Article

Understanding and Enhancing Soil Biological Health: The Solution for Reversing Soil Degradation

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Abstract: Our objective is to provide an optimistic strategy for reversing soil degradation by increasing public and private research efforts to understand the role of soil biology, particularly microbiology, on the health of our world's soils. We begin by defining soil quality/soil health (which we consider to be interchangeable terms), characterizing healthy soil resources, and relating the significance of soil health to agroecosystems and their functions. We examine how soil biology influences soil health and how biological properties and processes contribute to sustainability of agriculture and ecosystem services. We continue by examining what can be done to manipulate soil biology to: (i) increase nutrient availability for production of high yielding, high quality crops; (ii) protect crops from pests, pathogens, weeds; and (iii) manage other factors limiting production, provision of ecosystem services, and resilience to stresses like droughts. Next we look to the future by asking what needs to be known about soil biology that is not currently recognized or fully understood and how these needs could be addressed using emerging research tools. We conclude, based on our perceptions of how new knowledge regarding soil biology will help make agriculture more sustainable and productive, by recommending research emphases that should receive first priority through enhanced public and private research in order to reverse the trajectory toward global soil degradation.

Keywords: soil biology; sustainable agriculture; soil health; soil management; soil organic matter (SOM)

1. Introduction

One of the most unexplored frontiers associated with understanding the dynamics of soil resources and their subsequent health or quality is that of soil biology. We suggest this reflects the challenges associated with understanding biological properties and processes when compared to soil physical and chemical manipulations that can be used to influence soil quality/health. As a result, multiple post-World War II developments leading to agriculture as we know it today [1] placed a greater emphasis on physical and chemical manipulation than on soil biology [2]. These developments included: (i) increased availability and use of synthetic fertilizers, herbicides, and pesticides; (ii) an improved understanding of plant nutrition and an infrastructure for delivering fertilizers to farmers; (iii) improved tillage, planting, harvesting equipment; (iv) cost-effective subsurface drainage; (v) increased efficiencies for both animal and crop

production systems; and (vi) development of global markets. Unfortunately, soil biological responses to these developments were often overlooked or not recognized, so the rapid changes also resulted in unintended consequences, especially with regard to soil health and long-term agricultural sustainability.

Optimistically recognizing the challenges associated with stopping and even reversing soil degradation, our objectives are to identify critical soil biological questions and to suggest various strategies for answering them through enhanced public and private research efforts focused on the concept of soil health. In order to identify knowledge gaps, we review previous literature on soil health and the role of soil biology, and frame future prospects in terms of emerging analytical capabilities.

2. What Constitutes a Healthy Soil?

2.1. Definition of Soil Health

Soil is a dynamic, living, natural body that is vital to the function of terrestrial ecosystems [3]. Farmers intuitively recognize the importance of healthy soils and have used qualitative terms (*i.e.*, color, taste, touch and smell) to describe soil condition and performance for crop production since the dawn of agriculture about 10,000 years ago [4]. At the beginning of the 20th Century, qualitative descriptions were gradually replaced by analytical procedures to assess and evaluate soil almost exclusively from the perspective of inorganic nutrients and crop yield [5].

Warkentin and Fletcher [6] were among the first to introduce the soil quality concept as an approach to improve the process of land use planning. The soil quality concept evolved rapidly during the 1990's, an outcome of increased emphasis on sustainable land use and a growing consensus that soil quality in agriculture should no longer be limited to productivity goals [3,7–12]. As the soil quality concept evolved, methods and tools for soil quality assessment were developed to facilitate comparisons between soil management systems and to document changes in soil properties and processes that occurred in response to land-use or soil management decisions [7,9,13–16]. There was agreement that the design of any generalized soil quality assessment tool must be flexible enough to capture multiple soil functions in various combinations [14] while respecting the broader goals of sustaining plant and animal productivity, erosion control, maintaining or enhancing water and air quality, and supporting human health and habitation [9,15,17].

Soil quality is most simply defined as "the capacity of the soil to function" [9]. Important soil functions include: water flow and retention, solute transport and retention, physical stability and support; retention and cycling of nutrients; buffering and filtering of potentially toxic materials; and maintenance of biodiversity and habitat [18]. A broader, ecologically-based approach was presented by Doran *et al.* [3], where they defined soil health as "the continued capacity of soil to function as a vital living system, within ecosystem and land-use boundaries, to sustain biological productivity, maintain the quality of air and water environments, and promote plant, animal, and human health." The terms soil quality and soil health are often used interchangeably, although farmers and some members of the research community favor the term soil health [19] because it more clearly conveys the idea that soil is a living dynamic system [3]. Most soil scientists, however, reluctantly prefer the term soil quality because of its focus on quantitative soil properties and the quantitative linkages between those properties and various soil functions [19].

Soil taxonomy (the set of innate soil characteristics conveyed by the classification) is the foundation for the soil quality/health framework. Each specific soil has inherent soil quality characteristics that are determined by the interaction of climate, topography, living organisms (vegetation, microorganism, humans) and parent material over long periods of time [20]. The term "dynamic soil quality" refers to the effects of human use and management on soil function [21,22], reflecting changes associated with current or past land use and crop and soil management decisions. Dynamic soil quality can be measured and used to compare different practices on similar soils or temporal trends on the same soil. The inherent properties of different soils may limit the extent of changes due to dynamic processes and need to be accounted for within management strategies to producer healthier soils.

2.2. Existing Soil Quality/Health Assessment

Assessment of soil quality is usually accomplished through direct measurement of a suite of soil biological, chemical, and physical properties and processes that have the greatest sensitivity to changes in soil function [14]. Soil quality indicators should correlate well with ecosystem processes, integrate soil properties and processes, be accessible to many users, sensitive to management and climate, and, whenever possible, be components of existing databases [23]. Selected groups of soil indicators, also referred to as minimum datasets (MDSs), that are used to indirectly measure soil function must also be sufficiently diverse to represent chemical, biological, and physical properties and processes of complex systems [23,24]. Researchers have given particular attention to soil indicators that can serve as early and sensitive indicators of longer-term changes in soil ecosystem function [25]. Frequently recommended soil quality indicators include: soil organic matter (SOM), particulate organic matter (POM), microbial biomass carbon (MBC), potentially mineralizable nitrogen (PMN), macroaggregate stability, electrical conductivity (EC), sodium absorption ratio (SAR), pH, inorganic N, P, potassium (K), and magnesium (Mg), available water-holding capacity (AWC), bulk density (BD), topsoil depth, and infiltration rate [9,23,26]. Soil enzyme activity, specifically β-glucosidase activity which is involved in plant residue degradation, and water-filled pore-space were recently added to the recommended list of important soil quality indicators because of their association with soil biological properties and processes [27].

The issue of spatial and temporal scale affects both the sensitivity of assessment and the choice of indicators that are evaluated. Both scales vary depending upon the type of soil management questions that are being asked or the purpose for which soil quality is being evaluated [28]. In general, soil quality evaluations at the farm, watershed, county, state, regional, or national scales are more general and less precise than those made at the point or plot scale [29]. Large-scale assessments often rely on databases, simulation models, and remote sensing in conjunction with statistically representative point sampling to verify the projections [21]. For instance, Potter *et al.* [30] used a combination of model simulations and data point measurements across the U.S. to assess soil organic carbon and identify areas most at risk for soil quality/health degradation and loss of soil function.

2.3. The Significance of Soil Health to Agroecosystems and Soil Restoration

The single most important soil quality indicator for nearly all soils throughout the world is SOM. It is also one of the most common deficiencies identified in degraded soils because of the numerous chemical, physical, and biological properties and processes it influences. Soil organic matter is generally

measured based on the concentration of soil organic carbon (SOC), because about 50% of the SOM is accounted for by SOC. Increases in SOM, particularly in biologically-available forms, are intimately linked to changes in the size, activity and composition of the soil microbial community, enhanced cycling and retention of nutrients, improved aggregate stability, and increased water-holding capacity.

Effective SOM management involves balancing two ecological processes: mineralization of carbon (C) and nitrogen (N) in SOM for short-term crop uptake, and sequestering C and N in SOM pools for long-term maintenance of soil quality, including structure and fertility. Agricultural land management options recommended to increase SOM and improve soil quality nearly always include some reduction in tillage intensity and implementation of integrated, multifunctional cropping rotations that include forage legumes, and/or small grains.

Integrated, extended crop rotations that include small grains and forage legumes have been shown to increase SOC compared to mono- or bi-crop rotations [31–34] with positive impacts being especially evident in the biologically active fractions of SOM [35–37]. Cover crops increase the complexity of rotations and extend the duration of photosynthetic capture in annual crop rotations, thus increasing organic C inputs to the soil and the potential for soil C sequestration—a critical process for restoring degraded soils and addressing increasing concerns regarding global climate changes.

Cover crops can also provide important ecosystem services when planted within corn (*Zea mays* L.) soybean [*Glycine max* (L.) Merr.] systems and extended cropping rotations. Environmental benefits such as decreased soil erosion [10,38] and decreased nitrate leaching [39–41] have been consistently demonstrated in cover crop studies. In general, leguminous cover crops provide the greatest potential for improving yields, but cereal crops generally result in higher levels of SOM, greater weed suppression, and more soil N immobilization, which can reduce nitrate leaching during winter months [42]. Planting small grains and *N*-fixing cover crops together may be an effective management strategy to simultaneously increase soil C and optimize soil N cycling processes, and thereby reduce both leaching and gaseous emission losses of N.

Conservation tillage increases surface SOC content compared to plow tillage [43–45], but some studies indicate subsoil C content is higher under plowing [46–48]. There is evidence that changes in tillage management alter C cycling processes, resulting in greater retention of corn-derived C in no-till (NT) compared to plowed systems. Type and intensity of tillage directly controls substrate availability to soil organisms and rate of decomposition of substrates by affecting the quantity and distribution of plant residues and roots [49,50]. Tillage factors can also exert indirect control on residue decomposition processes by influencing soil aeration, water content, soil temperature, and especially soil aggregate properties.

Soil management practices that increase SOM and enhance soil health create expanded habitat and greater niche diversity for soil biological communities. It is the inputs of organic matter from plant residues and exudates that provide carbon and energy sources for soil organisms. Net increases in SOM improve soil aeration, temperature, moisture, and aggregate stability, and provide a resilient resource base for a wide variety of soil organisms through the maintenance of a rich and varied source of OM and the efficient supply of nutrients. Improving the quality and health of the soil is important not only for those that manage the land, but for anyone who enjoys a cup of clear water or access to a plentiful and consistent food supply.

3. How Does Soil Biology Influence Soil Health, or What's Missing in a Degraded Soil?

3.1. Soil Biology Overview

Soil biology encompasses the collective biomass and activities of soil-dwelling organisms from an array of trophic levels that are present in staggering quantities, even though individuals may not be visible to the unaided eye. For example, it is estimated that there are at least one billion bacterial cells per gram of soil distributed among thousands to millions of individual species [51]. It has been calculated that the microbial biomass existing underground may approach the sum of all living biomass on the earth's surface [52]. Viewing the tree-of-life (based on genetic relatedness), one begins to understand the diversity of the unseen microbial world, especially since only the three branches at the top right (Animalia, Fungi, and Plantae) contain individual organisms that can be seen with the unaided eye (Figure 1).
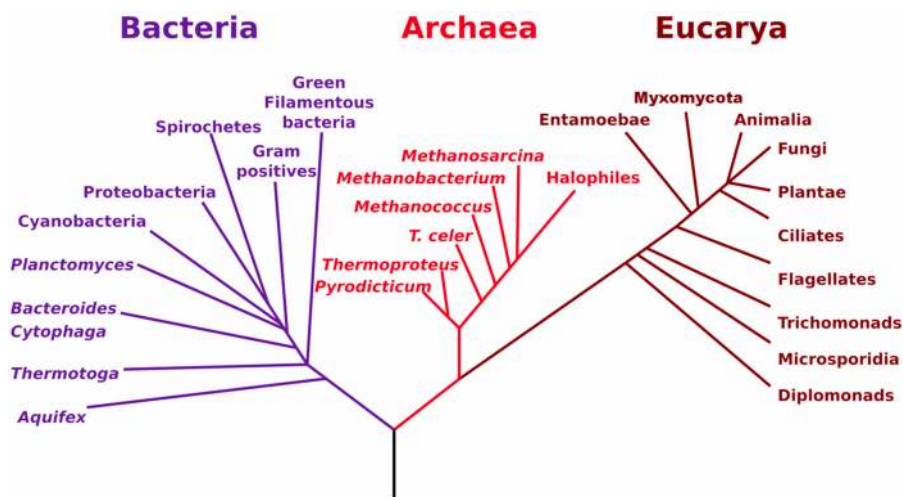

Figure 1. Tree of life based on genetic relatedness using the ribosomal RNA gene sequence.

One of the three domains (domain is the highest taxonomic level of life), the Archaea, was first described in 1977. Archaea appear morphologically similar to bacteria; however, they possess fundamental biochemical similarities with Eucarya and fundamental biochemical distinctions from Bacteria. In short, Archaea are genetically and phylogenetically as different from Bacteria as they are from any of the members of the Eukaryotic domain. The discovery of major taxonomic groups containing microscopic life continues at a rapid pace with a significant modification of the Archaeal domain now becoming apparent—all within in the last 25 years. In 1987 the domain Bacteria contained just 12 phyla (phyla is highest taxonomic group within a domain); today over 70 bacterial phyla are recognized or under consideration for recognition [53].

Each of the primary "Tree-of-Life" branches represents numerous species such that a detailed view would show each branch giving way to successively smaller branches, which are further studded with bushes. Within the two prokaryotic domains (Archaea and Bacteria), even the lowest taxonomic level of species often contains considerable diversity (*i.e.*, microdiversity) that manifests itself in strains, ecotypes, biotypes, serotypes, *etc.* For example, all *Escherichia coli* are considered the same species, but there are numerous strains that are distinctive not only genetically but functionally as well. This

means that one strain can be a deadly pathogen while other strains are either benign or even beneficial partners co-existing with plants and animals. This is just one example of the subtle differences associated with soil biology and why it can be difficult to identify exactly what's wrong in degraded soils that simply are not performing as expected.

The variety of physiological capabilities, tolerances, and energy sources of soil microorganisms are extraordinary, and new discoveries are common. A useful tool to comprehend the physiological diversity is the electron tower which displays standard electrode potentials of redox couples (Figure 2). Plants can photosynthesize by fixing CO_2 using water. Animals and plants respire organic compounds at the expense of oxygen as an electron acceptor. Microbes, on the other hand, can use all of these compounds (and more) as either an energy source or an electron acceptor so that energy can be gained from hydrogen gas (H_2) and inorganic molecules in their reduced form (e.g., nitrogen, sulfur, iron, manganese, *etc.*), while CO_2 and those same molecules (e.g., nitrogen, sulfur, iron, manganese, *etc.*) in their oxidized forms can be used as electron acceptors. Bacteria that can oxidize ammonium using nitrite as an electron acceptor have been described in the 21st century and have been found to play key roles in wastewater treatment. In addition to heterotrophic metabolism using exogeneous electron acceptors, microbes can ferment organic compounds, reducing one part while oxidizing the other. Microbes can fix CO_2 by not only standard photosynthetic processes, but also by anoxigenic photosynthesis using other compounds (e.g., sulfur) as electron donors in lieu of water, plus three other pathways not found in eukaryotic organisms [54]. As recently as 2000, it was discovered that some bacteria contained a protein, bacteriorhodopsin, which creates energy from light allowing photo-heterotrophic growth [55]. Similar bacteriorhodopsin molecules had previously only been detected in extremely halophilic archaea. This previously overlooked bacterial metabolism has since been found to be performed by a significant fraction of the world's marine bacterioplankton.

Microbes can even partner with others to perform metabolic processes thought to be energetically unfavorable such as anaerobic methanotrophy which couples methane oxidation with sulfate reduction. Anaerobic oxidation of methane has been described largely in the last decade, and new details such as the use of nitrate (in lieu of sulfate) in this reaction are still emerging.

The physiological tolerances of bacteria far exceed that of eukaryotes. Biological activity of microorganisms can proceed at environmental extremes including temperatures below freezing and above boiling, at pH approaching acid and alkaline endpoints, under very low water tensions, at very high ionic strength, in high radiation fields, and in the presence of high concentrations of toxic compounds. Viable bacteria have been retrieved from 2 miles below the earth's surface [56]; in fact, the existence of a sterile location on earth is difficult to prove.

Several recent findings highlight the on-going transformation in understanding of soil organisms and their processes. In 2006, it was determined that members of the Archaea were actually responsible for most of the nitrification occurring in many soils [57]. This completely changed what was "known" for decades—that nitrification was performed strictly by a very limited number of Bacterial genera. Bacteria belonging to the phylum Acidobacteria are now thought to be the numerically-dominant organism in many soils, but were first described in 1991 and virtually unheard of 15 years ago. Unfortunately, due to their resistance to laboratory culturing, there is yet insufficient information to establish their functional roles. Clearly, the basic understanding of the microbial world remains incomplete, and therefore represents an impediment to assessing and promoting soil health. The continuing exponential increase

in soil biological knowledge is also why we are optimistic that the pathway for mitigation and even reclamation of degraded soils is through an increased emphasis on research and education.
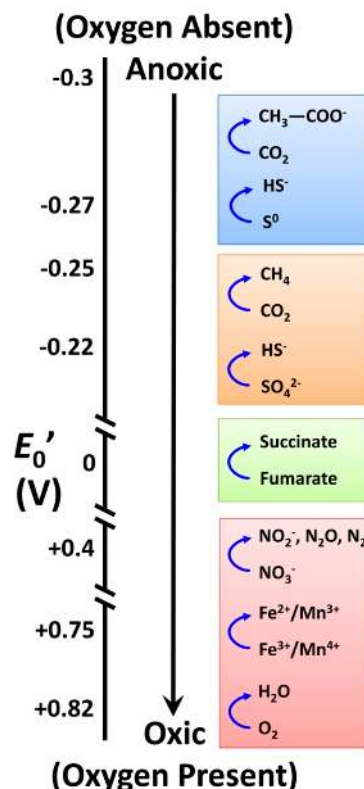

Figure 2. Standard electrode potentials of selected redox couples.

Frequent gene exchange, even between members of different domains [58], by multiple mechanisms, further emphasizes the genetic and functional fluidity of the unseen world that exists in soil. From a scientific standpoint, gene exchange among unrelated organisms greatly complicates attempts to classify them, to study their ecological relationships, and to develop useful models that will lead to predictive power necessary for applications. Yet, these difficulties do not diminish the potential value of understanding and influencing the power of the soil biota.

In addition to the prokaryotic organisms, there are enormous numbers of microscopic eukaryotes living in the soil. The net result is that in one gram of soil, there may be a million fungi comprised of hundreds of different species that can produce over 100 m of mycelial filaments. Add to the mix some thousands to millions of algae (classified as Plants), and millions of Protozoa belonging to several different phyla, and several dozen microscopic nematodes. Beyond the microbiota, soil supports a great diversity of invertebrates, ranging across many Phyla and Classes of organisms that are frequently larger and termed meso- and macro-biota. Phyla include Annelida, Nematoda, Nematomorpha, and Arthropoda, of which the last is by far the best studied group. At least five Classes of Arthropods reside within soil food webs: Arachnida (spiders, mites, *etc.*), Chilopoda (centipedes), Diplopoda (millipedes), Crustacea (isopods), and Hexapoda (insects, collembolans, diplurans, *etc.*). Constraints of modern taxonomic tools notwithstanding, scientists regard insects, spiders, and mites as the most diverse macro-taxa within soil food webs, and their numbers are overwhelming. Within conventional agroecosystems, density estimates reveal 100,000–160,000 insects and spiders per ha near the soil surface in soybean, and

340,000–680,000 per ha within the soil column in corn. Healthy soil arthropod communities within agroecosystems are composed of hundreds of species, each with a distinct function and biology. Altogether, soil inhabitants form a food web (Figure 3) that extends above-ground to plants and all other living organisms. Some of the more notable roles for soil fauna in contributing to healthy functioning soils are recognized in the next section; however, the remainder of this review is largely confined to the consideration of microbiota living in the soil. For literature reviews on the contribution of soil fauna to soil health, please refer to Lavelle *et al.* [59] and Blouin *et al.* [60].
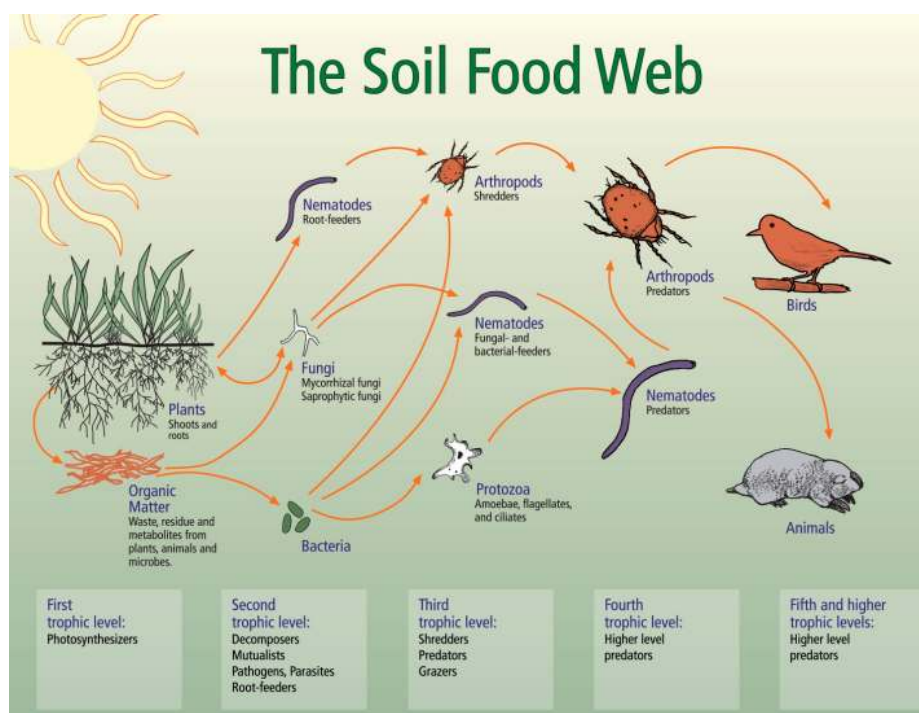
Figure 3. Soil food web (Reprinted with permission from: Soil Biology Primer. 2000. Soil and Water Conservation Society, Ankeny, IA, USA). Please note that the graphic does not represent all the important groups of soil organisms such as enchytraeids and earthworms.

3.2. Relationships between Soil Biology, Soil Quality and Restoration Strategies

Soil was characterized by Doran and Parkin [7] as having good "quality" if it could:

(1) Accept, hold and release nutrients and other chemical constituents.
(2) Accept, hold and release water to plants, streams and groundwater.
(3) Promote and sustain root growth.
(4) Maintain suitable soil biotic habitat.
(5) Respond to management.
(6) Resist degradation.

All of these attributes of soil quality are largely a function of soil biology and why we continue to emphasize that the most optimistic solution for reversing soil degradation is to enhance soil biology. It is widely recognized that soil microorganisms enable other forms of life to exist on Earth [61,62]. By catalyzing redox reactions, soil microorganisms directly mediate the biogeochemical cycling of carbon, nutrients and trace elements. These activities moderate atmospheric composition, water

chemistry, and the bioavailability of elements in soil. Soil fertility and other properties of soil (e.g., texture, aeration, available moisture, *etc.*) that support agricultural production are directly dependent on the biomass, metabolites, and activities of microorganisms. Specific populations of microbes are known to exert largely beneficial effects on plants (*i.e.*, symbiotic nitrogen fixing bacteria, mycorrhizal fungi) while others may exert deleterious effects (*i.e.*, pathogens). These microbes can be endophytic (living inside the plant) or free-living soil organisms living adhered to the root surface (*i.e.*, the rhizoplane), in close proximity to roots (*i.e.*, the rhizosphere) or further away in the bulk soil. At their most basic level, microbes and soil invertebrates are an important source of carbon and other nutrients. Soil invertebrates alter the structural components of the soil, increasing soil porosity, changing aggregate structure, and redistributing nutrients throughout the soil column and across the landscape. Invertebrates return nutrients and organic matter to the soil, either directly by breaking down plant material, or indirectly by consuming animal waste (e.g., dung beetles) or saprophytes like fungi. It follows that a well-poised and active soil biological community will be responsive to management and resist degradation.

3.3. How does Soil Biology Influence Ecosystem Services that Are Crucial for Well-Functioning Soils?

Soil biota are integral providers of fundamental ecosystem services such as those listed in Table 1. These are also among the most critical functions that need to be restored in degraded soil resources. Using a meta-analysis of published studies, Benayas *et al.* [63] documented the positive linkage between total biodiversity and provision of ecosystem services in terrestrial ecosystems. The multifaceted contributions of soil macroorganisms to ecosystem services has been well-described by Lavelle *et al.* [59]. The overall economic benefit of soil biodiversity to ecosystem services, and thus well-functioning soil resources, was estimated to be 1.5 quadrillion U.S. dollars [64]. In recent publications, biodiversity was also shown to influence global C [65] and greenhouse gas budgets [66], enhance water quality [67], moderate soil organic matter decomposition [68,69], regulate nutrient retention and availability [69], and determine the susceptibility of soil to invasion by a pathogen [70]. Synthesis papers by Kremen [71] and Hooper *et al.* [72] have summarized the established linkage between biological communities and ecosystems services, while emphasizing the need to understand biological complexity to properly manage the systems, particularly in agroecosystems.

Table 1. Ecosystem services provided by soil biota [†].

Ecosystem Services Provided by Soil Biota
Regulation of biogeochemical cycles
Retention and delivery of nutrients to primary producers
Maintenance of soil structure and fertility
Bioremediation of pollutants
Provision of clean drinking water
Mitigation of floods and droughts
Erosion control
Regulation of atmospheric trace gases
Pest and pathogen control
Regulation of plant production via non-nutrient biochemicals

[†] Modified from [73].

3.4. The Significance of Soil Biology to Sustaining Agriculture and Restoring Soil Health

Numerous examples of failed societies can be linked to degradation of soils by agricultural practices [74]; which by definition, must be considered examples of unsustainable practices. The characteristics of sustainable farming practices which maintain and/or restore soil resources are those that can be used over the long-term to produce adequate yields without severe degradation of soil, water and air resources that would limit agricultural production, cause human morbidity and mortality, and otherwise incur off-site economic costs. In practice, this means the soil and crop management practices must: (1) maintain soil carbon; (2) control erosion; (3) maintain soil structure; (4) maintain soil fertility; (5) increase nutrient cycling efficiency; (6) reduce export of nutrients and thus the need for increased inputs; and (7) reduce pesticide input requirements and potential export of either the materials or their residuals [73]. Once again, these are all attributes of a well-functioning soil and thus our premise that to restore degraded soils, the first step must be to enhance and maintain soil biological properties and processes.

The mechanism to achieve all of these goals is take advantage of inherent biological services to the greatest extent possible. Obviously, in entirely undisturbed grasslands, there is no human management to achieve the seven sustainability goals listed above, but on cultivated and range lands, soil and crop management practices can have positive or negative effects and thus influence the potential for soil degradation or enhancement. Sustainable agricultural management systems strive to integrate complexity into the management approach to include cover crops, filter strips, and non-crop landscapes such as grasslands and forest areas that provide vital habitats for beneficial organisms and serve as nutrient sinks to capture soluble nutrients and trap contaminants before these impact aquatic ecosystems [75].

The biomass of soil organisms nominally accounts for 2% of the SOC, but contribute to a much larger proportion of the actively cycled carbon fraction. At the decomposer level and higher, soil organisms represent the transformers of all fixed soil carbon and determine its fate. Soil microorganisms are well-documented to promote soil aggregation by their biomass and by their secretions. Microcolonies of bacteria and thin coatings of bacteria known as biofilms are held together and attached to their substrata by extracellular secretions largely composed of polysaccharides. Arbuscular mycorrhizal (AM) fungi have been shown to produce a glycoprotein, glomalin, which is responsible for aggregating soil particles [76]. Filamentous microbes, largely fungi, are particularly effective in mechanical binding of soil particles with their thread-like morphology. Plant roots, proliferating throughout the upper soil profile, support microbial communities actively involved in soil aggregation by providing organic carbon through rhizodeposition and thus helping stabilize soil structure and abate potential erosion [15]. Macro-invertebrates promote soil aggregation and create structures at a larger scale by tunneling, ingesting and depositing organic matter, producing secretions, and transforming organic residues [77]. The activities of ants [78] and earthworms [60] are widely recognized for promoting soil structure. Naturally, the degree of soil aggregation is directly related the soil's resistance to degradation and erosion by wind and water. Soil structure promoted by soil organisms is also central to soil water dynamics, increasing water infiltration and holding capacity.

Soil microorganisms are responsible for mineralizing organic compounds, including potential contaminant molecules such as pesticides. Half-lives of agrichemicals are based on the biodegradative abilities of the soil microbial community, as well as the local environmental conditions. In mineralizing organic compounds (native or added), microbial communities release combined elements (e.g., N, P)

in their chemically-reduced forms, generally increasing their availability to plants. Soil microbes also perform direct redox transformations of many inorganic elements using them as electron donors or acceptors in energy-yielding metabolic processes. In short, microorganisms moderate the abundance, speciation, and plant bioavailability of nutrients in the soil. Nitrogen-fixing bacteria exist in symbiotic and associative relationships with plants and as free-living communities in the soil to provide N to plants. Symbioses of N-fixing bacteria with soil invertebrates have been shown to be particularly important to the N cycling in some soils [79]. Nitrogen-transforming microorganisms (e.g., nitrifiers, denitrifiers) also moderate the speciation and therefore mobility of soil N affecting its propensity to stay or leave the system. Phosphate-solubilizing bacteria and fungi produce organic acids that either complex P or change microsite local pH to increase plant-available P. General activities of soil microbes result in the release of extracellular phosphatase enzymes which mineralize organic P, some of which becomes available to plants. Obligate plant symbiotic fungi, AM fungi, use a variety of mechanisms to uptake and translocate immobile nutrients (*i.e.*, P, Zn, Cu) and water to their host plants in exchange for fixed carbon [80]. A healthy soil food web with a diversity of macroinvertebrates has been shown to increase the release of P via the activities of grazers and predators [81]. The activity of tunneling organisms such as earthworms redistributes carbon and nutrients in the soil profile [60].

Phosphorus is a major nutrient with dwindling global supplies and rising prices. At the same time, only a small amount of P applied (20%) to crops is taken up by plants in the year of application [82,83]. The remaining P becomes sequestered in the soil, with limited availability to plants, or is lost by erosion and leaching (including tile drainage) to the watershed where it impacts other downstream populations and water quality by eutrophication which may culminate in the formation of marine dead zones. Similarly, only about one-quarter of annually applied N is taken up by crops in the year of application; some of the remaining N enters the watershed by leaching through the soil profile, tile drainage, or by overland flow processes to cause eutrophication and water treatment costs at downstream sites.

Nutrient-use efficiency is often defined based on the amount of N or P accumulated by a crop in comparison to the amount applied through manures or inorganic fertilizers. However, a portion of the P and N in the crop has originated from within the soil, where it was already present and probably in a stable organic form resistant to export. Therefore, traditional nutrient use efficiency calculations often overestimate the efficiency of fertilizer application and fail to reflect added nutrients that were lost from the soil by leaching and/or erosion. A more reasonable goal would be to export fewer nutrients and consider how much of the added nutrient remains in the soil [84]. This should mean that inputs are reduced, while increasing the amount being provided by the soil through biologically-fixed N, or mineralization of P and N from organic matter at just the right time. In the case of P, there are large amounts of P already in the soil, unavailable to plants without the appropriate microorganisms and proper levels of activity. By considering the nutrient balance of the entire system, agricultural soils could be managed to stabilize at lower soil nutrient levels that make more efficient use of resources [85,86]. Some P exported with the crop will have to be replenished from external sources, but there is great room for improvement in promoting organic P cycling in soils and biological mobilization of "occluded" P already present in the soil.

There is a long history of using bacteria and fungi as control agents for a variety of insect pests [87]. One example is the use of the entomophagous fungi to control insect pests such as aphids [88]. Contemporary use of proteins native to *Bacillus thuringiensis*, as whole cells, protein extracts,

or expressed by genetically-engineered plants to control insect pests is widespread. Among the many potential benefits that AM fungi have been shown to confer to their plant hosts is pest- and pathogen-resistance [89,90]. Predatory insects and spiders within the soil readily attack soil-dwelling pests, often maintaining these pests at low levels [91]. Invertebrates are also important herbivores of weeds, and reduce weed seed density and emergence by consuming many of the weed seeds that fall to the soil surface [92–94]. Microbes also affect weed seed banks, either directly by degradation [95] or indirectly as symbionts within insects, influencing their consumption of weed seeds [96]. Soils which inherently reduce weed seed germination are known as "weed-suppressive soils". Although the exact biological qualities that contribute to control of weeds are not well known, one of the mechanisms is the production of allelochemicals that reduce weed germination [97]. Similarly, some soils are considered to be "disease suppressive" wherein often poorly-defined components of a diverse soil microbial community confer disease resistance to plants [70,98,99]. Use of inherent (or perhaps added) organisms to manage pest, disease, and weeds in agroecosystems would provide opportunities for lowered use of biocidal agrichemical use, export, and residuals.

Soil bacteria that produce a positive effect on plant growth and vigor have been termed "plant growth promoting bacteria" (PGPB), or if they are located in the rhizosphere, rhizoplane, or inside the root (endophytic), they are termed "plant-growth promoting rhizobacteria" (PGPR) [100–102]. Sometimes the endophytes are considered separate from other PGPR [103]. There are, of course, also fungi that are endophytic like AM fungi and some *Trichoderma* sp. [104] which are often considered beneficial to the plant host. Soil organisms belonging to these groups have been identified to specific strains (*i.e.*, *Enterobacter* sp. 638 [105]) or have been more generally categorized (*i.e.*, fluorescent pseudomonads [106]). The functional contributions of the PGPR/B include repression of pests and diseases, and so there is overlap with the phenomena of disease-suppressive soils and pest protection discussed above. The putative mechanisms for pest and pathogen resistance include the production of antibiotics and siderophores, the physical (preventive) colonization of root tissue, interspecific-competition for resources, biodegradation of biogenic toxic substances, and the production of chemical signals (e.g., salicylic acid) that induce systemic resistance by the plants [102,107–109]. There are also PGPR/B that contribute to plant nutrient acquisition like the well-know symbiotic nitrogen fixers, *Rhizobium*, but also free-living N_2 fixers such as *Azospirillum* and *Azotobacter* [110]. Some PGPR assist in mobilizing P for plant uptake using mechanisms such as production of acidity, organic ligands including siderophores, and extracellular phosphatases [110]. Other PGBR assist plants by degrading toxic organic compounds in the soil or immobilizing toxic metals [102].

Another distinct soil microbial function is the production of growth factors and metabolic products that positively influence plant metabolism in ways not directly associated with pest or pathogen resistance. For instance, the enzyme 1-aminocyclopropane-1-carboxylase (ACC) produced by soil bacteria degrades an ethylene precursor that, in turn, depresses the plant's stress response to a variety of biotic and abiotic stress factors [111]. Soil microbes also can stimulate plant growth via the production of plant hormones such as auxins and cytokines. The auxin, indole acetic acid (IAA), is a phytohormone produced by soil bacteria which influences plant physiology, often resulting in enhanced root growth [112]. Naturally, microbial metabolites that positively influence plant vigor also impact plant resistance to pests and pathogens.

Biological production and reception of chemical signals are a common feature of the integrated biome present in agricultural soils and the net outcome of these interactions on crop production may be positive as described above, or negative [113]. In opposition to PGPR/B is a loosely-defined group of microorganisms termed "deleterious rhizosphere bacteria" (DRB) [114,115]. These soil bacteria have been determined to have negative consequences for plant growth and vigor via mechanisms that include phytotoxin and phytohormone production, nutrient competition, and inhibition of AM fungi [115]. The DRB are usually not considered to be plant pathogens, but this is not always the case. Interestingly, groups such as the fluorescent pseudomonads have been identified as DRB [116], even though other studies have identified them as PGPR/B [106]. One view is that a single organism can be a DRB under one set of environmental conditions and a PGPR/B under a different set of conditions [115].

4. How Can Soil Biology Be Used More Effectively to Mitigate Soil Degradation?

4.1. Strategies to Manipulate Soil Biology Focusing on Soil Microorganisms

The benefits of a healthy soil and the role of the biological community in soil health have been covered in the previous two sections. Therefore, we now shift our focus to examine the potential for influencing soil biological communities to (i) increase nutrient availability for production of high yielding, high quality crops; (ii) protect crops from pests, pathogens, and weeds; and (iii) manage other factors that limit or threaten the stability of production and ecosystem services. As with any management decision, the process or tools selected to manipulate soil biological communities will be defined by the desired goals and objectives. With this in mind, we envision two strategies for management of soil microbial communities to obtain beneficial functions: (i) specific approaches; or (ii) general approaches. Specific approaches will require knowing the service that specific microbes are providing (*i.e.*, nutrient acquisition, disease suppression) so they can be targeted to provide immediate relief for problems or degraded soil conditions identified within a specific field, farm or other location. Typical options for this approach include selection of disease resistant plants and/or cultivars with desired exudates. The specific approach is hindered by the lack of reliable information on the specific role(s) of more than a handful of the diverse taxa in soil. In contrast, the general approach seeks to provide a suitable environment to enrich the abundance and/or diversity of the entire microbiome through management practices. However, as with the specific approach, this will require knowledge of the current plant-soil-microbiome status in order to focus on any missing or limiting conditions for establishment of a robust and diverse soil microbial community.

4.2. Specific Approach: Plant Selection and Microbial Amendments

Plant root exudates include a variety of sugars, amino acids, flavonoids, proteins, and fatty acids [117], that can serve as growth substrates, signal molecules for suitable microbial partners, or growth deterrents for microbes [118]. The composition of plant root exudates can vary by plant species, and even cultivars within a species [119–121], resulting in concomitant changes in the composition of the soil microbial community [122–124].

Despite a general knowledge of the growth requirements for microbes in culture (which may or may not translate to the field), knowledge of the relative importance of various root exudates with regard to

shaping soil microbial communities or restoring degraded soils is lacking. Can selective effects be explained by a small number of high-impact compounds? How important are the diversity, quantity, or consistency of exudation to host plant-selective effects? The impact of particular aspects of root exudation on soil microbes has begun to be addressed for model plant species [117,125] through the use of ABC transporter mutants to alter root exudates; however, this should be made a priority for agriculturally relevant species as well.

With emerging extreme climatic changes, another critical question is whether cropping system sustainability can be increased by using plants that can interact with a variety of PGPR/B that are capable of increasing photosynthetic capacity [126,127], conferring drought and salt tolerance [126,128–130], and improving the effectiveness of the plant's own iron acquisition mechanisms [129]. A variety of companies have begun to offer new products that consist of PGPR/B inoculants (soil and/or seed treatments), or chemicals aimed at increasing root exudation to help foster PGPR/B establishment. However, field studies with PGPR/B inoculants often result in limited PGPR/B establishment and colonization, highlighting the need to better understand the factors involved in successful PGPR/B establishment.

The use of amendments, either as live organisms or solutions applied in small amounts that are promoted to stimulate microorganisms, is increasing. The use of seed-applied, symbiotic N_2-fixing bacteria to enhance the performance of legumes has a long, successful history. However, there are few other well-documented success stories to report. The use of AM fungi inoculants has been rising, but few refereed publications exist to support the benefits of this practice in production agriculture. In a three-year field study, the application of PGPR and AM fungal amendments was reported to positively affect plant nutrient uptake and conservation in corn plots [131]. However, for many commercial live biological amendments, there is little data beyond yield comparisons from company-sponsored field trials to evaluate these products. It is impossible to determine the potential benefits or risks of amendments without an increased basic understanding of soil microbial functional groups, their distributions, and their ecology (e.g., dispersal, survival).

Agricultural chemicals applied to the foliage of crops or in-furrow can also impact soil organisms. Biostimulants (e.g., products containing plant hormones and other organic and inorganic compounds) and liquid fertilizers affect soil microorganisms by providing additional nutrients or growth factors that alter soil and plant metabolic activities for improving crop growth and productivity [132–134]. Biostimulants applied at extremely low dosages affect rates of organic matter decomposition, nutrient mineralization, and soil microbial activity [132,134]. Depending on the product, amendments could be classified as either a specific or general strategy. Developing a more complete understanding of how biostimulants and other formulations could be used to help restore degraded soils also provides a strong argument for increased public-private partnerships designed to address these complex and "wicked" [135] problems. Such partnerships could be very effective for overcoming current barriers to understanding appropriate uses and modes of action for the various amendments created by the proprietary nature of product formulations.

4.3. A General Approach: Modify the Whole Soil Community

The future of any soil microbial community is determined by the capacity of its individual members to adapt or modify to "negative" soil characteristics [136], and to challenges such as climate change. Any potential manipulation of soil microbial communities must consider that ambient soil characteristics (e.g., water potential, aggregation, salinity, legacy of past management, pH, texture, SOM content/quality) influence the existing community and will consequently influence attempts at manipulation. Some of these soil factors can be positively manipulated through management (within local limitations), with considerable feedback from the soil biota (e.g., SOM, aggregation), while other soil factors are more resistant to modification (e.g., pH, texture). For example, one of the most influential factors on the microbial community is soil pH as different strains exhibit optimum pH in which they can function. Soil pH not only affects the cell functioning (*i.e.*, enzymes), but also reactions altering the availability of nutrients and metals. Studies on several soils have observed a positive correlation between bacterial diversity and soil pH within a range of 4 to 7 [137,138]. In terms of the response between different groups, the fungal community composition appears to be less strongly affected by pH than the bacterial community composition, and thus, wider pH ranges are observed for optimal growth of the fungal community [139].

Different microbial communities can be expected under different soil types due to variation in soil physical properties (*i.e.*, texture, bulk density, water infiltration), chemical properties (*i.e.*, mineralogy, SOM, nutrient availability, pH) and other factors (*i.e.*, soil genesis and morphology, climatic conditions). The challenge of selecting approaches to manipulate the microbial communities is, therefore, site-specific. For example, soils with higher SOM and clay content will show higher microbial community size and activities than a sandy soil, but it is still not clear whether a soil that is higher in organic matter and clay content is more resistant to manipulation. Even within a given soil profile, distributions of organisms and activities will vary according to heterogeneity in key soil properties. Further, the plant-microbe interaction is difficult to separate from the influence of soil characteristics on the microbial diversity as there are many examples of shifts in microbial community composition without changes in the SOM as affected by vegetation. Vegetation also introduces heterogeneity to the soil habitat. As studies are designed to determine how to most effectively remediate degraded soils, they will have to recognize that each set of soil characteristics and environmental boundaries will be an important determinant influencing the response of microbial communities for that soil.

There is no doubt that agricultural management practices can influence soil biological populations and processes and thus have a positive or negative effect on soil health. Agricultural management effects on soil health, in turn, influence the type and magnitude of ecosystem services provided by the soil biota. One measurement of soil health is biodiversity, which has been shown to influence global C [65] and greenhouse gas budgets [66], water quality [67], SOM decomposition [68,69], nutrient retention and availability [69], and the susceptibility of soil to invasion by a pathogen [70]. Many assessments of soil health based on measurements of soil microorganisms have relied on estimates of total biomass and activity. The following agricultural practices have been observed to modify the whole soil biological community (biomass, numbers, diversity, activity) in a generally positive manner: no till or conservation tillage, cover cropping, elimination of fallow, incorporation of perennial crops, retention of crop residues, diverse crop rotation, use of organic fertilizer sources, and implementation of integrated pest

management practices (Figure 4) [75,140–142]. Many of these same practices have been shown to increase PGPR/B and reduce DRB [100,101].
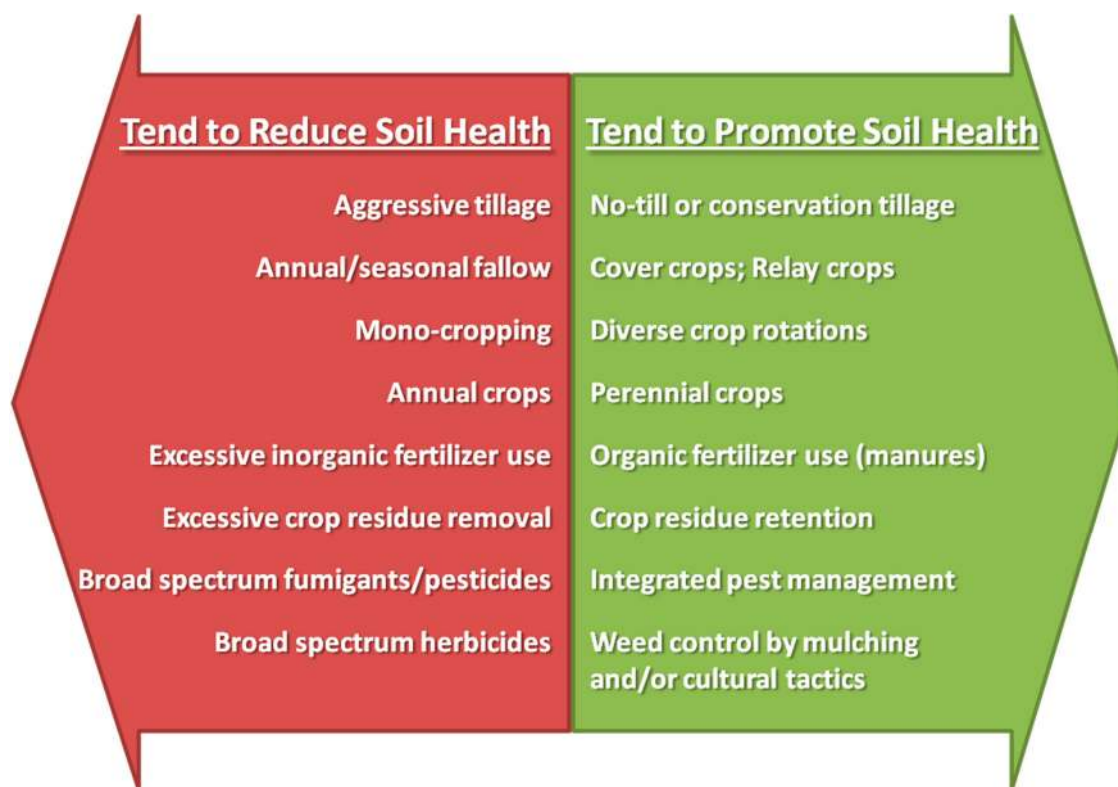

Figure 4. Generalized Effects of Agricultural Management Practices on Soil Health (information compiled from: [75,140–142]).

Tillage represents a disturbance of the soil habitat and can mechanically disrupt filamentous organisms, decrease soil structure, temporarily increase organic matter decomposition, and alter water and nutrient content and distribution [143,144]. Tillage-induced disturbance often has a negative impact on soil biota and the services that they supply [144–146]. Tillage most noticeably impacts large soil biota like earthworms [144] and filamentous organisms like fungi, particularly AM fungi [147]. Reductions in tillage are frequently linked to increased fungal biomass, and therefore have been suggested as strategies to increase microbial C use efficiency and soil C sequestration potential [148]. Reduced tillage is generally thought to increase microbial biomass in the long term [149] and has been associated with reductions in DRB in wheat cropped fields [150]. The combination of reduced or no-tillage with crop rotation or incorporation of perennial crops for integrated livestock and cropping systems promote AM fungi which enhance plant uptake of phosphorus and water, and disease resistance potential [151]. Although conservation tillage has been reported to impact beneficial microbial communities in certain scenarios (e.g., soils in humid regions), Acosta-Martinez *et al.* [152] reported that semiarid soils under different cropping systems showed no differences in microbial community size or structure when no-tillage and conventional tillage systems were compared after five years.

Cover crops were originally defined as crops grown to protect the soil from erosion and nutrient losses [153]. However, it has become clear that cover crops have a wide array of benefits that depend on local soil-climatic conditions [154]. By reducing seasonal fallow, cover crops have enormous influence

on soil biology by increasing the quantity and variety of C entering the soil through plant biomass, exudates, and residues. Additionally, cover crops increase N in the soil by stimulating the free-living N fixing bacteria and symbiotic N fixers when leguminous cover crops are planted. The inclusion of cover crops in a variety of corn production systems has been shown to significantly increase native AM fungal numbers and diversity [155–157] and P availability [158]. Recent research suggests that the benefits of cover crops include many additional factors, such as weed suppression and pest management that are likely connected to the larger soil biological community [159]. A study comparing four different cover crops in potato systems of the San Luis Valley show that they can support a disease-suppressive microbiome (Manter, unpublished data). In particular, the soil community under Sudan grass 79 is enriched for siderophore microbes that can not only provide disease suppression against fungal pathogens but also increase nutrients available to the subsequent crop species.

Conversion of lands for biofuel feedstocks using either perennial vegetation such as switchgrass (*Panicum virgatum* L.) or rotations using corn or sorghum (*Sorghum bicolor* L.) may help meet increasing national energy demands, but require careful evaluation of impacts on overall ecosystem functioning. Despite the potential negative impact of excessive corn stover removal on SOM dynamics in the Midwest [160], other studies have shown that conversion of marginal lands to rotations involving high-residue crops (e.g., cotton (*Gossypium* spp.)) to high-yielding sorghum on low SOM soils can increase microbial biomass and metabolic capacity related to biochemical cycling [161]. In experimental cellulosic ethanol production systems where corn stover was harvested, no-till and addition of cover crops limited extensive changes in soil microbial communities [162]. Additional studies quantifying biofuel-cropping system effects on soil microbial communities are also needed to be sure such practices are not detrimental to biological soil quality.

Crop rotation has long been noted for disrupting pest cycles and adding N fertility with legume crops [85,86,163]. In a study of five long-term diversified cropping systems, crop diversity (rotation) increased soil microbial biomass and activity and was associated with positive changes in soil C and nutrient dynamics [164]. Crop rotations have been specifically noted for increasing soil fungal biomass, which in turn aids in soil aggregation and C sequestration [148]. Rotating corn with other crops increased soil microbial biomass, C availability [165] and numbers of AM fungi [166]. In comparison to continuous corn, rotating corn with canola resulted in greater microbial biomass, activity, and functional diversity [167]. On the other hand, continuously cultivated crops are most commonly associated with increased incidence of DRB which impair plant growth through numerous modes of action [115,168]. The absence of a crop (fallow) is an obvious factor in decreased soil health as there is no plant host for obligate symbionts, no exudates for the rhizosphere community, and no residues for the bulk soil community. Fallow is associated with poor nutrient conservation [169], lowered AM fungi populations [140,170] and other impacts to soil health that affect crop production [171]. While crop rotation is known to benefit crop production via modification of the soil microbial communities, many details are still unknown [142]. Specific crop sequences have been shown to be particularly effective for controlling weeds, but often the mechanism remains unexplained, and probably involves modification to the soil biota [172].

Organic amendments enhance the physical environment for nutrient retention and bioavailability causing alterations to the existing microbial community. Depending upon their composition and nutrient content, they can also cause significant shifts in the existing microbial community of soil by introducing another diverse microbial pool plus their metabolites into the soil. However, some researchers argue that

organic amendments seem to have less prolonged effects on soil microbial communities than seasonal variations or other anthropogenic factors such as the mechanical management of the soil [173]. Recent studies using molecular techniques have identified detectable changes within *Proteobacteria*, *Acidobacteria* and *Bacteroidetes* with the use of organic amendments [174,175]. Another recent study suggested that compost effects were mainly caused by physicochemical characteristics of the compost matrix rather than by compost-borne microorganisms and that there was no resilience of microbial characteristics during the study (6–12 months) after applying a high amount of compost [176]. However, a comprehensive meta-analysis showed that organic amendments routinely increased soil microbial biomass in agricultural soils [177]. And, while excessive inorganic P fertilization is known to suppress AM fungi [80,140,178], meta-analysis results show equivocal effects of mineral N fertilizers on aspects of the entire soil microbial community [179]. Thus, more information is needed on actual comparisons of the microbial communities within different organic amendments and the extent of alteration and resilience of the inherent soil microbial community over time.

While the effects of fumigants are relatively easy to predict—they are used as a soil biocide—the non-target effects of other agrichemicals such as insecticides, herbicides, fungicides on soil biota are less clear. Determining agrichemical effects on soil biota is complicated by different modes of delivery (seed applied, foliar, soil drench, *etc.*), the concentration, mixtures, the specificity of the target(s), and the mechanism(s) of action. Most agrichemicals represent a C and nutrient source for some soil microorganisms. The most widely-applied herbicide, glyphosate, is relatively non-toxic to most soil biota in laboratory bioassays [180]. Largely negligible impacts on soil biota have been observed in field or greenhouse studies of potential glyphosate treatment effects [181–185]. On the other hand, extensive research has indicated negative impacts of glyphosate application on symbiotic N-fixing bacteria when applied to glyphosate-resistant soybean [186]. In the absence of any additional stressor, the inhibition of these symbiotic N-fixers is transient, and not expected to affect yields [186]. Some recent reports indicate the potential for indirect effects of glyphosate via its complexation with trace nutrients resulting in increases in pathogenic soil microorganisms, perhaps due to stressed plants [187,188]. However, there is a lack of consensus in the literature on the potential for glyphosate to select for soil pathogens [189]. One possible outcome that is not well-documented is that large areas that are devoid of vegetation due to glyphosate application will have lower soil microbial biomass and activities simply due to the lack plant hosts, exudates, and residues. The lack of weeds has been shown to negatively influence the diversity of some insects and birds in agroecosystems [190]. Some agricultural pesticides have been indirectly linked to increased DRB numbers [114,116,191,192], and it was recently concluded that the fungicide carbendazim inhibits AM fungal colonization of pepper plants [193]. It is difficult to generalize non-target effects of agrichemicals (herbicides, fungicides, and insecticides) on beneficial soil biota because the experimental conditions and results of individual studies are variable.

5. What Are the Primary Knowledge Gaps Limiting Manipulation of Soil Biological Communities and Mitigation of Degraded Soils?

Despite the amount of research already conducted, we do not know how soil microbial communities are controlled. One model proposes that the control is balanced between the soil (texture), the plant (maize or Arabidopsis), and the particular microorganism (an actinomycete or *Pseudomonas* sp.) [99]

(Figure 5); however, the actual situation is most assuredly more complicated. If we are to manipulate soil biology in order to optimize ecosystem services and restore degraded soil resources, we need to understand what controls soil microbial community structure, function, and biomass under a given set of conditions, how much it varies according to conditions, and distinguish these effects from seasonal influences. Further, the duration of effects due to changes in management or crop is an unresolved question with conflicting research findings.
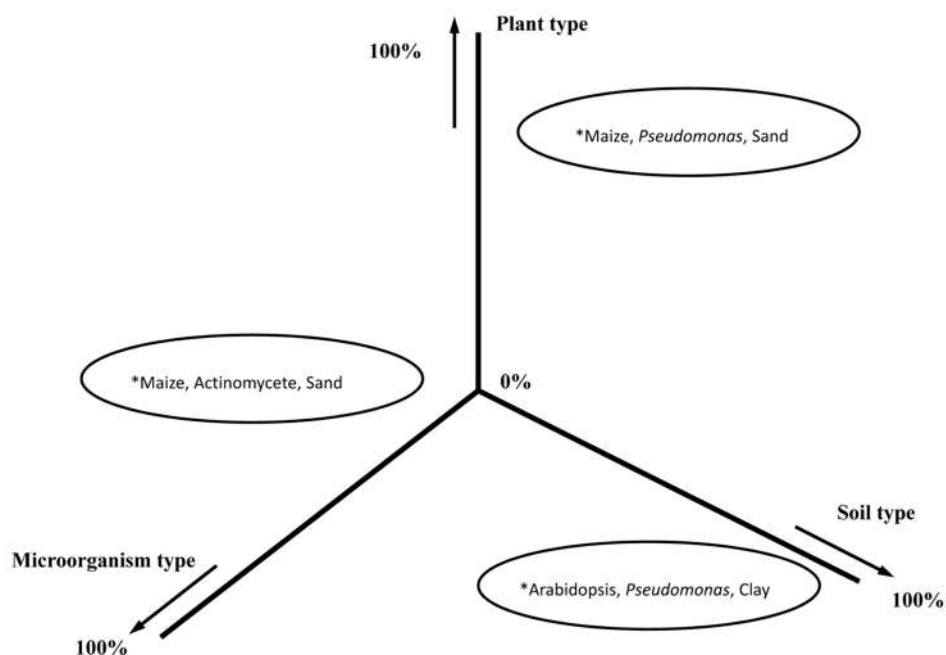

Figure 5. Conceptual model of the relative strengths of forces shaping microbial communities in the soil (from Garbeva *et al.* [99], with permission of the publisher).

While microbial community function should theoretically vary with community structure, it is not known how common this linkage actually is within soils. If functional redundancy is very high across different phylogenetic groups, large changes in microbial community structure could occur without corresponding changes in soil function or possibly resiliency. If functional redundancy occurs across ecotypes, changes in soil conditions could occur yet function might remain unchanged. The distribution of soil microbial populations and functions at local and larger scales (*i.e.*, biogeography) and their colonization abilities are largely unknown for most taxa. The extent of microbial species endemism and functional redundancy are central to measurement of soil health and resilience, particularly in relation to biodiversity [194].

We do not know how soil microbial community function is related to microbial biomass. As biomass increases, the potential for function should increase due to a higher number of organisms carrying out that function, but other factors may limit gene expression or enzyme activity and therefore function. While soil microbial community function should be related to the number of copies of that functional gene in the community and the degree of expression of that gene, in many cases we do not know how gene expression is controlled or the factors controlling enzyme activity in soil microbial communities.

A predictive model that combined all of these factors to explain how soil microbial community structure, relative abundances, and function were controlled would permit us to maximize soil health

and optimize ecosystem services on a site and management-specific basis. In part our understanding has been limited by available methodology. Only recently has a method (next- generation sequencing) been developed which has the potential to identify changes in soil microbial communities at the species or genus level. Before next-generation sequencing, scientists could detect alterations in microbial community structure but could not determine which genera changed, or were restricted to the very small proportion of soil microbes that could be cultured in the laboratory. Similarly, functional genes and gene expression of the entire soil metagenome can now be measured using microarrays and next-generation sequencing.

6. What Are the Highest Priority Research Needs to Improve Soil Health and Reverse Soil Degradation?

6.1. Framing High Priority Research Questions

Soil microbial communities can be manipulated to enhance ecosystem services and improve crop productivity, but this requires an understanding of the genetic potential of the soil microbiome [195]. Given this enormous amount of functional diversity, substantial research is needed to link microbial species, or assemblages, with key function(s) in the soil, and in particular how they are influenced by management [152,196–198]. Furthermore, addressing emerging challenges such as climate change and land use will be reliant upon the identification of microbial species and/or assemblages that enhance soil structure, nutrient and water uptake by plants, and protection from pathogens, pests, and weeds. Our goals are to understand these interactions and apply that understanding to increase agroecosystem productivity, to document suitable indicators of soil health, and to provide guidelines for restoring and then maintaining the health of degraded soil resources.

6.2. Fundamental Information Lacking Regarding the Identities, Distributions, Ecology, and Functionality of Soil Biota

Fundamental information is required to answer simple questions like "What organisms are there?" and "What are they doing?" Projects such as TerraGenome (www.terragenome.org) are an important step in our efforts to better understand the true diversity of genes and functions residing in the soil. When a sufficient amount of the census information exists, the next questions that require more complete answers are: "How are they distributed?" and "What do we know about their ecology?" Determining the extent of a biogeography for individual taxa or functional capabilities is key to understanding how factors influence communities and their function, and what management practices will inhibit degradation of soil health. For instance, if certain AM fungi with specific functional abilities or host preferences are endemic to a given soil-climatic region, and they are eliminated by soil-degrading practices, then appropriate management will be required for re-establishment. The required management will depend on the ecological characteristics of the AM fungi such as life-cycle and dispersal abilities. Management options could be creating better conditions (*i.e.*, cover cropping, crop rotation, avoiding fallow) or inoculation with non-native, commercial AM fungal inocula, or on-site amplification of native AM fungal inocula [199], depending on what information is available for local conditions.

Basic descriptive information is required for taxa associated with soil biological functions that are fairly cosmopolitan (e.g., denitrification), but also for more specialized functional guilds (e.g., symbiotic N-fixers). The current information void concerning soil organisms and consortia that are known, or suspected to be particularly influential to plant development (e.g., AM fungi, PGPR/B and DRB), limits opportunities to exploit these organisms to improve soil health and function.

The nature of interactions of plants and rhizosphere microbial communities deserve special attention. Future research should investigate plant characteristics that are related to aspects of microbiome diversity, *i.e.*, the richness and evenness of species composing the community. For instance, how important are adaptation or long-term association in maintaining evenness among rhizosphere microbes? Over long time scales, does rhizosphere microbial evenness increase as many microbial community members undergo adaptation or niche differentiation in the context of a stable assemblage of interacting organisms? Does increasing exudate diversity sustain greater microbial richness in the rhizosphere? Or, can simple exudates be transformed by microbial activity into sufficiently diverse metabolites to allow for niche differentiation of many microbes? If so, simply increasing exudate quantity may be as effective in maintaining a rich microbiome as increasing exudate diversity. The relative importance of carbon source identity *vs*. diversity has begun to be explored through simple studies of resource amendment using defined compounds [200] but much more work of this sort is needed.

Research should consider the role of soil microbial richness and evenness on plant performance and address whether a greater functional gene diversity and/or functional redundancy associated with increased taxonomic diversity leads to a more resilient and consistent functioning of the soil microbiome across changing environments [201]. Furthermore, while only a portion of the soil microbial pool is metabolically active (at different rates) at any given time [202], a more diverse community should increase the metabolically active pool of microbes, but also provide the genetic diversity to function under changing environmental conditions. A more abundant and diverse community would also maximize microbial competition and/or niche saturation rendering the soil more resistant to new invasion. For example, soils with higher microbial biomass and/or diversity have been found to be more disease-suppressive [203–205] and resilient to invasive organisms [98]. The role of community evenness has received less attention than richness or diversity; however, evidence supports an important role for evenness in community functioning and plant productivity, particularly under stresses or perturbations [206]. The mechanistic basis behind these benefits still need to be explored; however, like community richness and diversity, may be associated with a more complete resource utilization that reduces niche space available for invaders. In particular, community evenness has been shown to be important to limit invasive plants [207] or insect pests [208].

6.3. Defining Relationships among Climate, Edaphic Factors, and management with Respect to Soil Biota

Overall, there remains insufficient information to quantify effects of agricultural management practices on key soil biological functions under a range of soil-climatic conditions. It is also essential to incorporate the temporal element as the timing of disturbances (managed or natural) could determine their significance, and length of time needed to recover critical soil functions.

While numerous studies have found the effect of one or more specific factors (edaphic, management) on soil microbial communities to be significant, very few researchers have integrated a wide range of factors into one study, and interactions were generally not identified. In one of the very few attempts to look at this problem on a broad scale, a study on bulk soil from field plots in California found that microbial communities were affected by the following variables, in order of decreasing importance: soil type > time > specific farming operation > management system > spatial variation [209]. Studies like this need to be repeated with modern methods across a wide range of soil types and climate. New metagenomic tools including high-throughput sequencing and functional gene arrays now make it possible to directly address this question. This is a critical question which must be answered in order to build a model that uses agricultural management and environmental factors to predict soil biological health and ecosystem services. A step in this direction has been made with the inclusion of AM fungi in modeling the services provided by cover crops [154].

Both short term and long term disturbances affect the soil biological community and its function. An example of a short term or acute change would be the transient change in overall biomass or activity due to a single event such as tillage or fertilizer application. These changes may or may not be significant depending on the stage of crop growth and its current requirements. Long term changes in the soil biological community are those occurring in response to persistently applied management approaches such as tillage regime, crop rotation, or cover cropping. These changes result in alterations within the soil communities as some members are lost while others become dominant. If an organism that is lost has limited dispersal mechanisms, such as AM fungi, then recovery of these populations may take a lot of time or require intervention by inoculation.

6.4. Development of Improved Indicators of Soil Health

Another challenge is to identify those soil biological functions or variables that are sensitive and have short-term biological relevance but also integrate management history. Measuring such functions could then be used to inform management decisions. The natural temporal or spatial scales of some soil functions will likely not correspond to the scale of management. Highly variable, but biologically important, soil parameters such as soil moisture, temperature, mineralization rates, and pools of labile C and N may be most useful for understanding short term, localized patterns of soil functions but their relatively high spatial and temporal heterogeneity hamper meaningful measurement and limit their use for determining prescriptive management activities at the field scale [210]. Moreover, parameters with variable tendencies may not adequately detect baseline shifts in key soil biological activities without a robust temporal and spatial historical dataset. Conversely, relatively large scale soil parameters that impact soil biological functions may not be manageable (soil texture) or change slowly (soil organic matter), making them less useful for modifying management plans in the short term. A truly defensible measure of *in situ* biological function remains a challenge, as the act of measuring or sampling will influence the target measurement. Improved relevance of functional measurements is imperative for understanding the dynamic processes occurring in soils.

Identification of optimal soil functions and a suitable set of representative soil variables must be specific enough to be useful at the local scale but also capture information that will allow meaningful comparisons across geographic gradients or over time. Coordinated research, using standardized

methodology and development of appropriate methods for normalizing soil biological functions may be one means for such comparisons. A related but more difficult task is the development of forward-looking information to accommodate anticipated, but uncertain changes to soil-climate linkages in the future. Future changes are expected to manifest as shifts in the overall trends of major environmental factors such as temperature and precipitation but accompanying these may be increasing variability and thus risk.

One challenge to understanding the relationships between management and soil function, whether under different management options, combinations of soil climate, or scenarios of change, is to move beyond descriptive soil biology towards mechanistic characterizations of community composition and activities that are directly related to productivity or sustainability and are amenable to management [210]. Productivity is relatively easy to measure but sustainability is more complicated given our imprecise understanding of how the communities of soil biota link to ecosystem functions and how they can respond to change, whether planned or stochastic. It has proven difficult to comprehensively define "ambient" or "optimum" levels of soil health in part because these are context dependent terms that depend on intended land use. Thus further work is needed to provide suitable baseline criteria about manageable, functionally-related soil traits in order to compare among various management approaches such as conventional *versus* low input *versus* integrated approaches that combine livestock and crop production. Such comparisons may be at the local scale (e.g., nutrient cycling, pathology, or aggregate stability) or have broader consequences (e.g., water quality, C sequestration, greenhouse gas formation erosion).

One area that demands a comprehensive level of effort is the role of soil biology in improving nutrient use efficiency by plants. Current nutrient recommendations are primarily based on a single, point-in-time measurement of soluble and easily-exchangeable soil nutrients. However, the chemical speciation of nutrients changes frequently, often catalyzed by biological processes. However, nutrient recommendations are commonly developed under standard test conditions, usually similar to conventional farming practices, where soil biological contributions to soil fertility are likely to be minimized. Consequently, while nutrient recommendations do predict the average crop response, they do not reliably predict plant response and soil fertility under many site-specific conditions, particularly where soil biology has been enhanced by management practices [211–213]. Typical calculations of nutrient use efficiency contribute to excessive nutrient application because they fail to account for loss of nutrients from the system [84]. Improved nutrient use indexes that account for nutrient loss from the system implicitly include the extensive effects of soil biota on nutrient dynamics. Plant nutrition models fail to capture many biological rhizosphere processes, particularly the kinetic aspects, and enhancement of root-rhizosphere processes is the most probable path for ecologically-sustainable intensification of agriculture [214]. Managing the nutrient balance of the entire soil system allows the system to stabilize at lower nutrient levels that take advantage of biological means of nutrient retention and makes the most efficient use of resources [85,86].

Simple and effective indicators of soil quality/health which have meaning to land managers remain inadequate for assessing the sustainability of management. Indices and models are needed to link changes in microbial community composition and activities to a change in metabolic functions (*i.e.*, C cycling, and nitrous oxide (N_2O) and methane (CH_4) fluxes) for different soils and crop scenarios. A recent report by a group of scientists for the American Academy of Microbiology (AAM) stressed the importance of incorporating microbial processes into climate models [215]. Currently, no index includes

the microbial portion of soil, which poses another challenge to assess the success of benefits to soil health provided by conversion of cropland to conservation programs (*i.e.*, The Conservation Reserve Program). Quality and quantity of SOM is coupled with composition and functioning of the microbial community and therefore, SOM quality assessments must also be a component of future research/indices. Perhaps, soil microbial community characteristics (e.g., size, composition and specific activities) and changes occurring with management can be assigned a ranking number to guide management decisions and policy.

The proposed introduction of several new organic amendments or 21st Century by-products (e.g., biochars or nanomaterials) that can last longer in the environment than traditional amendments, create another level of complexity. Critical assessments are needed to quantify the impacts of these products on resident microbial communities and their associated—but largely unknown—activities. Similarly, the use of microbial amendments and stimulants are difficult to justify without better understanding of the baseline contributions of soil biota and suitable indicators to evaluate if modification of the soil biota results in significant improvements to soil health and function.

7. Soil Biology Research Investments Needed to Ensure Our Future by Promoting Soil Health and Mitigate Soil Degradation

The challenge for agriculture in the 21st century is to implement more sustainable farming systems that are economically viable and accommodate changing technologies and climate. The production of food and fiber continues to increase agriculture's C footprint through the increased use of fuel and fertilizer, and contributes to widespread soil and water quality degradation, and loss of habitat diversity and biodiversity. To decrease this footprint, nutrient management in sustainable systems must be a top priority [216]. Soil biology is the foundation for soil health and the biological processes which moderate nutrient availability to plants, in addition to buffering plants from changes in water availability and pest, pathogen, and weed pressures. The health of the soil biota is strongly linked to the resistance of soils to erosion. Soil biological diversity is positively linked to ecosystem level processes such as C and nutrient dynamics [69] and has a central role in agroecosystems that are operated in an environmental- and economically-sustainable manner [217,218]. Soil biology is the key to ensuring the ability to "Feed the World" [219] and reversing the degradation of soils that support crop production.

As farming systems constantly change due to economic and technical drivers, soil biological functions need to be continually re-evaluated [220]. Synthesis papers by Kremen [71] and Hooper *et al.* [72] detail the linkages between biological communities and ecosystems services; understanding soil biological complexity is essential to properly manage agroecosystems. Recent advances in DNA and biochemical methods in characterizing biological activity and biodiversity will help better understand the complex nature of life in soil, provide new insights into functional mechanisms of soil microbial communities, and thus be useful for restoring degraded soil resources. This new knowledge will also greatly aid and drive development of innovative agricultural production systems that are economically and environmentally sustainable [220].

Climate change models suggest that modified cropping systems will be needed for optimal production under extreme weather events, such as the recent drought facing much of the U.S. The resiliency and resistance of agroecosystems depends, in part, on the functioning of the microbial community. Changes

in cropping systems resulting from an earlier growing season, emerging plant pathogens and lower yields, and cropping sequence disruption due to drought cycles in certain regions will challenge land and water resources to maintain food, fiber, and feed production for the growing population. For example, frequent drought cycles in the U.S. Southern Plains have resulted in transition from irrigated to dryland production with possible total crop abandonment and/or interruptions in production cycles [152,221]. Identification of key soil microbial assemblages and the soil management practices that support these key microbial assemblages may assist the recovery of soils from major disturbances. Climate change may result in even more soil degradation through greater wind erosion and increased use of fallow periods to compensate for periodic droughts in some rotations. Greater knowledge of microbes and their roles in essential soil processes will aid in quickly adapting to these climate changes and other factors contributing to soil degradation. As cropping systems evolve with changing technologies, producer views and environmental constraints, specific bacterial-fungal assemblages that foster efficient nutrient and water uptake under modified or new cropping systems will need to be identified.

Research investment is required to significantly advance basic knowledge of soil biology and to properly assess soil biological responses in agricultural systems. Research should be designed with particular agricultural applications in mind and sites need to accommodate regionally- different soil-climatic regimes and agricultural practices. Long-term, multi-location, multidisciplinary team research with shared goals and protocols is required to thoroughly and productively advance this area of research.

Significant progress toward enabling predictable application of soil biology manipulation in agricultural systems could be made using currently-available analytical tools provided a critical mass of effort is assembled. A hierarchical set of analyses should be applied, such as that proposed by Kowalchuk *et al.* [222] to assess the effects of GM plants on soil microorganisms (Figure 6). These analyses would include basic measures of the size of the microbial community (e.g., biomass and numbers), bulk activities (respiration, enzyme activities), community composition (PLFA, molecular profiles) as well as quantification of subsets of microbes and their activity potentials using molecular probes and soil metagenomic approaches.
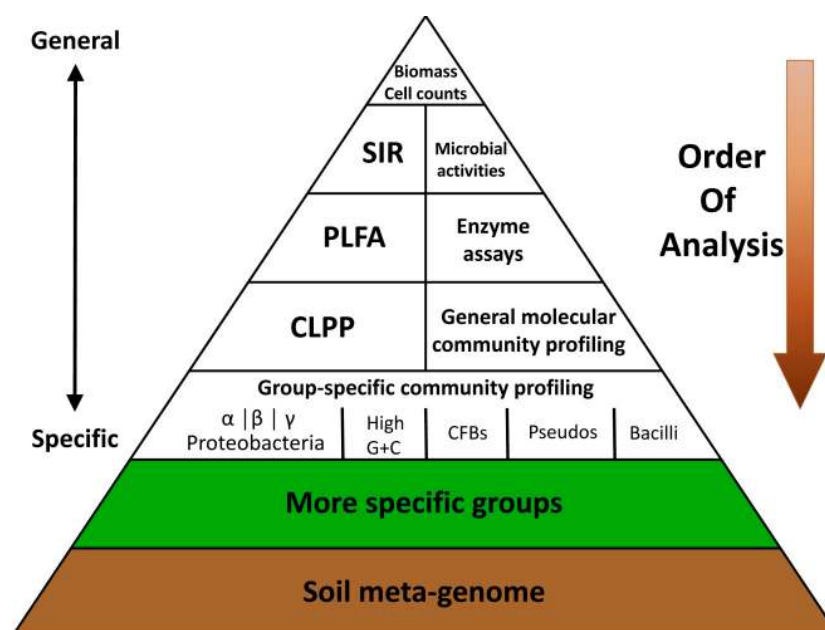

Figure 6. Hierarchy of soil microbial analyses to characterize soil microbial communities. Modified with permission from Kowalchuk *et al.* [222]).

8. Summary and Conclusions

After reviewing what's known and unknown regarding soil microbial communities and their relationships to soil health, we remain optimistic that one of the most promising strategies for mitigating and even reversing soil degradation around the world is to significantly increase public-private research efforts focused on soil biology. Of the three indicator regimes (physical, chemical, and biological) influencing soil health/quality at all scales, biological relationships are by far the most complex with large deficiencies in basic understanding. Many new tools and techniques have been or are being developed, thus making it more feasible to unravel these complex systems. Ultimately, this new knowledge will be used for informing management to restore the degraded soils that humankind desperately needs to meet the rapidly increasing food, feed, fiber, and fuel needs of an expanding global population.

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Author Contributions

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Conflicts of Interest

The authors declare no conflict of interest.

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