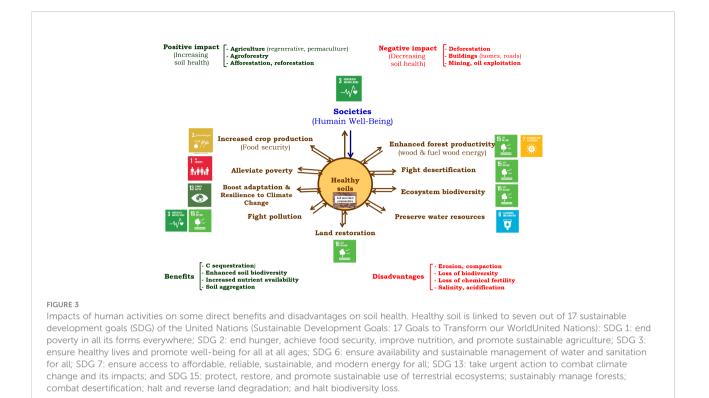
Overall effect of human activities on soil health

Human activities may shape the environment and affect processes within plants, soils, and the environment driven by soil biota (31, 35, 44, 54). In the review, these impacts have

been evaluated mainly at the soil level, especially with regard to its health (37, 40, 41, 52, Figure 3). It is well known that SOM dynamics involve changes in soil health and enhance soil functions, with further impact on ecosystem biodiversity and the environment (32, 35, 61). Soil functions have the potential to influence human health by enhancing or inhibiting some processes that are regulated by soil organisms, leading to secure food, mitigating climate change, and sustaining soil management (land restoration) and ecosystem biodiversity (35, 37, 53). The overall schematic representation of the review is considering soil, especially its health, which relies on the interaction between the environment, soil functions driven by soil organisms, and human activities and well-being. At the very beginning are the human activities that positively or negatively impact soil health. Negative impacts may be direct as those mentioned in this review, i.e., deforestation, building (roads, houses), mining, and oil exploitation. There are also indirect negative impacts, such as those linked to climate change or land degradation initiated by humans.

Positive impacts of human activities may also be direct and indirect. Only direct impacts have been considered in this review (good agricultural practices, agroforestry, afforestation, and reforestation). These human activities foster soil health by enabling goals such as food security, reduction of poverty, adaptation and resilience to climate change, fighting pollution and desertification, restoring degraded lands, preserving water resources, boosting ecosystem biodiversity, and sustaining forest productivity (providing wood and fuel energy and conserving natural forests). These goals may contribute to seven out of the 17 United Nations SDGs (Sustainable Development Goals: 17 Goals to Transform our World | United Nations), i.e., SDG 1 "No poverty," SDG 2 "Zero hunger," SDG 3 "Good health and Wellbeing," SDG 6-"Clean water and sanitation," SDG 7 "Affordable and clean energy," SDG 13 "Climate action," and SDG 15 "Life on land." On the contrary, human activities inducing negative impacts on soil health will threaten the mentioned above goals, i.e., the seven out of 17 SDGs (Figure 3).

Carbon sequestration, enhanced soil biodiversity, increased nutrient availability, and soil aggregation are among the benefits resulting from the positive impacts of human activities on soil health. Disadvantages (erosion, compaction loss of biodiversity, loss of chemical fertility, salinity, and acidification) on the opposite lessen the ability of soil to fulfill its functions and meet the seven out of 17 SDGs of the United Nations. It is very important to notice that soil microbial communities, i.e., soil organisms in general, are at the center of this schematic representation (Figures 2, 3). It shows that soil organisms drive and regulate soil functions at the first level and then ecosystem services at the second level through soil functions (31-33, 56). Human activities may shape the environment (42, 43), but the functions of soil, ecosystem, and environment rely strongly on their interaction i.e., the interaction between soil organisms, plants, environment, and human activities.



Conclusions

This review highlights the potential impact of human activities on soil attributes in general and on soil bacterial community composition in particular. These impacts may positively or negatively affect soil attributes and boost or lessen soil health. It is also reported that the sustainability of forest plantations on infertile soils strongly relies on soil organisms that regulate the interaction between soil functions, the environment, and human activities. The current findings will not only help sustain forest productivity and promote soil health at the physical, chemical, and biological levels but also enable population welfare. They will also help to prevent land degradation, mitigate climate change, provide (wood and fuel energy), i.e., leading to preserve natural forests in the entire region of the Congo Basin, and finally, contribute to seven out of the 17 SDG United Nations goals.

Furthermore, the beneficial impact of the predominant phylum *Actinobacteria* on SOM decomposition is revealed by improved soil attributes (increased C, N stocks, and P availability). The potential impact of human activities (oil exploitation) on the bacterial community of forest ecosystems in the Congolese coastal plains must be confirmed. Further studies must be conducted on the forest plantations located in the coastal plains, areas neighboring Brazzaville, and the northern part of the country. These studies should attest to the strong reliance of forest plantations on the interaction between soil functions, human activities, and the environment. They will also show how the attributes of fragile and inherently infertile soils are strongly linked to the vegetation cover (afforestation) and the environment, determining their development and sustainability as well as the prevention of their degradation.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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