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Posted Date: 1 November 2024

doi: 10.20944/preprints202411.0003.v1

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Biofertilization and Bioremediation - How Can Microbiological Technology Assist the Ecological Crisis in Developing Countries?

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Abstract: The increasing global demand for food caused by a growing world population has resulted in environmental problems, such as the destruction of ecologically significant biomes and pollution of ecosystems. At the same time, the intensification of crop production in modern agriculture has led to the extensive use of synthetic fertilizers to achieve higher yields. Although chemical fertilizers provide essential nutrients and accelerate crop growth, they also pose significant health and environmental risks, including pollution of groundwater and and other bodies of water such as rivers and lakes. Soils that have been destabilized by indiscriminate clearing of vegetation undergo a desertification process that has profound effects on microbial ecological succession, impacting biogeochemical cycling, and thus the foundation of the ecosystem. Tropical countries have positive aspects that can be utilized to their advantage, such as warmer climates leading to increased primary productivity and, as a result, greater biodiversity. As an eco-friendly, cost-effective, and easy-to-apply alternative, biofertilizers have emerged as a solution to this issue. Biofertilizers consist of a diverse group of microorganisms able to promote plant growth and enhance soil health, even under challenging abiotic stress conditions. They can include plant growth-promoting rhizobacteria, arbuscular mycorrhizal fungi, and other beneficial microbial consortia. Bioremediators, on the other hand, are microorganisms that can reduce soil and water pollution or otherwise improve impacted environments. So, the use of microbial biotechnology relies on understanding the relationships between microorganisms and how they affect their environment, and, inversely, how abiotic factors influence microbial activity. The more recent introduction of genetically modified microorganisms into the gamut of biofertilizers and bioremediators requires further studies to assess potential adverse effects in various ecosystems. This article reviews and discusses these two soil correcting/improving processes with the aim of stimulating their use in developing tropical countries.

Keywords: microorganisms; biostimulation; biogeochemical cycles; extreme environments; soil pollution

1. Introduction

Developing countries face a series of critical environmental processes due to the mismatch between their pace of development and their role in the global context [1]. Given their relatively short history, they have not had sufficient time to catch up with the global pace set by developed nations. Consequently, these countries are already showing signs of the impact of recent industrialization and urbanization [2]. Rapid development, population growth, inadequate responses to climate and environmental risks, and inefficiencies in governance and environmental management pose substantial environmental challenges for developing countries.

A significant number of these countries are located in warmer climates, allowing them to become major global food producers and leading to the excessive use of their land for agriculture. This can lead to biomes rich in biodiversity being destroyed to make way for monocultures of food plants, depleting ecosystems and their soils. Chemical fertilizers introduced into these systems to boost agricultural productivity disrupt the local soil geochemical balance and affect adjacent environments such as rivers, lakes, and coastal areas [3]. Ultimately, this process can lead to imbalances in water bodies, resulting in hyperproductivity and subsequent eutrophication [4].

In these sense, tropical soil ecosystems exhibit a rich tapestry of diversity and complexity, setting them apart from their temperate counterparts. Within the expansive realms of the tropics, a myriad of ecosystems serves as the canvas for diverse microbial niches and evolutionary processes. The relationship between latitude and bacterial diversity is not statistically significant, but communities can be aptly characterized by their ecotypes and functional attributes. Delving into desert soils, where extremes of solar radiation, minimal precipitation, and fluctuating temperatures prevail, one discovers the existence of intricately diverse bacterial communities, a subject briefly touched upon here. In the semi-arid tropical biomes dominated by grassy vegetation, a resilient and dry-adapted bacterial biodiversity coexists harmoniously with plants [5]. Venturing into water-rich tropical environments, encompassing rainforest soils and the sediments of mangroves, unveils an astonishing array of diversity, harboring untapped biotechnological potential. It’s noteworthy that tropical soils play a crucial role in providing sustenance for around 40% of the world’s population, with a significant portion residing in developing countries. In Brazil, the application of microbial inoculants derived from tropical soils has yielded substantial improvements in large-scale food production. This particular brand of biotechnology is now being shared by Embrapa with tropical nations in Africa. The utilization of tropical soil bacteria extends beyond agriculture, with applications in remediating polluted soils, promoting reforestation, and safeguarding water resources. However, the imperative lies in scaling up these efforts across all tropical regions. Preserving designated areas within the intricate tapestry of tropical ecosystems becomes paramount, ensuring that the invaluable soil microbial gene pool remains intact for the benefit of future generations [6].

Soil, plant and water-associated microorganisms play a vital role in ecosystem functioning, participating in biogeochemical cycles and degrading organic matter [7]. Over 80 coexisting beneficial soil microorganisms, including photosynthetic bacteria, lactic acid bacteria, yeasts, actinomycetes, and fermenting fungi had been identified up to 2014 [8]; with the greater use of DNA-based technologies, this number has increased substantially. These microorganisms can be employed as biofertilizers, to replace the harmful chemicals still being used. Ranipa et al. (2023) [9] point out the role of biofertilizers in sustainable agriculture and review the organisms and their applications. Zhang et al. (2021) [10] investigated the role of arbuscular mycorrhizal fungi in symbiosis with plants, revealing their catalytic effect on organic matter decomposition. This symbiosis also promoted soil aggregation and contributed to soil stabilization through mycelial growth, ultimately enhancing nutrient uptake, particularly phosphorus, by plants. Kheirfam et al. (2017) [11] demonstrated that soil crusts enriched with beneficial microorganisms improved soil properties; poor soils could be improved by adding cyanobacteria, for instance. The application of these bacteria proved to be a rapid, long-lasting, environmentally friendly, and cost-effective technique for enhancing soil quality [11]. Liu et al. (2022) [12] demonstrated that the application of biofertilizers resulted in the increased presence of beneficial bacteria within the sugarcane rhizosphere, while reducing the population of pathogenic bacteria (such as *Leifsonia*). This shift in microbial communities could help mitigate or hinder the development of diseases.

These examples underscore the significance of biofertilizers, microorganism-based fertilizers, in sustainable agriculture; they have a long-lasting impact on soil fertility [13,14]. In addition, the ability of microorganisms to balance soils and water bodies and to degrade toxic compounds provides them with another important use, commonly referred to as bioremediation.

Biofertilizers and bioremediators are formulations comprising living microbial cells, either a single strain or multiple strains (a consortium), that enhance plant growth by increasing nutrient availability and acquisition and reducing adverse conditions. The term “biofertilizer” has evolved over the past 30 years and has received various interpretations [15,16]. Macik et al. (2020) [16] point out that the most common misconception in nomenclature arises when microbial inoculants with other beneficial activities (e.g., biopesticides and phytostimulators) are included under the umbrella of biofertilizers. Plant growth-promoting bacteria and rhizobacteria (PGPB/PGPR) may also be distinguished, as not all PGPB/PGPR function as biofertilizers [17]. However, it is worth mentioning that biofertilizers can offer additional direct and indirect benefits for plant growth, including phytostimulation, enhanced tolerance to abiotic stress, and control of plant pathogens [18,19,20].

2. Biofertilizers and Bioremediators

One of the key elements of fertile soil is the presence of beneficial soil microbiota, which play a crucial role in enhancing the nutrient pool through biogeochemical processes in the soil. Consequently, it is essential for biofertilizers (microbial inoculants) to be compatible with the soil environment [21]. However, a significant proportion of arable soils worldwide do not offer ideal cultivation conditions due to various abiotic stressors, such as organic pollutants [22], heavy metals [23], drought [24], salinity [25], and extreme temperature variations [26]. Among these stressors, the release of metals from diverse human activities [27–29] poses a substantial threat to the sustainability of crop production systems.

Biofertilizers and bioremediators consist of organic or composite products containing living microorganisms with the ability to enhance biogeochemical cycles and, as a result, increase primary productivity and environmental health. The basic difference between the two lies in their purpose and consequent composition: Biofertilizers are used to enhance crop productivity, while bioremediators are employed for the removal of excessive or toxic compounds [30]. In the particular case of biofertilizers, they are mainly used in agriculture as an alternative to traditional chemical fertilizers, since they can play a significant role in providing essential plant nutrients, such as nitrogen, phosphorus, and potassium, in a more sustainable manner. Various biofertilizer types are available, including nitrogen-fixing varieties, mycorrhizae fostering symbiotic associations between fungi and plant roots to enhance nutrient absorption, phosphorus-solubilizing bacteria, and liquid fertilizers containing microorganisms that facilitate organic matter decomposition, thus enhancing soil structure and nutrient availability [31]. In comparison to chemical fertilizers, biofertilizers are deemed more sustainable, as they reduce the dependence on harsh chemicals, promote soil well-being, and, in many instances, encourage environmentally-friendly agricultural practices [32–36]. Bioremediators, on the other hand, contribute to the reduction of pollution and the associated environmental impact stemming from conventional agriculture, deforestation of forests with concomitant soil degradation, and the ultimate contamination of soil and water bodies.

2.1. Agricultural Fertilization

The global human population continues to expand at a concerning rate, giving rise to various issues, including food insecurity [37,38]. To ensure the supply of food, it is imperative to enhance crop production through fertile agrosystems. Soil fertility and crop productivity are often used interchangeably; however, they differ significantly. Soil fertility refers to the inherent capacity of the soil to provide essential plant nutrients in sufficient quantities [39,40], while crop productivity is defined as H/P x Y, where H is acres harvested, P is acres planted and Y is the yield per acre. Both, however, rely on the availability of essential plant nutrients such as N, P, K, Ca, Mg, S, Cu, Cl and Si. These nutrients are produced by the natural decomposition of soil organic matter and the addition of chemical fertilizers. Inoculating biofertilizers represents a promising approach for enhancing crop productivity while decreasing reliance on synthetic fertilizers, thereby promoting environmentally sustainable agriculture [40–42].

Microbial inoculants play a crucial role in accelerating the decomposition process, which results in the release of these essential nutrients. This, in turn, leads to an overall increase in crop productivity [43]. As the global population currently stands at around 8 billion people and is projected to reach 9.7 billion by 2050, there is a pressing need to produce 321 million tons of food to feed this growing populace [44]. However, relying solely on chemical fertilizers is no longer a sustainable solution due to their cost and detrimental effects on soil health. The emphasis is shifting toward cost-effective, environmentally friendly, and sustainable biofertilizers, which not only enhance the physical, chemical, and biological properties of the soil but also boost crop yield per unit area [45].

Biofertilizers are also gaining attention for their potential use in challenging environments such as elevated temperatures, saline soils, water scarcity, fluctuating pH levels, and the presence of environmental stressors like protein and heavy metal contaminants [46]. Their impact extends to the modulation of microbial communities within the rhizosphere, thus exerting an influence on the soil's overall ecosystem [47].

The use of biofertilizers enhances both the function and structure of soil microorganisms and has implications for the physicochemical properties of the soil [48]. The effects of introducing plant growth-promoting rhizobacteria (PGPR) can be quite variable, impacting indigenous microbial populations in various ways. Some remain unaffected, while others may experience either stimulation or inhibition of their growth [49]. For instance, the probiotic strain *Stenotrophomonas acidaminiphila* BJ1 increased the bacterial population in the rhizosphere of *Vicia faba* in chlorothalonil-polluted soil [50]. Numerous studies have assessed the impact of microbial inoculants on soil microorganisms [51–53]. As early examples, we may cite Upadhyay et al. (2012a) [54], who reported positive effects on the growth and antioxidant status of wheat under saline conditions when inoculated with two PGPR strains, *Bacillus subtilis* SU47 and *Arthrobacter* sp. SU18, and Gangwar et al. (2013)[55], who observed enhanced root length, shoot length, root dry weight, and shoot dry weight of Mung Bean (*Vigna radiata* L.) following dual inoculation with plant growth-promoting *Pseudomonas putida* and *Trichoderma viride*.

2.2. *Afforestation and Biostimulation*

Afforestation involves the establishment of trees on land that has not been previously managed for forests or has been without forests for a minimum of 50 years (UNFCCC) [56]. It serves as a crucial restoration method for reclaiming abandoned agricultural and degraded land. A substantial portion of today's agricultural land was once covered by forests. The ever-increasing human population and the rising need for food and fiber led to the expansion of agricultural activities, resulting in the conversion of forested areas into agricultural land [57]. The global agricultural land area increased from 15.84106 km2 in 1983 to 16.79106 km2 in 2003 [58]. As depicted in Figure 1, the escalating demand for agricultural land has caused the world to lose approximately one-third of its forests over the centuries.

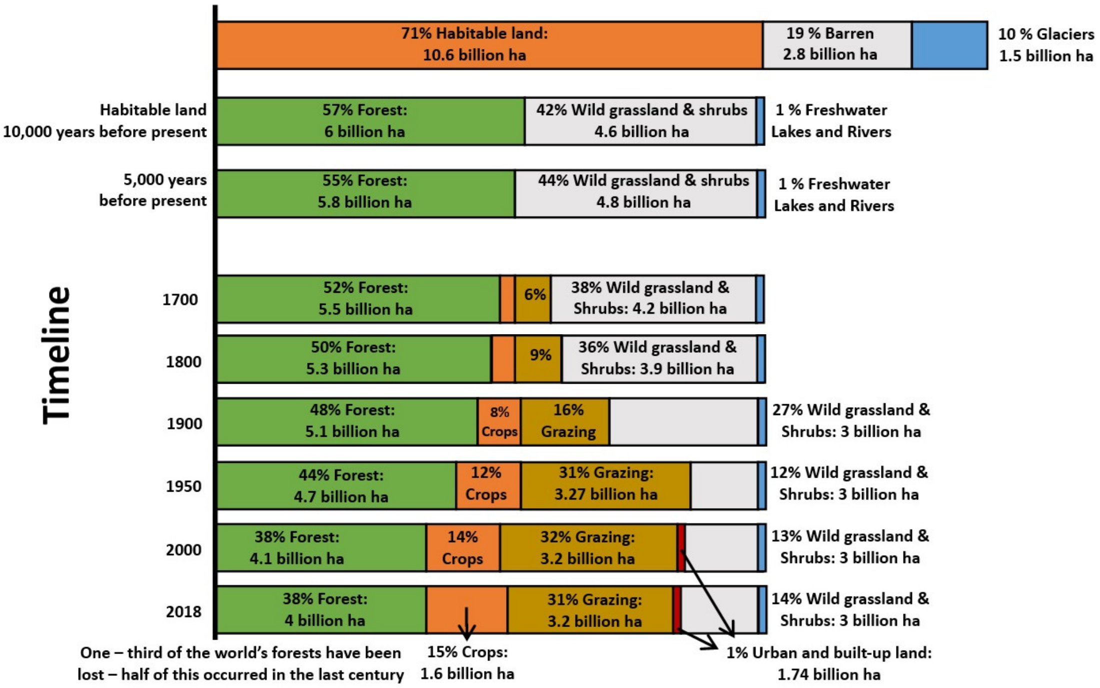

Figure 1. Land use variation over the millennia. (Modified from: https://www.weforum.org/agenda/2021/02/ice-age-forest-lost-demand-agriculture/).

The growing human and livestock population, uncontrolled extraction of forest resources, frequent forest fires, and mining operations have all contributed to soil erosion, diminished fertility, reduced moisture levels, and declining forest productivity. These issues create a multitude of challenges in ecosystem restoration. Consequently, soil-residing microbial inoculants play a vital and integral role in our soils, primarily by enhancing plant growth through nutrient accessibility, nitrogen fixation, the mobilization of otherwise unavailable nutrients, and the production of antifungal substances [59]. More specifically, deforestation for cattle production brings a series of impacts to the soil. Soil degradation can be classified as one of the most perilous human activities on the Earth's surface, due to the fact that soil is not immediately renewable [60]. When deforestation reaches a stage that makes reoccupation by secondary forest impossible, the soil becomes exposed or occupied by low grasses, leading to changes in several abiotic factors that may result in desertification. Factors such as inappropriate temperature and salinity can make it impossible for the reestablishment of plant ecological succession, thus preventing the recolonization of deforested areas. Below, some impacts of deforestation on the abiotic parameters of the soil are listed, mentioning how the application of biofertilizers can contribute to the environmental restoration process. It should be taken into consideration, however, that the majority of studies on biostimulation are related to agriculture, with limited tests conducted on native species in tropical forests.

2.2.1. Temperature

Once soil is exposed by deforestation, the direct incidence of sunlight on the soil surface causes an increase in ambient temperature. This affects plant physiology by increasing respiration rates and leaf transpiration, altering photosynthate allocation [61,62]. The enzyme ribulose bisphosphate carboxylase/oxygenase (Rubisco), which produces organic carbon from the inorganic carbon dioxide in the air (Figure 2), is one of those affected.

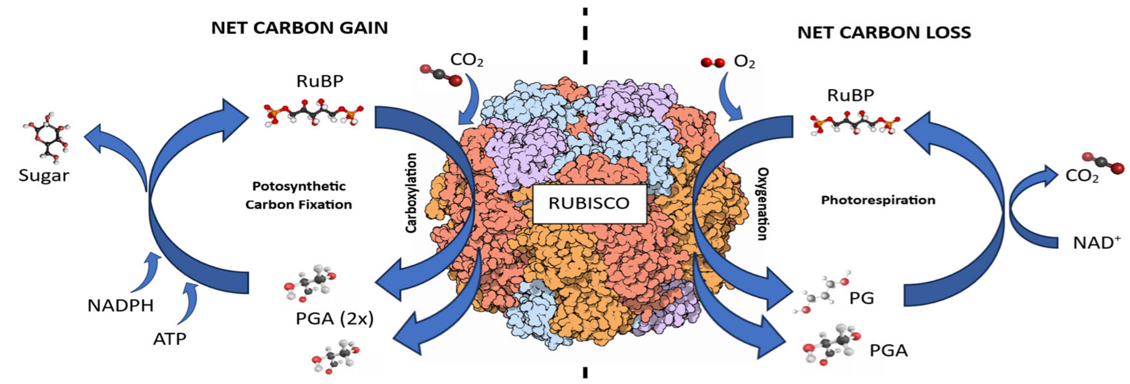

Figure 3. Role of the rubisco molecule in plant primary production and cellular respiration. Modified from Gupta and Kim, 2015 [63].

At high temperatures, Rubisco's affinity for carbon dioxide decreases, while its affinity for oxygen increases [64,65]. Carbon dioxide solubility decreases more than that of oxygen with rising temperatures, resulting in reduced carbon dioxide concentration in the chloroplast compared to oxygen [66]. Additionally, plants close their stomata to reduce water loss through evapotranspiration when temperatures rise. Stomatal closure leads to a rapid decline in carbon dioxide concentration, while oxygen concentration increases, limiting photosynthesis and increasing photorespiration [67].

Heat stress triggers complex molecular, biochemical, and physiological responses in plants [65], leading to the synthesis of heat shock proteins, reactive oxygen species (ROS), osmoprotectant compounds, amino acids, sugars, and sulfur compounds [68]. Consequently, heat stress stimulates oxidative stress and ROS production, which are detected by histidine kinases and heat stress factors (Hsfs). Redox-sensitive transcription factors downstream from these signals are activated through the mitogen–activated-protein kinases signaling pathway, subsequently turning on other transcription factors (e.g., BF1c and Rboh) to trigger the expression of genes involved in the synthesis of antioxidant enzymes [69]. However, although ROS accumulate during abiotic stresses, such as heat, ROS themselves are toxic and can react with cell components; the classical response to heat stress involves Hsfs, HSPs and various levels of ROS [70]. The heat shock response is a complex and finely tuned system.

Hormonal signaling plays a significant role in heat stress responses, with ethylene being one of the key players [71–73]. Ethylene is involved not only in processes like senescence, development, and plant physiology but also in plant responses to various abiotic stressors, including heat, salinity, and drought [72–74]. Protection of plants against heat stress can be enhanced by microbial biostimulants. For instance, the synthesis of enzymes that degrade ROS, such as superoxide, catalase, peroxidases, and dismutase, can improve heat stress tolerance in plants. This enhancement can be observed in plants colonized by beneficial bacteria like *Pseudomonas* and *Bacillus*, as well as mycorrhizal fungi like *Septoglomus deserticola* and *Septoglomus constrictum* [75]. Some available biostimulants contain *P. fluorescens* and *P. aeruginosa*, which contribute to improving soil quality and heat stress tolerance, working as bioremediators, phytostimulators, and enhancing soil fertility [65]. Similarly, *Bacillus* spp. have been developed not only as biopesticides but also in the form of biostimulant products. While these microorganisms are utilized in various commercial treatments, whether individually or in combination, their potential to mitigate heat stress is not always highlighted as one of their benefits [76].

The use of microorganisms capable of reducing ethylene emissions holds promise because decreasing ethylene levels during stressful situations could help plants avoid the detrimental effects of heat stress [77]. Bacteria that possess 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity appear particularly promising, including species like *Bacillus subtilis* BERA 7, *Leclercia adecarboxylata* MO1, *Pseudomonas fluorescens* YsS6, and *Pseudomonas migulae* 8R6 [78]. For example, the ACC deaminase-producing *Paraburkholderia phytofirmans* PsJN has been found to support normal tomato development under heat stress [79]; however, this strain has not yet been commercialized [65].

Despite the documented positive effects of biostimulants as mitigators of thermal stress, further research is needed to better understand their mechanisms of action and to develop efficient formulations that can mitigate the impact of heat stress in the recuperation of desertified areas.

2.2.2. Salinity

The soil serves as a reservoir of biodiversity, but the worldwide issue of soil salinization poses a significant threat to crop cultivation, affecting all living organisms and hindering the achievement of sustainable development goals, particularly in ensuring food security. Salinity in the soil can be attributed to a variety of natural and human activities. Reduced water availability and osmotic pressure in saline soil are indicated by poor seed germination, leaf wilting, and in extreme instances, the death of plants [80]. Mitsuchi et al. (1989) [81] conducted a review of both natural and human-induced factors contributing to soil salinization. Of the various human-induced factors, salinization resulting from deforestation was considered to be prevalent. In saline soil, the accumulation of solutes reduces the osmotic potential of the liquid phase, limiting water absorption by plant roots [82]. Soil salinization affects approximately 30% of total arable land in Mediterranean regions [83]. Drought stress and the resulting soil salinization are major contributors to desertification in overexploited regions, affecting soil biodiversity and composition, and leading to plant deterioration, reduced soil coverage, and subsequent soil erosion [84]. Drylands now cover 46% of the world’s land surface, impacting around 250 million people in developing countries [85].

Plant tolerance to drought and salinity can be enhanced by microbial biostimulants through various direct and plant-mediated processes. For example, microbial biostimulants can produce bacterial exopolysaccharides that improve soil structure by forming micro and macroaggregates [86], promoting plant growth under water stress conditions [65]. Additionally, exopolysaccharides form hydrophilic biofilms, creating a microenvironment that retains water by shielding microbes from drought stress [87] and binding Na+ ions to reduce their uptake by plants [88,89]. Examples of bacteria that produce protective exopolysaccharides include *Pseudomonas* spp. PF23 [88], *Pseudomonas putida* GAP-P45 [90] and *Bacillus licheniformis* [91]. Root capacity can also be strengthened by mycorrhizal fungi [92], leading to increased root biomass, improved soil structure, enhanced water retention, and reduced leaching of mineral nutrients [93,94]. For instance, the arbuscular mycorrhizal fungus, *Glomus* sp., produces a glycoprotein called glomalin, which enhances soil structure, plant growth, and drought tolerance [95]. Similarly, ascomycetes (*P. glomerata* LWL2, *Exophiala* sp. LHL08, *P. formosus* LHL10, and *Penicillium* sp. LWL3) colonize cucumber plants, enhancing leaf development and chlorophyll content under drought stress [92,96].

In addition to promoting root development, mycorrhizal fungi can improve water absorption through aquaporins [97], a family of integral membrane transporters that facilitate water movement through the cell membrane [98]. For example, *Glomus intraradices* colonizes common bean plants and mitigates water stress by affecting aquaporin activity and improving water conductivity in the roots [97,99]. *G. intraradices*, often found in commercial products, is typically formulated in combination with various beneficial bacterial and fungal strains or is available in single formulations [76].

Microbial biostimulants offer various supplementary benefits when it comes to alleviating the effects of drought stress in associated plants. These advantages encompass the enhancement of antioxidant defenses, the synthesis of protective osmolytes such as glycine betaine, phytohormones, and the emission of volatile organic compounds (VOCs) [100,101]. Drought stress often triggers increased ethylene production, which impedes plant growth. Microbial biostimulants, like *Pseudomonas fluorescens*, can address this issue by reducing aminocyclopropane-1-carboxylic acid (ACC) levels, consequently restricting ethylene production and mitigating ethylene-mediated inhibition [77]. Numerous microbial species, including *Staphylococcus sp*. Acb12, *Staphylococcus sp.* Acb13, *Staphylococcus sp*. Acb14, *Bacillus, Achromobacter, Klebsiella*, and *Citrobacter spp*., also synthesize ACC, offering the potential to alleviate the consequences of drought and salt stress [102,103]. Beneficial microorganisms that possess ACC deaminase activity, such as *Achromobacter piechaudii*

ARV8 in pepper and tomato plants [104] and *Pseudomonas fluorescens* TDK1 in peanut seedlings [105], can assist in mitigating these unfavorable impacts. Furthermore, *Achromobacter* spp. and *Pseudomonas* spp. are recognized for their ability to stimulate plant growth and enhance soil quality [76].

According to Ouyang et al. (2017) [106], microbial biostimulants have the ability to biosynthesize indole acetic acid (IAA), which serves to stimulate the growth of plants and the proliferation of their root systems when they are exposed to drought stress. These authors suggested that this phenomenon is observed in various bacterial species, such as those falling within the genera *Alcaligenes, Sinorhizobium, Serratia, Bacillus*, and *Arthrobacter*. The bacterium *Pseudomonas chlororaphis* TSAU13, renowned for its ability to produce IAA, can bolster the resistance of cucumber and tomato plants to drought and salinity when introduced in salt-stressed conditions [107]. Similarly, the mycorrhizal fungus *Funneliformis mosseae* elevates IAA concentrations in the roots, fosters the development of root hairs, and stimulates the growth of orange plants experiencing drought stress [108]. Specific commercial products derived from *Funneliformis mosseae* can enhance plant nutrient and water uptake [65]. Microorganisms proficient in producing cytokinins and gibberellins can alleviate water stress by promoting stomatal opening and encouraging shoot growth in conditions of restricted water availability [109]. Plant growth-promoting rhizobacteria (PGPR) of the *Acinetobacter*, *Pseudomonas*, and *Burkholderia* genera can generate gibberellins, and can augment the growth of cucumber plants under salt and drought stress [110]. Despite their promising attributes, there are presently no commercially available products based on these species.

Following exposure to drought stress, the production of abscisic acid (ABA) increases, leading to stomatal closure. In soybean plants, the introduction of *Pseudomonas putida* H-2-3 decreases abscisic acid (ABA) levels, reducing the impact of drought stress [111]. *P. putida* is commonly used in conjunction with *B. subtilis* to enhance soil fertility, rather than specifically for alleviating drought stress. Similarly, the inoculation of lettuce with *Glomus intraradices* leads to a reduction in ABA concentration and increased resistance to salt [112]. ABA and water scarcity typically lead to increased ethylene production, which can inhibit plant development.

Water stress leads to the generation of reactive oxygen species (ROS) and subsequent oxidative damage to lipids, nucleic acids, and proteins. Many microorganisms can counteract the effects of elevated ROS by either producing antioxidant compounds or increasing the activity of antioxidant enzymes, such as peroxidases and catalase, in plants [113]. *Pseudomonas* species increase catalase activity in basil plants under water stress [113]. Similarly, *Pseudomonas* species, *Bacillus lentus*, and *Azospirillum brasilense* are microbial bioinoculants that have been employed individually or in consortia to mitigate drought stress in crops [65]. Ascorbate, peroxidase, and glutathione peroxidase in *Pseudomonas* species, *Bacillus lentus*, and *Azospirillum brasilense* have been utilized to alleviate drought stress [114].

The accumulation of osmocompatible solutes is a strategy employed by plants to combat water stress, allowing the buildup of inorganic and organic solutes in the vacuole and cytosol, respectively. This lowers the osmotic potential of the cell and maintains turgor pressure in water-stressed conditions [65]. Numerous bacteria can produce osmolytes [115], which often collaborate with osmolytes synthesized by the host plant, such as proline, to reduce osmotic potential and stabilize cell wall components [116]. The phosphate-solubilizing bacterium *Bacillus polymyxa*, when introduced to specific plants, produces proline, reducing the effects of water stress [117]. Betaine, produced by osmotolerant bacteria such as *Streptomyces tendae* F4 in the rhizosphere, can work in conjunction with the betaine produced by the host rice plant, increasing its tolerance to water stress [118]. Despite these promising results, *Bacillus polymyxa* is not yet available as a commercial product.

Some bacteria can interact with plants through volatile organic compounds (VOCs), which can induce stress adaptation responses related to mineral uptake, water conservation, and root growth [119]. Although the significance of hormone signaling pathways has been established [120], the underlying mechanisms of VOC-mediated interactions between plants and microbes under extreme conditions remain largely unexplored. Microbial VOCs can have positive effects on plants, such as the synthesis of osmoprotectants and regulation of stomatal closure [121] and increased plant fitness by 2,3-butanediol [65]. Compounds like 1-heptanol, 3-methyl-butanol, and 2-undecanone produced by *Paraburkholderia phytofirmans* enhance salinity tolerance [122], while butyrolactone and 1-butanol promote root growth and carbon exchange in the rhizosphere [123]. The production of VOCs by *Bacillus thuringiensis* AZP2 has been instrumental in mitigating drought stress in wheat [124]. The future development of VOCs for plant promotion will likely depend on the identification of stress-induced signaling pathways.

Although numerous microorganisms have demonstrated the ability to protect plants from water stress, only a limited number of commercial biofertilizers are available. Many of these are based on combinations of microorganisms, including *Azospirillum brasilense, Bacillus altitudinis, Bacillus amyloliquefaciens, Bacillus licheniformis, Cellulomonas cellasea, Pseudomonas fluorescens, Pseudomonas putida, Pseudomonas stutzeri, Streptomyces albidoflavus*, *Glomus* species, and *Trichoderma* species. These microorganisms exhibit not only the capacity to mitigate water stress but also the ability to enhance plant yields through the production of exopolysaccharides and the enrichment of nutrients and soil organic matter [76]. The development and production of more universally applicable commercial products, effective across various ecosystems, will greatly contribute to the mitigation of water stress in plants.

2.2.3. Flooding, Water Pooling, and Heavy Precipitation.

The root systems of trees help stabilize the soil, which in turn reduces the risk of flooding and erosion; trees also play a crucial role in soaking up excess water during the rainy season. However, when trees are removed from the environment, heavy rains, typical of tropical countries, can lead to severe consequences. Precipitation washes away essential topsoil and whatever nutrients remain in the soil. Flooding impacts approximately 13% of the Earth's surface, and it is anticipated that the frequency and intensity of heavy rainfall events will increase globally in the future [65]. Heavy floods and rain result in water stagnation, causing root anoxia and hypoxia. When roots are subjected to flooding, they produce substantial amounts of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) synthase, which is involved in ethylene production [65]. ACC oxidase, another enzyme required for the final step in ethylene biosynthesis, depends on oxygen for its catalytic activity. ACC is transported to the aerial parts of the plant through the xylem [125], where it is converted into ethylene, leading to symptoms such as wilting, chlorosis, leaf necrosis, fruit and flower loss, and reduced crop yields (Glick, 2014). Microbial biostimulants, through their ACC deaminase activity, can help to alleviate the stress caused by water stagnation by reducing endogenous ethylene levels [77,126]. Plants inoculated with ACC deaminase-producing strains of *Pseudomonas* spp. and *Enterobacter* spp. exhibit reduced anoxia stress and improved germination [65,127]. *Pseudomonas* and *Enterobacter* spp. can increase stress tolerance, although they do not specifically protect against waterlogging. *Pseudomonas* sp. [128] and *Streptomyces* sp. GMKU 336 [129] can increase chlorophyll content, plant growth, biomass, adventitious root formation, and leaf area, while reducing ethylene levels. *S. lydicus* WYEC 108 and *Streptomyces* K61 are beneficial bacteria often used against biotic stresses [130,131]. Future research should aim to develop more microbial biostimulants and comprehensively explore the potential of existing commercial products for mitigating water stress.

2.2.4. Imbalanced Nutrient Recycling

Forest degradation has profound effects on nutrient cycles. Along with its impact on ecosystem functions, it is exacerbated by changes in terrestrial environments. The primary anthropogenic influences on forests are logging and excessive pollution loads. Both processes result in detrimental effects on the soil, which subsequently hinder the natural regeneration of the forest [132]. The harm inflicted on forest soils jeopardizes the potential restoration of the original plant community because environmental fluctuations become deregulated. The soil's ability to regulate environmental fluctuations relies on the continuous cycling of organic matter and sustained fertility. Disruption in forest nutrient cycles hampers effective land management, including sustainable landscape management [133].

An example is the Brazilian Amazon rainforest, which faces a significant threat from the expansion of cattle ranching activities [134,135]. During the process, farmers not only extract valuable

doi:10.20944/preprints202411.0003.v1

timber, but also burn the remaining vegetation and replace it with fast-growing grasses [136]. This slash-and-burn technique alters the physical, chemical, and biological properties of the soil, facilitating the establishment of pastures in the Amazon region [137]. This practice is unsustainable, and pastures experience a rapid decline in productivity, ultimately becoming degraded and abandoned [138]. Under ideal conditions, 'secondary forest' is gradually formed [139], but studies suggest that deforestation is becoming increasingly common in the Brazilian Amazon region. Even though Carvalho et al. (2019) [140] state that these secondary forest areas are expanding, covering more than 100,000 km^2, there is a need for more research on the re-establishment of secondary forests, especially with respect to soil microorganisms and nutrient cycling [141].

Phosphorus is considered an essential nutrient for plant growth and can limit primary productivity in various environments, including tropical and subtropical forests [142]. These regions typically have soils with high levels of iron and aluminum oxides due to intense weathering processes, which are exacerbated by the heavy rainfall and high temperatures in these areas. Fe and Al oxides can bind P, making it less available to plants [143,144]. Consequently, many plants rely on the recycling of P from litterfall and microbial P turnover [145].

Land-use changes negatively impact soil P dynamics in the Amazon region [144,147]. This is because the conversion of pristine forests to pasture using the slash-and-burn method alters P lability and increases P levels in more recalcitrant pools [144]. It can also release substantial amounts of nitrogen and P from forest biomass, which can be lost through leaching and runoff [148,149].

There is limited research and information available regarding the effects of secondary forest re-establishment on P dynamics. Existing studies suggest that secondary forest re-establishment has the potential to promote a gradual recovery of soil P [150–152]. According to these authors, the increase in plant diversity, the restoration of certain soil physicochemical properties (e.g., pH), and enzymatic activity (e.g., C, N, P, S enzymes) may favor specific bacterial and fungal groups such as P-mineralizing and P-solubilizing microorganisms. These groups play crucial roles in P transformation processes and availability. They are primarily involved in three key soil processes: (i) mineralization, (ii) solubilization, and (iii) immobilization [153] (Figure 4). These microorganisms produce enzymes that break down ester-phosphate bonds, releasing orthophosphate from recalcitrant organic P forms, as explained by Arenberg and Arai (2019) [154]. They possess genes encoding enzymes such as phytase (appA), alkaline phosphatase (phoD), acid phosphatase (olpA), phosphonatase (phnX), and C–P lyases (phn), which can mineralize organic-P compounds in soils [155,156].

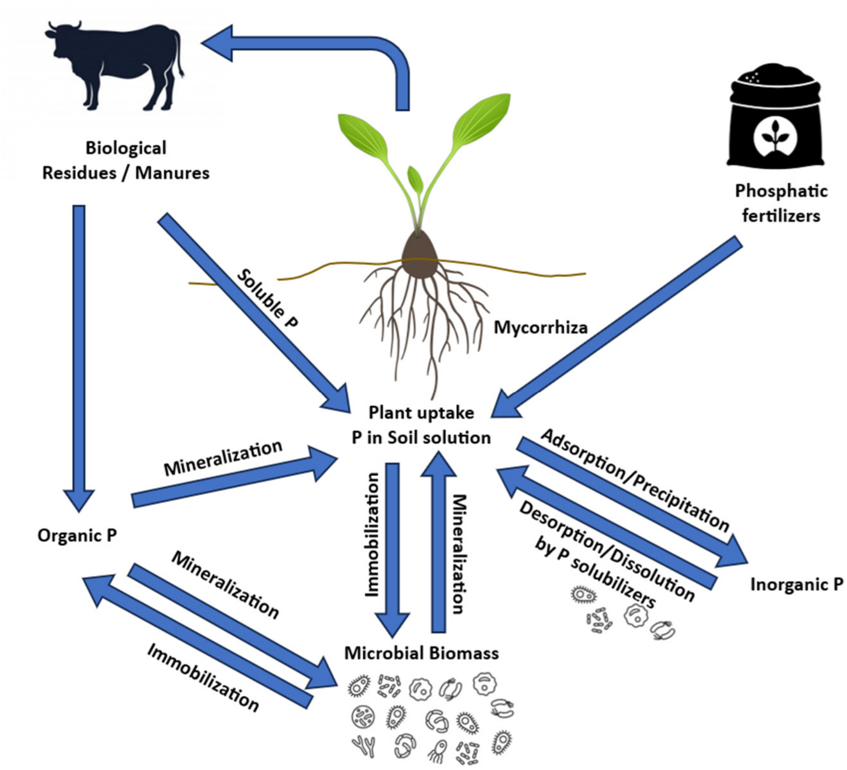

Figure 4. An overview of the phosphorus cycle in nature (Modified from Shrivastava et al., 2018 [146]).

P-solubilizing microorganisms can also produce and release organic acids like oxalic acid, malic acid, formic acid, citric acid, and gluconic acid. These acids can solubilize recalcitrant inorganic-P forms in soils [155,157]. They possess genes such as GCD (encoding glucose dehydrogenase) and the cofactor PQQ gene (encoding pyrroloquinoline quinone) that regulate the solubilization of unavailable inorganic P forms [158].

Microorganisms involved in P immobilization, on the other hand, can assimilate inorganic P into their biomass, competing with plants for available P [153]. They possess pst and pit transporter genes, which assist in the assimilation of inorganic P under P-limited and P-rich conditions.

The microbial groups involved in P transformations are ubiquitous in soils, but their population and activity are influenced by different environmental requirements [159]. They are also sensitive to disturbances, particularly changes in soil physicochemical properties [160,161]. This is a significant concern; previous studies have indicated that the conversion of pristine forests to pasture in the Amazon region alters soil physicochemical properties and the overall composition of the soil microbial community [162–164].

2.2.5. Soil Compaction by Cattle

Cattle trampling of agricultural soil can cause the collapse of larger soil pores, producing smaller pores. This leads to increased soil density and greater resistance to soil penetration, ultimately promoting more soil compaction. This, in turn, hinders the regrowth and renewal of pastures, resulting in reduced overall productivity [165]. Thus, soil compaction is closely linked to significant soil degradation processes, which manifest as reduced soil aeration, diminished water infiltration rates, and an increased risk of flooding and surface runoff [166–169]. These processes collectively have a negative impact on soil productive capacity [170]. Factors such as soil type, moisture content, and grazing management practices (like stocking rate, stocking density, and timing of activities) can exacerbate this soil compaction [165,171]. It is well-recognized that the risk is heightened when soil moisture content is increasing [172,173], as generally occurs in the wet summer seasons, which are thus the most vulnerable to soil compaction.

Currently, there are no reported studies that involve microorganisms and the impact of soil compaction resulting from cattle farming. However, some authors address the use of biochar to mitigate this problem. Gao and DeLuca (2022) [174] suggest that soil compaction and the consequent reduction in soil moisture and aeration may affect nutrient cycling, hindering natural repopulation with vegetation. There is thus a potential for enhancing nutrient cycling through the addition of specific microbial strains. The above authors noted an increase in soil organic matter and P content with biochar application. The use of microorganisms could further enhance this. Soil biofertilization could also stimulate primary production, leading to bioturbation by roots and detritivorous animals, thus promoting soil aeration. However, specific studies in tropical soils need to be carried out to substantiate this hypothesis. Porous materials can also play a crucial role in substrate enhancement [175–177]. Incorporating porous materials into the substrate augments soil porosity, elevates aeration rates [178], provides a conducive environment for microbial communities to thrive [179,180], and fosters the development of plant roots [181].

2.3. Treatment of Polluted Soils (Bioremediation)

The use of industrial effluents to irrigate agricultural crops is particularly prevalent in poor and less environmentally aware countries. This leads to the buildup of toxic substances in the soil with resulting effects on agricultural production and produce. Over the last decade, there has been a consistent growth in the number of publications discussing the application of microorganisms for the remediation of heavy metals and other contaminants in such polluted environments. While bacteria and fungi have been the predominant choices, yeasts and algae are also employed, the latter phylum mainly, but not exclusively, in aqueous environments [182]. Bioremediation usually relies on the metabolic activity of either a single organism or a consortium of microorganisms [183]. In this process, the transformation of contaminants may not provide significant benefits to the cell, when it is termed non-beneficial biotransformation [184,185]. Numerous studies have demonstrated that many organisms, both prokaryotes and eukaryotes, possess a natural capacity for biosorbing toxic heavy metal ions [186,187]; the biosorption sites may be located on or in the cells, or in the extracellular polymeric layer (EPS) of the microorganisms [188–191]. Alternative methods of bioremediating heavy metal contaminated soil include the use of microorganisms that change the toxicity of the metal by altering its oxidation state or by methylation [192–195] Examples of bacteria, fungi, and yeasts that have been studied and strategically employed in bioremediation applications for heavy metals in soil are shown in Table 1.

Table 1. Some microorganisms that have been used for bioremediation of heavy metal-contaminated soils.

Microbial inoculum	**Heavy metal(s)**	**Reference**
Bacteria:		
Arthrobacter spp.	Cd	Roane et al., 2001 [197]
Pseudomonas veronii	Cd, Zn, Cu	Vullo et al., 2008 [198]
Burkholderia spp.	Zn, Pb, Mn, Cd, Cu, As	Yang et al., 2016 [199]
Kocuria flava	Cu	Achal et al., 2011 [200]

Bacillus cereus	Pb, Cd, Cr	Ayangbenro and Babalola, 2020 [201]
Sporosarcina ginsengisoli	As	Achal et al., 2012 [202]
Serratia sp.	Ni, Cd	Li et al., 2016 [203]
Enterobacter cloacae KJ-46, *E. cloacae* KJ-47, *Sporosarcina soli* B-22, and *Viridibacillus arenosi* B-21	Cd, Pb, Cu	Kang et al., 2016 [204]
Enterobacter cloacae B2-DHA	Cr(VI)	Rahman et al., 2015 [205]
Brevibacillus parabrevis OZF 5	Cr(VI), Zn	Wani et al., 2023 [206]
Cupriavidus metallidurans LBJ and *Pseudomonas stutzeri LBR*	Pb	Ridene et al., 2023 [207]
Acinetobacter sp. LSN-10	Mn(II)	[208]
Achromobacter denitrificans, Klebsiella oxytoca, and *Rhizobium radiobacter*	Cd, Hg, As, Pb, Ni	[188]
Cyanobacteria		
Gloeomargarita lithophora and Cyanothece sp	Sr	[209]
Nostoc minutum and *Anabaena spiroides*	Pb, Cd, Ni	[210]
Fungi		
Simplicillium chinense	Cd, Pb	[211]
Penicillium sp.	Hg	[212]
Penicillium chrysogenum FMS2	Cd	[213]
Aspergillus versicolor	Cr, Ni, Cu	[214]
Aspergillus fumigatus	Pb(II)	[215]
Aspergillus spp.	Cd, Cu	[216]
Gloeophyllum sepiarium	Cr	[200]
Perenniporia subtephropora, Daldinia starbaeckii, Phanerochaete concrescens, Cerrena aurantiopora, Fusarium equiseti, Polyporales sp., *Aspergillus niger, Aspergillus fumigatus,* and *Trametes versicolor*	As, Mn, Cu, Cr, and Fe	[217]
Yeasts		
Candida tropicalis	Cr(VI)	[218]
Saccharomyces cerevisiae	Pb, Cd	[219]
Saccharomyces cerevisiae	Cd, Hg	[220]
Mixed consortia		

Chlorella thermophila SM01, *Leptolyngbya* sp. XZMQ and *Bacillus* XZM	As	[221]
Leptolyngbya sp. XZ1 and *Bacillus* sp. S1	Cd	[222]

Rhizobacteria have been suggested to be particularly useful for the bioremediation of heavy metal-contaminated soils; the mechanisms of metal removal include chelation by siderophores, biotransformation (change to a less damaging oxidation number or methylation to reduce toxicity), biosorption and bioaccumulation in the cells, precipitation, ACC deaminase action, and biomineralization [223]. Biotechnological approaches by other microorganisms encompass bioleaching, bioextraction, and bioencapsulation [224], although not all of these are applicable to soil in situ.

When a contaminated site contains various pollutants, effective remediation requires a diverse array of microorganisms. Many microorganisms can degrade petroleum hydrocarbons, using them as a source of carbon and energy. The selection of these organisms for bioremediation varies based on the chemical nature of the pollutants and must be made carefully, as they can only thrive in the presence of a limited range of chemical contaminants. The efficiency of the degradation process is linked to the microbial capacity to introduce molecular oxygen into the hydrocarbon and generate intermediates that enter the cell's energy-yielding metabolic pathways. Some bacteria have chemotactic responses, actively seeking out contaminants [225,226], while many produce powerful surface-active compounds that emulsify oil in water, aiding its uptake by the cells and hence removal from the soil [30,227]. Bacteria capable of degrading petroleum products include genera such as *Pseudomonas, Aeromonas, Moraxella, Beijerinckia, Flavobacteria, Chromobacterium, Nocardia, Corynebacterium, Streptomyces, Bacillus, Arthrobacter, Aeromonas*, as well as cyanobacteria [225,228], and certain yeasts [30]. One example is *Pseudomonas putida* MHF 7109 isolated from cow dung, which can be used for the biodegradation of selected petroleum hydrocarbon compounds, including benzene, toluene, and o-xylene (BTX) [186].

Genetically Modified Microorganisms for Bioremediation

Genetic engineering is a fundamental method to modify the metabolic pathways of microorganisms and improve their bioremediating activity, increasing efficiency and reducing the time required to produce the required effect. Genetic engineering can be applied to modify microorganisms to exhibit features like accelerated growth, tolerance to extreme environmental conditions and pH fluctuations, and cost-effective cultivation. Omics technologies, genomics, transcriptomics, proteomics and metabolomics, are being employed to increase our understanding of relevant microbial metabolisms, such as responses to heavy metals and high salt concentrations, and to indicate the appropriate engineering of potential microbial inoculants, with increased resistance and degrading activities for soil pollutants like heavy metals and hydrocarbons [229,230]. Perceived hazards in the release of genetically-modified organisms (GMOs), however, have led to problems in legislation for their placement on the market [231]. Similarly, care must be taken when releasing genetically-modified microorganisms (GMMs), defined as "microorganisms in which the genetic material has been altered in a way that does not occur naturally by mating and/or natural recombination" [232]. For this reason, genetic manipulations included in GMMs may include inbuilt senescence genes, so that unexpected negative interactions with native organisms will be limited [233]. Nevertheless, research on the use of GMMs in soil bioremediation in situ is now rather restricted.

The techniques used in the production of GMMs are beyond the remit of this article, but for those interested there is a wealth of papers published on this topic [234–238].

3. Environmental Parameters Influencing Microbial Fertilization and Bioremediation in Soils

Bioremediation involves harnessing microorganisms, including bacteria, algae, and fungi, as well as plants, to expedite the breakdown, alteration, elimination, immobilization, or detoxification of diverse physical and chemical contaminants in the environment. The microorganisms can employ metabolic pathways to accelerate biochemical reactions that break down pollutants [239,240]. For bioremediation to be effective, microorganisms must be supplied with the necessary energy and nutrients to support their growth. Various factors, including physical, chemical, biological, soil type, carbon and nitrogen sources and the type of microorganisms (whether single or a consortium), influence the efficacy of bioremediation [241]. Microbial consortia often exhibit multifunctionality and resistance, and thus are more efficient than a single microorganism [242]. These may be natural microbial communities. For instance, carbon, one of the most crucial nutrients, was found to enhance in situ bioremediation by increasing natural consortium metabolic activity and expediting the breakdown of existing pollutants [243]. Soil type also impacts bioremediation, with sandy soils generally allowing higher levels of pollutant bioremediation than clay [244]. The factors influencing bioremediation and the methods employed for soil remediation, both in situ and ex situ, are discussed by Sales da Silva et al. (2020) [245]. These factors include the microbial population, contaminant accessibility, and the physicochemical characteristics of the environment (Figure 5). The same considerations apply to the use of biofertilizers. Extra activities involved may be excretion of phytohormones, suppression of phytopathogens and protection of plants from various types of stress [246,247].

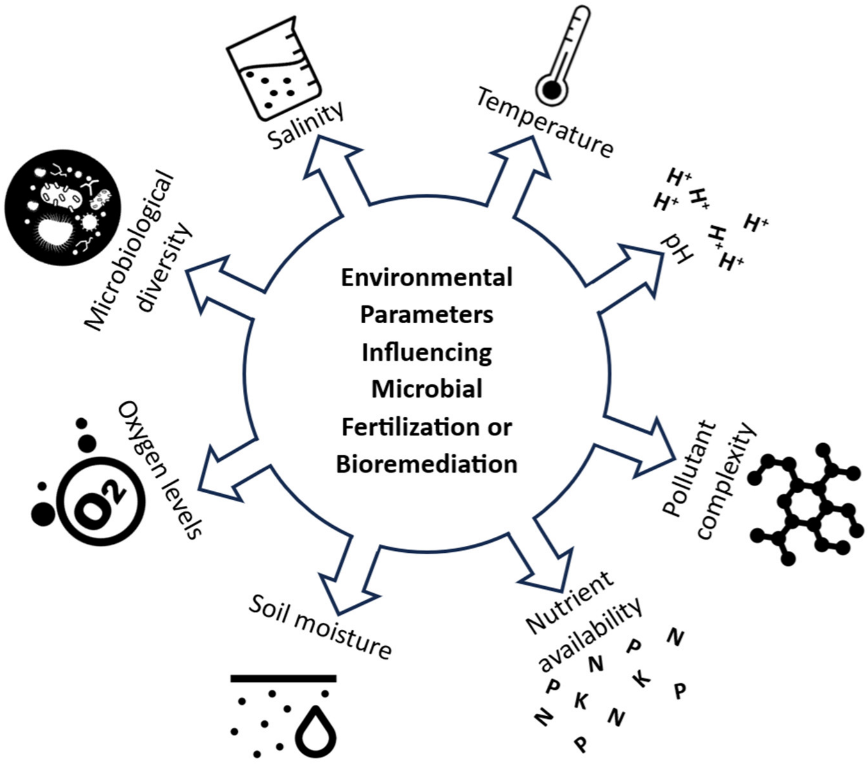

Figure 5. Environmental Parameters Influencing Microbial Fertilization or Bioremediation.

3.1. Temperature

An important physical factor that significantly influences the survival of microorganisms as well as the degradation of pollutants is temperature. For example, in cold regions such as the Arctic, the natural degradation of oil is slow, creating a greater reliance on microbes to remediate oil spills. In these conditions, sub-zero temperatures can freeze the transport channels of microorganisms, hindering their ability to carry out metabolic processes. Temperature also has a direct impact on the turnover of enzymes involved in degradation, which may vary depending on the pollutant. The physiological properties of microorganisms are influenced by temperature, which can either accelerate or decelerate the bioremediation process. Higher temperatures generally promote increased microbial activity up to a certain limit, and this activity typically decreases if temperatures rise or fall abruptly, eventually ceasing altogether at temperature extremes [248,249]. However, extremophilic microorganisms, thermophiles and psychrophiles, are active in extreme environments such as the tropics and polar regions and can be used in bioremediation and biofertilization in such areas, as well as in other extreme environments [250–254].

3.2. Salinity

One of the factors that can limit bioremediation and that could be tackled by the use of extremophiles is salinity. Salt levels in soils used for agriculture are rising because of natural and anthropic activities [255]. Unsustainable soil management, such as irrigation with brackish water or overapplication of fertilizers, are responsible for some of this [256]. Hypersaline soils not only reduce plant growth, but also limit the possibilities of bioremediation. Non-saline soils have been shown to have approximately four times higher total petroleum hydrocarbon biodegradation compared to saline (1% NaCl) soils [257]. Salinity reduces the bioremediation of motor oil [258] and petroleum hydrocarbons [259,260] in soil. Nguyen et al. (2021) [261] suggest that salinity exposure may influence Cr(VI) bioremediation; Cr-resistant microorganisms may be able to deal with this problem [195]. There are several examples of the use, or potential use, of halophiles in bioremediation of polluted environments [195]. Although still undergoing considerable research effort, the use of halophilic microorganisms for bioremediation in, or of, saline environments appears to be a real possibility [267–269]

3.3. pH

The acidity, alkalinity, and basicity of a compound influence microbial metabolism and the bioremediation process. Soil pH, similarly, has an impact on nutrient availability as well as enzyme activity. Soil pH can be used to predict microbial growth since even slight pH variations have a notable effect on metabolic processes [270]. In the case of petroleum hydrocarbon biodegradation, a pH close to neutrality is optimal [271], but this will clearly vary depending on the pollutant and the microorganisms. For example, modeling the removal of the antibiotic, azithromycin, from contaminated soil by various fungi showed pH to be the most important physicochemical parameter and the optimum to be 5.5 [272], and acidophilic methanotrophs, growing optimally at pH 5 or below, have been suggested for the bioremediation of chlorinated volatile organic compounds in groundwater aquifers [273]. It should be noted, however, that biofertilizers themselves may be able to alter soil pH advantageously [274].

3.4. Microbiological Diversity

Quite apart from the microorganisms added to attain the desired effect, the resident microbiota will have a large part to play in the final outcome of a bioremediation or biofertilization treatment. There will be competition between the autochthonous and the added species, as well as between the indigenous microorganisms themselves [275,276]. For example, when petroleum degrading bacteria (PDB), Acinetobacter radioresistens KA5 and Enterobacter hormaechei KA6, were inoculated into soil containing indigenous microorganisms, the level of petroleum breakdown was considerably lower than that produced by the PDB alone [277]. When two different types of pollutants require removal, or when biofertilization is the aim, the choice of augmenting microorganisms becomes much more complex; antagonistic or highly competitive interactions must be closely monitored. The negative effects of one pollutant on the degradation of another are discussed and exemplified by Olaniran et al. (2013) [278], but double bioremediation is achievable, although perhaps not at maximum efficiency. In the case of metal-contaminated soils, one approach is to use metal-resistant microorganisms. Roane et al. (2001) [279] isolated 4 bacterial strains of different genera that reduced soluble Cd levels in the contaminated soil and also supported the degradation of 500-µg ml^{-1} 2,4-D by the cadmium-sensitive 2,4-D degrader Ralstonia eutropha JMP134, while Wani et al. (2023) [280] reported that Brevibcillus parabrevis OZF5 removed both Cr and hydrocarbons from contaminated soil, enhancing growth of beans. Microbial surfactants, such as surfactin, rhamnolipid, and sophorolipids, may also be used to augment bioremediation of various pollutants, including DDT, atrazine, hexachlorocyclohexane and cyprodinil [281], as well as the obvious hydrocarbons [282].

Finally, it must be noted that any change in the structure of the microbial community can result in shifts not only in temperature adaptation at the community level but also in growth strategies: copiotrophs can promptly respond to favorable environmental conditions and proliferate rapidly when labile carbon sources are available. In contrast, oligotrophs display gradual, sustained growth under conditions of low carbon and nutrient availability, finally yielding a higher biomass per unit substrate [283,284]. As eloquently articulated by Neidhardt (1999) [285], when the primary objective is growth, delving exclusively into individual enzymes and genes, or even isolated pathways and mechanisms, is insufficient. There comes a point where one must return to the holistic perspective of the entire cell and consider the coordinated orchestration of various processes. When several microbial species are mixed, the community must work together and support each other to grow and become active in the bioremediation/biofertilization process in a symbiosis (Moqsud et al., 2015) [286].

3.5. Oxygen Levels

The biodegradation process is directly related to the available oxygen content in the environment. Most bioremediation systems run under aerobic conditions [287]. Often, however, in aquatic sediments, sludges or compacted soils, for example, there is limited oxygen available. With the impossibility to aerate the environment, the use of anaerobic decomposers or facultative organisms can be more effective [288]. Ji et al. (2014) [289] investigated how the activities of microorganisms were influenced by the presence of dissolved oxygen (DO) in polluted river water. Their study revealed that the removal efficiency of different substances, such as chemical oxygen demand, total phosphorus, and ammonia nitrogen, increased with higher levels of DO, showing improvements of 4.59%, 18.18%, and 34.34%, respectively, suggesting that this bioremediation works even under aerobic conditions.

Petroleum-contaminated sludge is a particular problem in coastal wetlands, where costly physicochemical treatment is currently the norm [290]. Anaerobic bioremediation, utilizing sulfate-reducing bacteria, denitrifying bacteria, iron and manganese reducing bacteria, and, particularly, methanogenic bacteria is more economical, although currently less efficient than aerobic bioremediation [290]. Intermittent oxygen supplies may also be useful in some cases, For example, Chen et al. (2023) [291] found that intermittent microoxygenation facilitated codegradation of trichloroethane and toluene; the main bacterial genera responsible for the dechlorination were Dehalogenimonas, Dehalococcoides, and, mainly, Dehalogenimonas. One possibility could be the use of cyanobacteria, which can grow anaerobically, under the correct conditions and produce oxygen by photosynthesis. Their potential as biofertilizers in green technology is discussed by Bhuyan et al. (2023) [292].

3.6. Soil Moisture

The soil's moisture content is also an important factor in accelerating biogeochemical processes. Soil that is excessively waterlogged is not suitable for microbiological treatment [293]. The moisture level in the soil impacts the movement of water and soluble nutrients in and out of microorganisms and excessive moisture diminishes oxygen levels during the aerobic process [294] and hence bioremediation [295]. With this effect of soil moisture in mind, Naorem (2022) [296] considered the potential effects of climate change on biodeterioration efficiency. Bahmani et al. (2018) [297], using laboratory experiments and various moisture levels in hydrocarbon-contaminated soil, developed a mathematical model for the process. They defined a first-order rate equation for removal of total petroleum hydrocarbons (TPH); this equation held good between a specific moisture value at which the constant is zero and that at which the constant reaches its maximum.

$$\nu\ d\theta/dt=q_{in}-q_{out}\ (1)\ q_{in}=0\ (2)\ q_{out}=APET\ (\theta-\theta r\ /\theta sat-\theta r)$$

Where, ν=volume of beaker, θ=water content, q=volumetric flow rate of water, A=surface of beaker, PET=potential evaporation (constant during their experiment at 0.00495 m day^{-1}), θr=residual water content, θsat=saturation water content.

In their study, the best TPH removal from a sandy clay soil was achieved by adjusting the water to 60% capacity and adding water every 2 days. This moisture level is higher than that quoted by other workers; for example, Kumari et al. (2023) [298] suggested 35%. However, Zeng et al. (2023) [299] and Norozpour et al. (2023) [300] suggest 60% and 70-80% respectively. These authors were all working with PAH-contamination.

3.7. Nutrient Availability

Nutrients play a crucial role in influencing the growth of microorganisms and the rate of biodegradation. Enhancing the soil C:N:P ratio can significantly enhance biodegradation efficiency, particularly when vital nutrients like nitrogen and phosphorus are provided. When these nutrients are present in low concentrations, the degradation of hydrocarbons is constrained. Addition of extraneous nutrients, such as glucose, can augment pollutant removal by stimulating microbial activity [301]. Introduction of nutrients is particularly important for bioremediation activities in cold environments; it can boost the metabolic activity and diversity of microorganisms and, consequently, the rate of biodegradation [80]. Microbes that consume oil rely on these essential nutrients to thrive, and they are typically present in limited quantities in natural settings [302,303].

Cavazolli et al. (2023) [304] used DNA sequencing techniques to investigate the bacterial populations of soil co-contaminated with heavy metals and hydrocarbons. Bioremediation was carried out using meat and bone meal (MBM) as nutrient addition and cyclodextrin (Cdx), as a surfactant to release previously unavailable nutrients. After 12 weeks, only Cdx had increased bacterial diversity more than the control soil; MBM accelerated the change in populations, but final diversity after 12 weeks was not altered. Oil-degrading groups of bacteria increased in prevalence during the procedure, but hydrocarbon and heavy metal levels were not determined. The effects of addition of any specific nutrient, or nutrients, to contaminated soil are difficult, perhaps impossible, to predict and should be carefully monitored.

3.8. Pollutant Complexity

The release of diverse chemical pollutants into the environment by industries can disrupt the delicate equilibrium of ecosystems. These anthropogenic pollutants, in particular, tend to exhibit greater complexity and heightened resistance to degradation, necessitating the use of specific bioremediating strains capable of withstanding the toxicity of substances such as metals and hydrocarbons [305]. It has been suggested that GMOs and mixed strains of microorganisms may be the preferred route for future treatment of complex pollutants [306,307]. While the potential of GMOs in bioremediation is substantial, its practical application is circumscribed in various ways [308] and the discussion above (Section 2.3.1) points out the problems of this approach.

Li et al. (2020) [309] suggest that fungi may be more appropriate for the degradation of complex pollutants. Fungi may oxidize pollutants extracellularly using laccases, manganese peroxidases and lignin peroxidases, or intracellularly using cytochrome P450, reductive dehalogenases, and nitroreductases [309]. Recently, innovative remediation techniques have been proposed, including the utilization of extracellular and/or cell-free enzymes, together with metabolomics and proteomics to study the response of the microorganisms to complex and mixed pollutants [310,311]. Using a single microbial species in a bioremediation treatment for complex molecules is unlikely to obtain success; microbial consortia are now being intensely studied to find species that can survive and work together. The engineering of microbial consortia is discussed by Li et al. (2021) [312]; they consider 2 main approaches, “bottom-up” and “top-down”. Interactions between microorganisms include antagonism and symbiosis; the bottom-up approach involves reconfiguring negative interactions to ensure co-survival and continued activity. The top-down approach involves modifying the environment to compel the organisms to perform the desired activities; it is not an easy option because of the complexity of the microbial interactions. The bottom-up approach requires a detailed knowledge of the metabolism and interactions of the consortium members. The new omics techniques have allowed this to become a less onerous and more achievable goal and will assist the development of consortia for the bioremediation of complex pollutants such as PAHs.

Cell-free systems have also been investigated for bioremediation of pollutants such as organophosphate pesticides [313], aromatic polymers like chlorophenols [314] and nitrile and amide-based xenobiotics [315]. Immobilization of the enzymes on a suitable, and economic, material can be advantageous to ensure their continued activity, but the support must be carefully chosen to prevent any reduction in efficacy [316]. Screening of microorganisms for enzyme activities, in addition to being used for the identification of potential enzymes to be extracted or engineered, could also be used in place of laboratory biodegradation tests for detection of efficient functional isolates for bioremediation procedures [317].

4. Risks to Ecosystem Health: Impact on the Local Biota

In theory, the biofertilization and bioremediation approaches should lead to minimal or well-controlled consequences concerning factors such as dispersal, persistence, alterations to microbial function and biogeochemical cycles, and shifts in the ecosystem communities [318]. A substantial area of concern lies in the potential impact of introduced microorganisms on the existing microbiome, which may result from direct ecological interactions, whether they are cooperative or antagonistic in nature. Invasive, alien species are bad for ecosystems, since they may reduce biodiversity and disrupt food chains, including our own. Species from other regions that establish self-sustaining populations in the invaded area are referred to as naturalized species. Among naturalized species, those that quickly spread beyond the site of their initial introduction in the invaded region are classified as invasive, as described by Richardson et al. (2000) [319], Pyšek et al. (2004) [320], and Blackburn et al. (2011)[321]. For instance, the chestnut blight fungus entered North America surreptitiously through contaminated nursery stock [322], leading to the demise of four billion trees over a span of 40 years. Especially in tropical regions, like South Asia and South America, plant invasions are one of several factors that threaten the local biodiversity. However, the economic and social challenges resulting from plant invasions are on the rise across all continents. The expenses directly associated with the harm caused by invasive species are thirteen times greater than the costs incurred for their management [323].

Finally, biological invasions rank as the fifth most significant driver of global environmental change, according to IPBES 2019 [324]. Approximately 14,000 taxa, constituting about 4% of the world’s flora, are recognized to have naturalized from the global plant species pool [325,326]. Among them, around 2,500 species are identified as invasive (Pagad et al. 2018), with the Asteraceae family contributing the highest number of naturalized taxa [327]. The escalating international trade has led to a global increase in the number of invasive species [328].

The phenomenon of horizontal gene transfer has also been identified as a relevant consideration [329–331]. Horizontal gene transfer involves the transfer of genetic information between organisms, facilitating the dissemination of antibiotic resistance genes among bacteria, excluding those passed from parent to offspring. This process contributes to the evolution of pathogens [332]. For instance, the simple use of manure as an organic fertilizer in agriculture introduces fecal bacteria, along with their plasmids and antimicrobial resistance genes, into the soil. The exchange of genetic material, which includes plasmids [333] and even entire genomic segments, is particularly prevalent in the rhizosphere—an area rich in microbial activity. Such exchanges have been observed even between species that are quite distantly related. There have, for example, been documented cases of gene transfer between *Pseudomonas putida* and *E. coli* facilitated by the TOL plasmid (pWW0) [334]. Macedo et al. (2022) [333], through a microcosm study involving *E. coli*, recorded the successful transference of a broad host range plasmid to soil and manure bacteria by conjugation. Similar instances of plasmid transfer have been witnessed within various strains of *Azotobacter vinelandii*. Martínez-Carranza et al. (2019) [335] suggest that *A. vinelandii* may have a polyphyletic origin, with a genomic resemblance to the pathogenic bacterium *P. aeruginosa*. This hypothesis opens up the possibility of horizontal transfer from *P. aeruginosa* to *A. vinelandii* of genetic information encoding pathogenicity [335].

It has been suggested that microorganisms may influence ecosystem biodiversity or induce infections in humans, animals, or plants, thereby creating an adverse environmental impact. As a response to this concern, the European authorities have tried to protect humans, plants, animals and the environment by developing European Regulation (EU) 2019/1009 [336] on biofertilizers.

Current understanding suggests that plants are not isolated entities; instead, they exist in association with a diverse range of microbes [337]. Introduced microorganisms can indirectly alter resident microbial communities by influencing plant physiology and morphology, via the acquisition of nutrients, reduction of plant stress and suppression of plant diseases. For instance, some plant growth-promoting microbes are known to modify root architecture and exudation [338], which can impact rhizosphere communities [339,340]. In mixed plant communities, indirect effects on the resident microbiome could also occur if the introduced microorganism induces changes in plant diversity and composition, as has been seen with some AMF inoculants [341,342].

Inoculation with rhizobia, commonly used in biofertilizers, has shown significant effects on soil and plant-associated microbial communities in soybean [343], alfalfa [344] and common bean crops [345]. These effects can extend beyond the rhizosphere; field inoculation of *Phaseolus vulgaris* with two native rhizobia strains (separately or combined) altered the structure and increased the phylotype richness of bacterial communities in the bulk soil [346]. Changes in microbial structure can result from both positive and negative interactions of rhizobia with the rhizosphere microbiome. The close relationship between root endophytes and root tissues facilitates the exchange of nutrients between plants and microbes [347]. For instance, *Azospirillum*, a bacterial genus known for its free-living organisms with nitrogen-fixing capabilities, among other plant growth-promoting traits, has shown variable effects on the resident microbiome [346]. Inoculation of maize with *A. lipoferum* induced a shift in the composition of rhizosphere bacterial communities lasting for at least one month [348]. However, variable results were observed when inoculating the same or other crops with *A. brasilense* [349–351], even though this bacterium can induce physiological and morphological changes in the root system.

According to Trabelsi and Mhamdi (2013) [346], the effects of *Azospirillum* inoculation on rhizosphere microorganisms are likely driven by nitrogen dynamics, although a wide array of factors are involved. While rhizobia and *Azospirillum* have been more widely studied regarding their effects on the resident microbiome, research on other taxa, such as *Pseudomonas sp*., remains limited, even though they could potentially modify both bacterial and fungal communities [352,353].

Arbuscular mycorrhizal fungi (AMF) biofertilizers are the most widely used and readily available, despite insufficient evaluation of ecological risks associated with their field application [341,354]. The introduction of non-native AMF can impact indigenous AMF communities in various ways, such as displacing them and reducing their diversity [355], or altering their composition [356], although these effects on the native AMF community may not always be evident [357]. In a study conducted by Jin et al. (2013b) [358], a diverse AMF inoculum had a less pronounced positive impact on plant fitness but had a milder influence on the composition of subsequent AMF communities. In addition to affecting native mycorrhizal fungi, introduced AMF can disrupt other soil microbial communities, especially those associated with their extraradical mycelium, known as the mycorrhizosphere [346].

The influence of AMF on soil microbial communities appears to be variable and is influenced by multiple factors [359–361]. For instance, among the principal factors influencing microbial activity lies the microbial capability to reduce organic materials, utilizing them as sources of energy. The average oxidation state of carbon in a contaminant stands as an effective energy source for aerobic heterotrophic organisms. A heightened oxidation state, consequently, correlates with a diminished energy yield, thereby offering a reduced energy output for microbial degradation. The outcome of any biodegradation undertaking is contingent upon various factors, encompassing microbial dynamics (population diversity, enzyme activities, and biomass concentration), substrate attributes (physical and chemical properties, molecular concentration, and structure), and an assortment of environmental determinants (pH, moisture content, temperature, electrical conductivity, availability of electron acceptors and carbon, and energy sources). These parameters exert influence on the adaptation period of microorganisms to the given substrate. The concentration and molecular structure of contaminants wield substantial influence over the feasibility of bioremediation practices and the nature of microbial metamorphosis, determining whether the compound will function as a primary, secondary, or co-metabolic substrate [362].

Notably, bacteria residing in the mycorrhizosphere have demonstrated plant growth-promoting activity and are believed to work in synergy with AMF [363]. The impact of non-AMF fungal inoculants has received less attention, but there is evidence that endophytic fungi [364,365] and *Trichoderma* spp. [293] can induce changes in local microbial communities.

The impact of introduced microorganisms on the existing microbial communities hinges, to some extent, on their abundance, survival, and persistence within the ecosystem [366]. This intricate relationship implies that the very traits that contribute to successful plant growth promotion also elevate the risk of ecological invasion. Surprisingly, there is a dearth of comprehensive studies that delve into the consequences of large-scale, repeated inoculations, as well as the enduring effects, both in the long term and across subsequent crops [330,346]. Hart et al. (2018) [341] emphasize the significance of long-term repercussions, particularly concerning AMF inoculants. The assessment of the establishment and endurance of AMF inoculants is compounded by their complex genetic makeup. These concerns become all the more alarming when considering that the effects of inoculation may linger even as the population of introduced microorganisms diminishes [346]. One of the underlying mechanisms responsible for these enduring "legacy" effects is the phenomenon of plant-soil feedback. This is more likely to occur when the introduced microorganism has a symbiotic relationship with or a strong affinity for a specific plant, potentially affecting non-target plants within the agroecosystem [342,366].

The diverse outcomes witnessed when introducing microorganisms through inoculation into the resident microbiome imply a multifaceted interplay of influencing factors, notably including the host plant [359]. Correa et al. (2007) [351] found that the plant's genetic makeup exerts control over the genetic and physiological responses of phyllosphere and rhizoplane bacterial communities to *A. brasilense* seed inoculation. Rhizosphere bacterial communities were found to respond differently to *A. brasilense* at distinct growth stages of the crop, displaying more pronounced effects during the jointing stage than the grain-filling stage [367].

The resident microbiome susceptibility and buffering capacity can vary considerably depending on its diversity [346,368] and the presence of specific antagonistic or synergistic taxa [369,370]. Environmental conditions, such as soil moisture [361,371] and light intensity [359], may emerge as pivotal factors in regulating the influence of introduced microorganisms.

In general, it appears that the majority of studies investigating the effects of biofertilizers tend to place emphasis on structural attributes rather than functional aspects [346]. Recognizing the functional implications of these alterations is of paramount importance, as they exert a direct influence on ecosystem operation and well-being. To tackle the complexities of these ongoing dynamics and foresee microbial responses in natural conditions, multidimensional omics and advanced data analysis serve as indispensable tools [366,372]. The question remains as to the lasting environmental impact of introduced microorganisms, encompassing their potential for long-term and legacy effects. Additionally, there is a need for more in-depth exploration regarding genetically modified microorganisms, encompassing considerations of metabolic load [329] and the associated risks of horizontal gene transfer and dispersion [273,274]. Diverse inoculants may emerge as a more environmentally benign alternative, as implied by studies on AMF or *Bacillus spp* [76].

Bioremediation as a method presents its own set of constraints. The microbial breakdown of specific chemicals may lead to the creation of intermediary substances that not only prove more toxic but also exhibit greater mobility than the original compound. For example, the reductive dehalogenation of TCE can result in the accumulation of vinyl chloride, a highly toxic and carcinogenic byproduct. Hence, bioremediation is a technology demanding extensive research and a comprehensive understanding of microbial processes prior to its implementation. Failure to do so could yield even more severe repercussions for the ecosystem than the initial contaminant itself [375].

5. Conclusions and Perspectives

Currently, developing countries are going through particular historical phases compared to those experienced by developed nations. This is due to both globalization, which defines their role in the global context, and their geographical characteristics, which directly influence their ecological, cultural, and productive dynamics. Consequently, they are currently grappling with issues stemming from their rapid industrialization, lacking the necessary infrastructure and cultural maturity to address the adverse effects of development. On the other hand, their natural attributes bestow upon them advantages that have not yet been fully harnessed. The warm climate, coupled with increased sunlight and more intense weathering, results in higher primary productivity and, thus, greater biodiversity, which could serve as a key to their sustainable development. Throughout this review, we briefly discussed characteristics related to the communities of microorganisms in nature, as well as the effects of microbial coexistence. It becomes evident that there is a direct relationship between environmental health and the microbial balance. The targeted use of these microorganisms can lead to beneficial effects on ecosystems. Introducing microbial strains into low-quality soils, which are typically unfavorable for plant growth, has a dual benefit. It not only enhances soil fertility, boosts nutrient cycling, and mitigates soil salinity, but also enhances the profitability of cash crops and fosters the sustainability of farming practices. Thus, the key to sustainable development lies in the proper management of these biological tools. Understanding the product of the interaction between microorganisms and environmental factors is essential for the development of cost-effective sustainable environmental management techniques.

Bioremediation is a burgeoning technology that can be employed in conjunction with other physical and chemical treatments to comprehensively address a wide range of environmental pollutants, in addition to helping to solve a range of other environmental issues, further in-depth studies on its other uses should be undertaken to fully explore the potential of microbial biotechnology, which appears to offer a sustainable approach to environmental pollution management. It is imperative to establish a synergistic relationship between the environmental influences on the fate and behavior of environmental contaminants and the selection and efficacy of the most suitable bioremediation technique, as well as other pertinent methods, to ensure the efficient and successful execution and monitoring of bioremediation processes.

The vast majority of articles published on the effects of using microorganisms in bioremediation, particularly studies on the use of microbial strains in the remediation of natural environments, reveal a range of methodological limitations, like the use of known and secure microbiota species, the use of the host species with a short-life cycles, the control and manipulation of mineral nutrients level in soil and the appropriate combination of micobiota species and host plant. It is essential to bear in mind that the majority of this research has been conducted in temperate climates. This article proposes that the environmental conditions of tropical regions could offer an advantage for the utilization of this more ecologically sustainable technology, which could usefully be employed to tackle problems in developing countries.

Author Contributions: Christine C. Gaylarde and Estefan M. da Fonseca: conception; development of the theory; discussion of results and contribution to final manuscript.

Ethics approval and consent to participate: Not applicable.

Consent for publication: Not applicable.

Acknowledgments: This research was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Competing interests: The authors declare that they have no competing interests.

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