

SOIL MICROBES ARE SHAPED BY SOIL PHYSICO-CHEMICAL PROPERTIES: A BRIEF REVIEW OF EXISTING LITERATURE

Abstract: Soil consists of very complex, inter-related community of microorganisms which interact with one another, and with plants and animals, forming a complex web of biological activity. The microbes determine health and potential of soil to perform a multitude of ecosystem processes, which depend on the community composition and functioning. The microbial community structure and functions in soil are influenced by physico-chemical properties of soils. Abiotic controls like surrounding climate, environment, land use, nutrients, pH and rhizosphere control the composition of microbes in soil, which in turn modify soil properties. In this review, we investigate the existing body of research exploring studies which have explored how microbes are shaped by soil properties.

Keywords: microbial diversity, rhizosphere, soil texture, ecosystem functioning, biodiversity.

1. Introduction

“Biodiversity”- or biological diversity- is a term used to explain the variety of life on Earth. The Convention on Biological Diversity (CBD) defined biodiversity as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species, and of ecosystems.” The diversity of the living organisms has created a support system in our biosphere, which has been used to develop and sustain all ecosystems.

Biodiversity is mainly classified into:-

- (a) Genetic Diversity : the variety in the genetic make-up among individuals within a species.
- (b) Species Diversity : the variety among the species or distinct types of living organisms.
- (c) Ecosystem Diversity : the variety between the ecosystems like forests, deserts, grasslands, lakes, oceans, wetlands and other biological communities.

(d) Functional diversity : the biological and chemical processes of function such as energy flow and matter cycling needed for the survival of species and the biological communities (http://www.cyen.org/innovaeditor/assets/Biodiversity_module.pdf).

The soil biodiversity refers to the mix of living organisms in the soil, which interact with one another, and with plants and animals, forming a complex web of biological activity.

Soil is a complex, inter-related community of soil organisms, which influence, yet are partially determined by the physico-chemical properties of the soil [1]. Soil microorganisms play a pivotal role in various biogeochemical cycles. They also influence above-ground ecosystems by contributing to plant nutrition [2], plant health [3], soil structure [4, 5] and soil fertility.

Although microbial population in a soil is considered as a characteristic property, the extent and nature of it is continually subject to changes that are occurring in nature. Therefore, microbiological properties are more sensitive than soil physico-chemical properties, to changes in management and environmental conditions (Figure 1). Changes in the composition of soil microflora are fundamental in assessing the functional integrity of soil [7]. Soil microbial diversity determines soil fertility, productivity, and ecological stability [8]. The idea of biodiversity and ecosystem stability being intimately connected is a core dogma of early ecosystem theory. Tilman (1982) [9] stated that when an area is barren in terms of resource availability, it cannot sustain many species and its productivity would be low. Yachi and Loreau (1999) [10] said that species richness enhances the performance of ecosystem, by buffering against disturbances. Hence, understanding of microbial diversity is a necessity, in an age when we are facing threats of soil degradation and soil erosion. In this review, we look into the existing body of literature which have probed into influence of physico-chemical properties of soil on soil microbial composition and diversity.

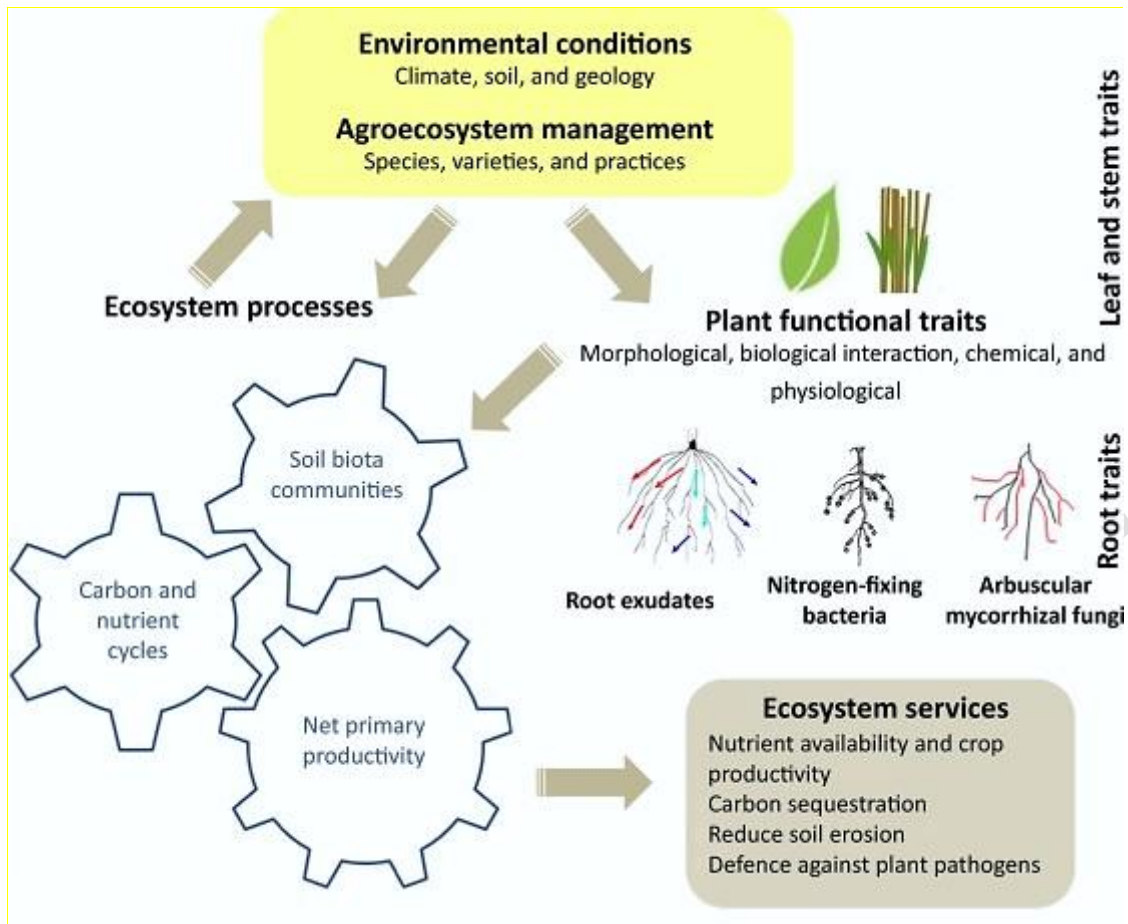


Figure 1: Linkages showing how soil microbes help shape ecosystem processes (from Faucon *et al.*, 2017[6])

1.1 Factors influencing the occurrence and distribution of soil microflora

Some notable factors, in this study, which manipulate the soil microbial population are environment, soil nutrient status, soil pH, soil texture, rhizosphere and host plants. Their effects and influences in soil are briefly reviewed.

a. Environment

Climatic changes alter species distribution and affect the interactions among organisms [11, 12]. These interactions can be beneficial or antagonistic or may have little or no functional impact. The nature and extent of these interactions may change with environmental stress [13]. Barros *et al.* (1995) [14] studied the effect of moisture on soil microbial activity. He reported a positive correlation between the percentage humidity, total heat evolution and microbial growth rate constant, all measured by microcalometric method. Soil drying effectively reduces the substrate flow to microbial cells. With the gradual drainage of soil pores, the water films on soil surfaces become thinner, leaving a more

difficult path for the substrate molecules to diffuse into cells [15]. The relative importance of cytoplasmic dehydration versus diffusional limitations in controlling rates of nitrification in soil was studied by Stark and Firestone (1995) [16]. They reported decline in the activity of nitrifying bacteria at low soil water content.

An integrative measurement of microbial activity in soils is the efficiency by which microbes convert assimilated carbon into biomass carbon. It is called the microbial growth efficiency (Y). Changes in rainfall patterns and soil water content influences Y and affects nutrient cycling at ecosystem level [17]. The accumulation and decomposition of litter in soils under forests depend on climatic conditions. Rigobelo and Nahas (2004) [18] evaluated the effect of monthly rainfall and temperature, organic matter, total organic carbon and soil moisture on total bacteria, in a *Eucalyptus*-cultivated and *Pinus*-cultivated oxisol. They reported a positive correlation of organic matter, organic carbon and soil moisture on the total bacteria and dehydrogenase activities. Besides, all parameters in *Eucalyptus* soil were higher than *Pinus* soil, most probably due to higher soil pH and fertility status.

An increase in 5°C in a temperate forest altered the relative abundances of soil bacteria and increased the bacterial-to-fungal ratio of the community [19]. It has been reported that microbially-mediated processes (like N-mineralisation), which are very conspicuous, are more tightly correlated with abiotic factors like temperature and moisture than the composition of microbial community in soil. This may be since a variety of microbes drive these processes [20].

Ram *et al.* (2013) [21] studied the seasonal variation in microbial populations at different depths of normal and sodic soils of Varanasi, and found that winter season favoured an increase in population of soil bacteria and fungi, and summer season favoured soil actinomycetes in both sodic and normal soils. Subba Rao (1982) [22] reported higher phosphate solubilising bacterial count in soil under moist climate than under hot and dry climates in arid regions of India. Microbial studies related to climate change have been done in certain cases in India [23, 24], but they have not focussed on microbial diversity changes with respect to environment. Bhowmik *et al.* (2008) [25] showed that climate affects the phyto-diversity and microbial diversity of soils in Arunachal Pradesh. Dasgupta (2016) [26] found that soil culturable bacterial, fungal and actinomycetal populations did not significantly vary among the different agro-ecological sub-regions of West Bengal, although they did

show variations in correlation patterns with soil physico-chemical properties from one region to another.

In general, microbial population and diversity is higher in mild and moist climate [27] than hot and dry conditions. The direct influence of climate on microbial status is well-reviewed [28, 29] but the indirect effects are less acknowledged. They have huge significance in stimulation and mediation of important ecological interactions, and it is highly essential to explore the systems and mechanisms underlying these complex interactions.

b. Soil nutrients

Soil nutrient status is an important parameter which determines the proliferation of microbes in soil. Conversely, the microbes determine the soil nutrient status [27]. Microbial community composition, in most cases, is sensitive to the levels of nitrogen, phosphorus and potassium in soil [30]. It has been observed, that in unmanaged ecosystems, increasing N input suppresses the soil microorganisms [31]. Geisseler and Scow (2014) [32] reviewed and analysed the responses of soil microorganisms to mineral fertiliser using data from long-term fertilisation trials in cropping systems. They reported a 15 per cent increase in microbial biomass in fertiliser application trials above unfertilised control trials. Fertilisation tended to reduce microbial biomass carbon in soils with a pH below 5, but it had significantly positive effects at higher soil pH values.

The soil organic matter (SOM) is a vital component of the soil which determines the soil health due to many essential functions it provides and supports [33]. Main indicators for evaluating SOM status are the soil organic carbon ($\approx 50\%$ of SOM), organic nitrogen and readily mineralisable C and N [34]. Decrease in SOM leads to decreased biodiversity and soil fertility, loss of soil structure, increased soil erosion and soil compaction [35]. The soil organic carbon is a familiar and direct indicator of ecosystem performance. Most of the bacteria, fungi and actinomycetes have been shown to have positive correlation with the organic carbon content of soil [36, 37].

Swier *et al.* (2011) [38] studied the fungal population and diversity in organically amended soils of Meghalaya. They reported significant positive correlation between fungal populations and organic carbon in organic plots. Koorem *et al.* (2014) [39] studied how soil nutrient content influences abundance of soil microbes, in a herb-rich spruce forest. They reported that abundance of arbuscular mycorrhizal fungi was negatively related to soil phosphorus and positively influenced by soil nitrogen content.

Nutrients like calcium, magnesium and sodium are constituents of microbial cells. Das et al. (1991) [40] stated that actinomycetes and fungi in soil showed positive correlation with available K^+ , exchangeable Ca^{2+} , Mg^{2+} and the cation exchange capacity (CEC) of soil. Bashan and Vazquez (2000) [41] observed that increased levels of Ca in soil had detrimental effects on *Azospirillum* in soils. Magnesium leads to increased sporulation of oligotrophic bacteria, and also counters the toxicity caused by increased levels of cadmium in soils [42]. Markovitz and Sylvan (1961) [43] studied the effect of sodium sulphate and magnesium sulphate on heteropolysaccharide synthesis in Gram-negative soil bacteria. Vincent (1962) [44] studied the influence of Ca and Mg on the growth of *Rhizobium trifolii*. He reported that deficiency of Ca, in presence of Mg, caused reduction in growth rate, the level of maximum growth and the proportion of viable cells. Shortage of Mg, in presence of Ca, did not significantly affect the growth rate, but proportion of viable organisms was markedly decreased.

Princic et al. (1998) [45] studied the effects of different ammonium concentrations on the community structure of nitrifying bacteria from wastewater. Martikainen (1985) [46] reported that nitrifiers require sufficient Ca, Mg, P and Fe for sufficient growth. Patil et al. (2011) [47] reported that increased P-application in soil leads to growth of phosphorus solubilising bacteria, in maize fields.

Nutrient requirement for microorganisms varies from one group to another. Heterotrophs show increased growth in organically rich soils [48]. Autotrophs show less dependence on organic carbon. Increase in Mg^{2+} in soil triggers the proliferation of actinomycetes, whereas the increase in Ca^{2+} accentuates the proliferation of fungi. Small-scale resource heterogeneity is very important in determining the plant productivity, which influences the soil microbes [49].

c. Soil pH

One of the most influential factors affecting the microbial community of soil is pH. pH strongly influences abiotic factors like carbon availability, nutrient availability, and solubility of metals. Soil pH also influences biotic parameters like biomass of fungi and bacteria. Normally bacteria and actinomycetes are positively correlated with soil pH [40], whereas fungi show negative correlation with soil pH [50, 51]. Rousk et al. (2009) [51] reported approximately 30-fold increase in fungal importance when pH was reduced from 8.3

to 4.5. This shift in fungal and bacterial importance along pH gradient resulted in decreased carbon mineralisation.

Soil pH has been included in soil health tests to assess impacts of land use change and agricultural practices [52, 53]. Many crops grow best if pH is close to neutral (pH 6.0-7.5). In acidic soils, calcium, magnesium, NO_3^- -nitrogen, phosphorus, boron and molybdenum are deficient, while aluminium and manganese are abundant (often at toxic levels to plants). Phosphorus, iron, copper, zinc and boron are normally deficient in alkaline soils [54]. Nitrification and nitrogen fixation are inhibited by low pH. Various diseases of plants are also influenced by pH (eg: potato scab caused by *Streptomyces scabies*, which is more severe in pH more than 5.2. Take-all disease of wheat, caused by *Gaeumannomyces graminis* is favoured by alkaline pH. Clubroot of mustard caused by *Plasmodiophora brassicae* is a major problem in acidic soils of pH 5.7 or lower) [54, 55, 56].

Nicol *et al.* (2008) [57] studied the influence of soil pH on the diversity, abundance and transcriptional activity of ammonia-oxidising archaea and bacteria. The community structure and phylogeny of ammonia-oxidising bacteria and archaea, across a soil pH gradient of 4.9-7.5, was determined by amplifying 16S rRNA and amoA genes followed by denaturing gradient gel electrophoresis (DGGE) and sequence analysis. Rousk *et al.* (2010) [58] reported a doubling of bacterial diversity between pH 4 and 8. In contrast, the relative abundance of fungi was weakly related to soil pH. Martyniuk and Martyniuk (2002) [59] reported that soil populations of *Azotobacter* spp. rarely exceed several thousand cells per gram of neutral or alkaline soils, and in acid soils (pH<6.0), these bacteria are generally absent or occur in very low numbers. *Azospirillum* spp. optimally exist in soil at pH near neutrality [60], and drying the soil or increasing soil pH can reduce the adsorption of cells to soil particles [61]. However, the growing of wheat decrease soil pH. That is because plant exudates influence the soil solution [62].

Dancer *et al.* (1972) [63] reported that in soil pH range of 4.7 to 6.6, ammonification rates did not vary appreciably, but it had significant effect on the rate of nitrification. Rate of NO_3^- accumulation decreased with decrease in soil pH. Ste-Marie and Pare´ (1999) [64] studied soil pH effects on net nitrification on boreal forest stands. Increase in forest floor pH had a positive effect on net nitrification while acidification depressed it. Phosphorus solubilisers secrete organic and inorganic acids, which solubilise inorganic P and decrease the pH in basic soils [65].

Soil pH is a function of parent material, vegetation and climate which helps us identify trends in change **for several soil** biological and chemical functions [66].

d. Soil texture

Soil texture refers to the weight proportion, or the relative proportion, by weight percentage of sand, silt and clay. It plays a key role in carbon storage and influences nutrient retention and availability. It also governs availability for growth and important soil biological processes [67, 68, 69]. [Hamarashid et al. \(2010\) \[67\]](#) studied the effects of soil texture on microbial populations in soils. The results obtained showed that clay loam and silty clay loam soils had the highest bacterial populations, while sandy loam and silty loam recorded the least populations. No significant differences were noticed among the total fungi values. [Chau et al. \(2011\) \[70\]](#) reported that the bacterial species richness increased significantly with the coarseness of the soil. The increase in species richness in coarser soils was likely due to the increased number of isolated water films in soils with larger pores, suggesting that pore-scale hydrologic regime constrains bacterial richness in soil.

[Hassink et al. \(1993\) \[71\]](#) reported that the percentage of mineralized organic nitrogen was higher in sandy soils than in loams and clays; this was not observed for carbon. **The experiment was done on at least 8-year old grassland plots in Netherlands.** **The** C/N (carbon by nitrogen) ratio of the microbial biomass was higher in sandy soils than in loams and clays and was positively correlated with the nitrogen mineralization rate per unit of microbial biomass nitrogen. This agrees with the concepts of food webs that N mineralization is positively correlated with the C/N ratio of the consumer (bacteria) for a given C/N ratio of the substrate (organic matter). [Hassink \(1994\) \[72\]](#) reported a positive relationship between the amount of organic N in the soil and the clay + silt content. The relationship was affected by the groundwater table. There was a negative relationship between the percentage of soil N mineralizing during incubation and the clay + silt content of the soil. The amount of organic C was only positively correlated with soil texture in the soils with a high water table, but the relationship was less clear.

[Carney and Matson \(2005\) \[73\]](#) mentioned that fine-textured soils support more microbial biomass than coarse textured soils. [Heritage et al. \(2003\) \[74\]](#) stated that sandy soils cannot retain water very well and drain very quickly. Clay loam preserves water and retains soil nutrients for a longer time. This greatly influences microbial populations in soil.

e. Rhizosphere and host plants

Rhizosphere is characterised by greater microbial activity where most microflora along with their beneficial and harmful activities are present. Microbial activity is limited by the availability of carbon [75]. In the rhizosphere there is a constant supply of readily available carbon sources to the heterotrophic microorganisms. As a result, microbial activity, population and biomass in the rhizosphere of plants differ markedly from non-rhizosphere soils [76, 77].

Alpei *et al.* (1996) [78] found that the microbial biomass in the rhizosphere of wood-barley (*Hordelymus europaeus* L.) was almost double that of non-rhizosphere samples. Microbial respiration was also found to be higher in soils near roots than in soils away from roots. Other studies revealed that nutrients added to soil were rapidly immobilised by rhizosphere bacteria with only small portions returned to soil after the carbon supply ceased [79, 80, 81]. The constant supply of carbon compounds from plant roots fuels the complex interactions among rhizosphere organisms as well as between microorganisms and plants. Protozoa and microbial feeding nematodes are known to be the most important grazers of microflora in terrestrial ecosystems [82, 83]. Despite the crucial importance of interaction between roots (root exudates), microorganisms and their predators for plant growth, the knowledge of these interactions is still very rudimentary and poorly understood [84].

Lange *et al.* (2015) [85] showed, from observations accumulated from long-term biodiversity experiments in Jena, that higher plant diversity increases rhizosphere carbon inputs into the microbial community resulting in both increased microbial activity and carbon storage. Increases in soil carbon were related to the enhanced accumulation of recently fixed carbon in high-diversity plots. They showed that that elevated carbon storage at high plant diversity is a direct function of the soil microbial community, indicating that the increase in carbon storage is mainly limited by the integration of new carbon into soil and less by the decomposition of existing soil carbon.

The plant species, plant community diversity and microbial interactions significantly impact the soil microbial communities, but the effects are not explored in detail as of yet. Increasing plant community richness significantly altered soil bacterial community composition and was negatively correlated with bacterial diversity. Concentrations of soil carbon, organic matter, nitrogen, phosphorus, and potassium were similarly negatively correlated with bacterial diversity, whereas the proportion of antagonistic bacteria was positively correlated with soil bacterial diversity [86]. Host variation, among cultivars or

plant genotypes, affects the level of impact of beneficial as well as harmful microorganisms in soil. For example, *Rhizobium* sp. infects only the legumes, whereas the arbuscular mycorrhizal fungi infect a wider array of plant species [3]. Greater rhizosphere effect of plants was observed in bacteria than in actinomycetes and fungi [87]. Similarly, Edward and Tripathi (1972) [88], Shetty and Patil (1975) [89] studied how *Azotobacter* population in soils vary with different host plants. Dobereiner and Depolli (1980) [90] reported various *Azospirillum* species in the rhizosphere of cereals. Yahya and Al Azawi (1989) [91] reported that soil samples of vegetable crops had highest phosphate solubilising bacteria population, followed by legumes, grasses, cereals and orchards, from soils of Iraq.

Rhizosphere and host plants seen to affect the multitude of bacteria, fungi, actinomycetes, protozoa, viruses etc. in soil, and this field of soil biology needs to be explored in depth.

2. Microbial diversity as shaped by soil properties

Microbial diversity in soil exceeds that of eukaryotic organisms. One gram of soil may harbour upto 10 billion microorganisms of possibly thousands of different species [92]. Microbial diversity encompasses different levels of biological organisations. It includes genetic variability within taxons (species), and the number (richness) and relative abundance (evenness) of taxons and functional groups (guilds) in communities [93].

Tiedje *et al.* (2001) [94], Ranjard and Richaume (2001) [95] and Sessitsch *et al.* (2001) [96] studied the impact of soil structure and spatial isolation on microbial diversity. Soils subjected to proper agricultural practices, show stable aggregation of microbes in micropores [95]. Particle size has a higher impact on microbial diversity and community structure than factors like pH or organic nutrient content. The type and amount of available organic substrates strongly influence the abundance of microbial groups and their functional diversities in soils [97, 98].

Smit *et al.* (2001) [99] reported that in wheat fields of Netherlands, bacterial biomass did not change significantly among seasons, but culturing and molecular fingerprinting showcased variations in community compositions. Loreau *et al.* (2001) [100] reported that with increasing soil microbial diversity, there is a concurrent increase in productivity upto a certain level. Beyond that level, further increase in diversity results in decrease in plant production. Marcel *et al.* (1998) [101] revealed that mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity.

Reeve *et al.* (2010) [102] investigated the role of gene frequency and diversity, measured by microarray analysis, on soil processes in commercial organic and conventional strawberry fields in USA. Soil physical, chemical and biological analyses were conducted including functional gene microarrays (FGA). Soil physical and chemical characteristics were primarily controlled by soil texture (coarse vs. fine-textured), but biological and FGA measures were more influenced by management (organic vs. conventional). Organically managed soils consistently showed greater functional activity as well as FGA signal intensity (SI) and diversity. Overall FGA SI and diversity were correlated to total soil microbial biomass. Functional gene group SI or diversity were correlated to related soil chemical and biological measures such as microbial biomass, cellulose, dehydrogenase, ammonium, and sulphur. Management was the dominant determinant of soil biology as measured by microbial gene frequency and diversity, which paralleled measured microbial processes.

Zhou *et al.* (2002) [103] reported that in a site richer in organic carbon, microbial communities exhibited the uniform distribution pattern regardless of soil water content and depth. The uniform distribution implies that competition does not shape the structure of these microbial communities. Studies based on mathematical modelling suggested that spatial isolation could limit competition in surface soils, thereby supporting the high diversity and a uniform community structure. Carbon resource heterogeneity may explain the uniform diversity patterns observed in the high-carbon samples even in the saturated zone.

Microbial diversity has a positive effect on the cycling of nutrients and ecosystem processes. Microbial diversity ensures that all organic compounds are recycled in the biosphere [104].

Harish Kumar (2005) [105] studied the microbial diversity of 6 agro-climatic zones of Karnataka and calculated the Simpson index and Shannon-Wiener index of wetland, dryland and orchard ecosystem. He reported high biodiversity in dryland ecosystem of Eastern Dry Zone and wetland ecosystem in Eastern Dry Zone.

Wani *et al.* (2006) [106] studied microbial diversity associated with Lonar soda lake in India. 16S rDNA genes were amplified by PCR using primers specific to domains Bacteria and Archaea. After RFLP analysis, 44 unique phylotypes were obtained, out of which 34% were firmicutes, 29.5% proteobacteria, 6.8% actinomycetes, 4.5% *Deinococcus thermus*, 13.3% cytophages-flavobacterium-bacteroidetes, 6.8% planctomycetes, 4.5% cyanobacteria and 2.27% spirochetes.

Ramanathan et al. (2008) [107] studied the fungal and bacterial diversity with respect to behaviour of nutrients in the sediments of Sundarbans mangroves. *Aspergillus* and *Penicillium* were reported to be the most abundant fungal species in all the three sampling locations. The study also revealed that the existing environmental conditions plays a significant role in the proper determination of microbial diversity, as well as the behaviour of soil nutrients.

Srivastava et al. (2014) [108] undertook a study with an objective to investigate the impacts of bioclimates, soil depth, cropping systems, land use systems and management practices on the distribution of culturable microbial populations in the soils of Indo-Gangetic Plains. The research spanned 11 agro-ecological sub-regions encompassing states like West Bengal, Tripura, Uttarakhand, Uttar Pradesh, Bihar, Punjab and Haryana. They reported that bacterial and fungal populations are strongly and negatively correlated with soil depth. Sub-humid (moist) bioclimatic system recorded higher microbial population than sub-humid (dry) and semi-arid bioclimatic systems. Legume-based cropping system had higher microbial population than cereal or vegetable-based cropping.

Ciccolini et al. (2016) [109] explored the composition of microbial communities involved in nitrogen cycling in Mediterranean peaty soils drained for farming activity, and found that ammonia-oxidizing communities like AOA were shaped by clay content, AOB were shaped by bulk density, and both AOA and AOB were controlled by exchangeable calcium content. In ecologically restored lands, microbes have been seen to be influenced by changes in physico-chemical properties. In re-vegetated landscapes of Changting in China, which were previously degraded bare lands of red soil, soil bacterial diversity increased significantly with major phyla like Chloroflexi, Proteobacteria, Firmicutes and Cyanobacteria being positively correlated with soil chemical properties (Hou et al., 2019 [110]).

Most soil health conservation and land-use planning strategies do not consider monitoring microbial community composition and functions. However, general awareness regarding soil health and microbial contribution to maintenance and enhancement of soil health is increasing. It has been seen that soil microbes can be indicators of ecosystem processes and impacts of land use change, and can be integrated to provide relevant insights on soil properties and health. For example, Hermans et al. (2020) [111] used information on soil bacterial communities to differentiate soils, over 1300 km transects in New Zealand, with

different edaphological properties with 83% accuracy. Therefore, deeper research in this fascinating branch of ecology is warranted.

3. Conclusions:

Understanding the dynamics of soil microbial communities, structure and functions, and the factors that affect those dynamics is crucial for comprehending the processes affecting soil fertility and productivity in various ecosystems. In the wake of increasing awareness regarding sustainable agriculture and development, we are realising that we can exploit soil microbes to sustain ecosystem productivity for a significant amount of time. There is a lot of heterogeneity in terms of how microbes are shaped by edaphological properties. In this review, we see that many studies have investigated into such questions. However, inferences from such studies remain context-specific spatiotemporally. To that end, we need to build upon our understanding of how soil microbiomes are influenced by soil properties and try to find out wide-scale patterns and generalities, so that we can better judge their roles under land-use and climate change.

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