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FEATURE

Soil biology for resilient, healthy soil

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What is a resilient, healthy soil? A resilient soil is capable of recovering from or adapting to stress, and the health of the living/biological component of the soil is crucial for soil resiliency. Soil health is tightly coupled with the concept of soil quality (table 1), and the terms are frequently used interchangeably. The living component of soil or soil biota represents a small fraction (<0.05% dry weight), but it is essential to many soil functions and overall soil quality. Some of these key functions or services for production agriculture are (1) nutrient provision and cycling, (2) pest and pathogen protection, (3) production of growth factors, (4) water availability, and (5) formation of stable aggregates to reduce the risks of soil erosion and increase water infiltration (table 2). Soil resources and their inherent biological communities are the foundation for agricultural production systems that sustain the human population.

Table 1

Soil health is often coupled with the concept of soil quality.

Statement	Reference
"Soil quality is the capacity of the soil to function."	Karlen et al. (1997)
Soil health is "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."	Doran et al. (1996)
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.	Andrews et al. (2004)

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The rapidly increasing human population is expanding the demand for food, fiber, feed, and fuel, which is stretching the capacity of the soil resource and contributing to soil degradation. Soil degradation decreases a soil's production capacity to directly supply human demands and decreases a soil's functional capacity to perform numerous critical services, which are valued in trillions of US dollars (Pimental et al. 1997). The ability to reverse degradation of soil resources and improve soil services is intimately related to the ability to promote the biological functioning or health of the soil. Although this report primarily considers soil microorganisms, we fully acknowledge the importance of higher soil organisms to the maintenance of soil health and provision of soil services, but leave those phyla to future discourse. Emerging tools and technologies have become available to dramatically advance our understanding of microscopic soil biota and provide the foundation to manage soil organisms to enhance primary productivity, provide multiple ecological services, rejuvenate soil resilience, and sustain long-term soil resource quality.

RECOGNIZING SOIL MICROBIAL DIVERSITY AS THE FOUNDATION FOR SOIL FUNCTION

The soil has long been perceived to harbor the greatest microbial diversity among all ecosystems, and advances in analytical and computational tools have suggested that approximately one billion bacterial cells, grouped into 1,000 to 1,000,000 species, reside in a single gram of soil (Gans et al. 2005; Schloss and Handelsman 2006). The rate of discovering and characterizing bacterial diversity since 1987 is astounding, growing from a modest 12 phyla to more than 70 by 2009 (Pace 2009). However, many of these phyla contain few, if any, organisms that can be grown and studied in the laboratory. Within these new phyla are bacteria that can fix carbon dioxide (CO_2) via multiple pathways not found in plants (Thauer 2007) and bacteria that generate energy from sunlight using alternative light receptors not previously known (Beja et al. 2000). Given the recency of these discoveries, it is not surprising that the contribution of autotrophic soil bacterial organisms like these to terrestrial carbon (C) cycle and C sequestration has not been determined (Trivedi et al. 2013).

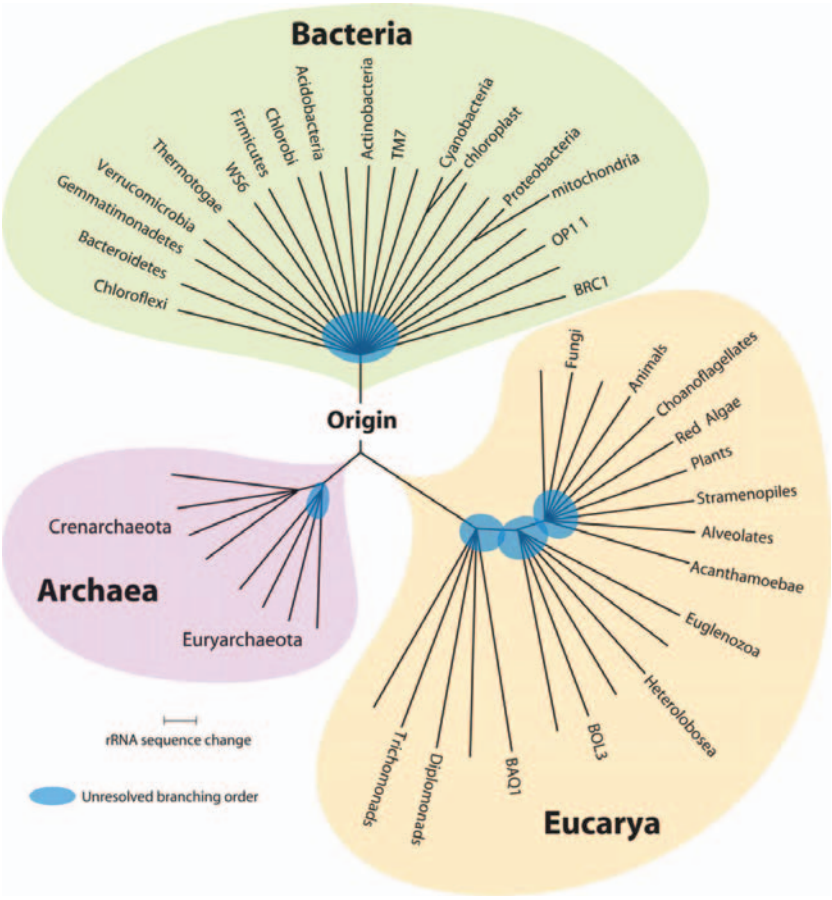
Table 2

Services provided by soil biota and related processes and benefits (Wall et al. 2004; Falkowski et al. 2008; Kowalchuk et al. 2008; Pritchard 2011).

Soil functions/properties	Processes involved	Agronomic services	Environmental services
Biogeochemical regulation, nutrient retention and delivery	Carbon, nitrogen, and phosphorus cycles Redox reactions Decomposition/humification	Provide plant nutrients	Mitigate atmospheric gases Sequester carbon Maintain/improve water quality
Symbiotic and compensatory associations	Nitrogen fixation (bacteria) Nutrient uptake via mycorrhizae (fungi)	Provide plant nutrients Enhance water acquisition	Maintain/improve water quality
Biodegradation/bioremediation of wastes, pollutants, and agrochemicals	Microbial degradation	Reduce pesticide legacy impacts	Maintain/improve water quality
Pathogen dynamics	Host-pathogen interactions (regulation and competition)	Suppress disease	Maintain/improve water quality
Soil structure and stability	Soil aggregation/porosity Build soil organic matter	Increase aeration Reduce compaction Improve water infiltration Increase water holding capacity	Reduce erosion risks Mitigate flood and drought Sequester carbon
Weed dynamics	Germination and growth	Suppress weed germination, growth, and persistence	Maintain/improve water quality

Figure 1

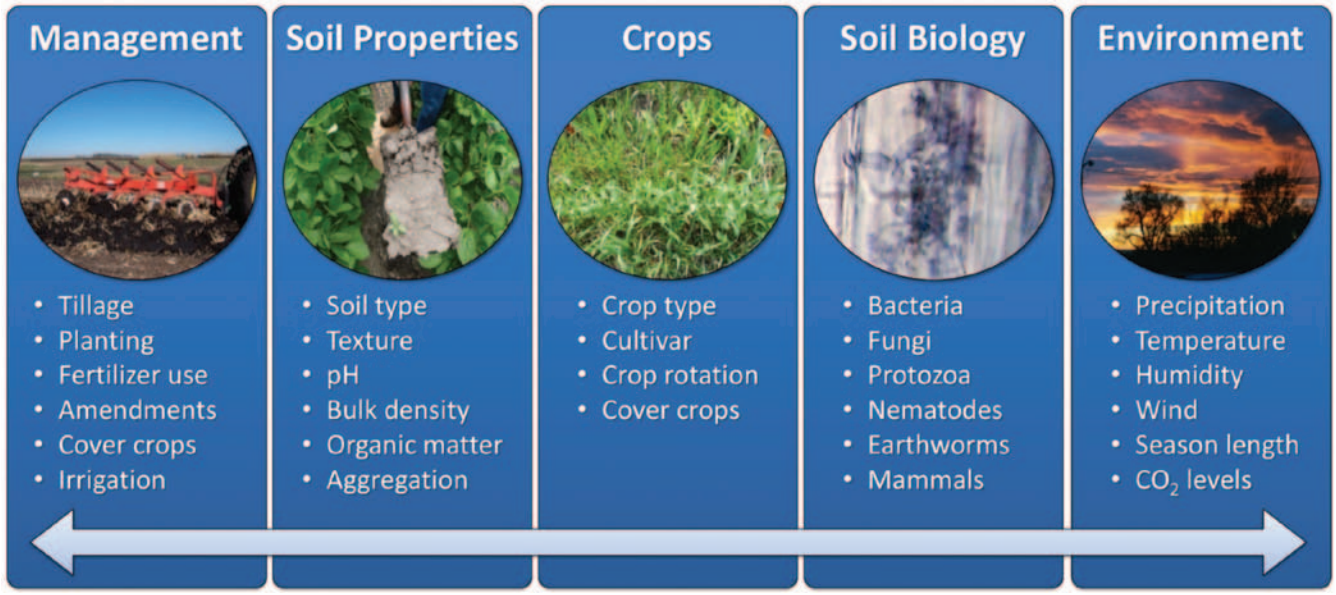
Tree of Life based rRNA gene sequence comparisons (reprinted with permission from Pace et al. [2009]).



It is now well-established that all life can be assigned to one of three domains: Archaea, Bacteria, and Eucarya (Pace 2009) (figure 1). Eucarya contains fungi and all visible (and some microscopic) plant and animal life. Archaea and Bacteria contain all of the prokaryotes that are commonly considered "bacteria" that collectively possess an enormous diversity of physiologies and environmental tolerances. In a startling example of the rapidly expanding knowledge of the microbial world, it was determined in 2006 that members of the Archaea domain were actually responsible for most of the nitrification occurring in some soils, which had for decades been thought to be performed strictly by a very limited number of Bacterial genera (Leininger et al. 2006). Members of a new phylum of bacteria, Acidobacteria, whose first representative was discovered in 1991, were virtually unheard of even 15 years ago and are now suspected to be the numerically dominant organisms in many soils. However, due to their resistance to laboratory culturing, there is insufficient information to establish their functional roles. An entirely new class of Fungi (Archaeorhizomycetes) that closely associate with plants and are ubiquitous in soils is just now being described, largely based on a single cultured member (Rosling et al. 2011). Other recent discoveries, such as rampant gene exchange within and between the three domains by multiple

Figure 2

Selected factors affecting soil functions and the provision of ecosystem services. The arrow represents interactions between factors and within each factor.



mechanisms, emphasize the genetic and functional plasticity of the microscopic world that exists in soil (Nelson 1999). Gene exchange has practical implications for antibiotic resistance (Forsberg et al. 2012) and also severely complicates attempts to classify microorganisms, determine their ecological relationships, and develop useful models with the predictive power necessary for management applications.

Advances in analytical and computational tools have accelerated the rate of discovery of soil microbial diversity and enabled renewed efforts to link microbial community structure to abiotic soil properties, vegetation, land management, and climate (figure 2). Because conclusions often depend on the particular methodology selected, the application of multiple molecular and biochemical assays (table 3) can be particularly useful. A recent study exemplifies this multipronged approach (Maul et al. 2014); these researchers used quantitative polymerase chain reaction (qPCR) and terminal restriction fragment polymorphism (TRFLP) of rRNA genes and phospholipid fatty acid microbial community analyses to provide phylum-level detail of community structure response to cover crop, mulch, season, and rhizosphere compared to bulk soil. Modern high throughput DNA sequencing of soil microorganisms has greatly increased the ability to characterize the taxonomic diversity within a particular arable soil (Acosta-Martinez et al. 2008; Sugiyama et al. 2010), yet most studies only characterize the dominant taxa (100 to 1,000 species) and provide little insight into the true genetic diversity and potential present in the soil. For example, considering a typical bacterial genome contains 3,000 to 4,000 genes, the number of microbial genes present in a single gram of soil may exceed 10^{12} genes, or 1,000 terabase pairs of DNA per gram of soil (Vogel et al. 2009). Assuredly, many great discoveries and surprises lie ahead.

LINKING SOIL MICROBIAL TAXONOMIC DIVERSITY TO THEIR FUNCTIONS

Soil microbial structures are frequently used to infer potential functional changes within the soil microbial community. Microbial biomass may contribute significantly to observed soil functions because more organisms carrying out a function may lead to higher rates of that function. Although there is an emerging understanding of the redundancy that exists within the soil microbial community gene pool, it is still unclear if there are (1) a small number of species that dominate the transcriptome (collection of all mRNA transcripts), (2) rare groups that dominate intermittently based on environmental conditions, or (3) microbial consortia that express genes in a coordinated fashion resulting in observed microbial community functionality. Linking microbial composition and biomass (e.g., who and how many) to analysis of soil microbial gene expression will be key to unraveling the regulation of soil functions that are desirable in agroecosystems.

It has often been assumed that changes in the phylogenetic community structure lead to changes in soil functionality as a result of differential niche specializations that have evolved among phyla. For example, certain functions can be associated with particular genera or species, (e.g., nitrogen [N] fixation). As more genomic information is collected within each phylogenetic clade, however, it is becoming clear that functional redundancy is most likely the norm among widely divergent microbial groups (Allison and Martiny 2008; Ollivier et al. 2012). Although individuals within a species or genera may all contain genes to carry out a specific function, it is rare that a specific function is exclusively maintained within only a single genera or species. This

Table 3

Techniques for soil microbial ecology analysis (Hill et al. 2000; Hirsch et al. 2010; Rincon-Florez et al. 2013).

Method	Notes	Benefits to soil production	Advantages	Disadvantages
Community DNA fingerprinting methods				
(Automated) ribosomal intergenic spacer analysis ([A]RISA)	DNA profiles/patterns generated for each bacterial community. Data is generated as polymerase chain reaction amplicons or fragments separated by size (e.g., T-RFLP) or sequence (e.g., DGGE). Some methods allow for downstream processing (e.g., DGGE) for methods such as DNA sequencing. Generally good for comparing community structure, possibly diversity. Require specialized software for post-run analysis and comparison.	Diversity has been used to assess soil health. Microbial community responses to changing soil conditions can also serve as a determinant of soil health. High throughput, low cost, and reproducible nature of several fingerprinting methods make them suitable for long-term monitoring of soils. Can be used for monitoring large areas and could be considered as potential standardized soil tests.	High throughput, cost effective, low technical demand.	Subject to overestimation of species richness.
Amplified ribosomal DNA restriction analysis (ARDRA)			Cost effective, low technical demand, no specialized equipment necessary.	Most effective to subtype individual species due to generating multiple bands per species.
Length-heterogeneity polymerase chain reaction (LH-PCR)			High throughput, highly reproducible, cost effective.	Limited database support.
(Denaturing/temperature) gradient gel electrophoreses ([D/T]GGE)			Fragments can be extracted and sequenced.	Variability between gels/experiments makes gel to gel comparisons difficult.
Random amplified polymorphic DNA (RAPD)			Rapid, high throughput, cost effective, low technical demand.	Random nature of amplification could be affected by DNA quality resulting in low reproducibility.
Single-strand conformation polymorphism (SSCP)			Fragments can be extracted and sequenced. Can identify new mutations.	Reannealing of DNA strands can increase number of bands. Heteroduplex DNA can be formed.
Terminal-restriction fragment length polymorphism (T-RFLP)			Rapid, high throughput, cost effective, method can be applied to multiple gene targets.	Fragments cannot be sequenced, distinct microbial groups may share profile.
Sequence-based methods				
Clone libraries	Provides DNA (e.g., pyrosequence) or RNA (e.g.,metatranscriptomics) sequence either directly or based on hybridization (e.g., microarray). Can allow for microbial identification down to genus and species levels. Provide excellent estimates of microbial activity, biomass, and diversity. If not contracted to an outside party, these techniques come with considerable start-up costs for equipment and reagents, though their high throughput, big data, nature generally tends to reduce costs on a per base pair rate. For a number of these methods, bioinformatics can be a bottleneck.	Provide insight into the following soil microbial characteristics: abundances (e.g., qPCR); diversity (e.g., 16S rRNA); and potential microbial activity (e.g., metatranscriptomics, qRT-PCR). Information can be measured both temporally and spatially, allowing for correlations with environmental conditions. Depending on the method, data generated can be very specific (e.g., qPCR) or broad in nature. In-depth analysis of soil microbial systems not provided by other techniques and can help identify management practices that are beneficial or deleterious to microbial communities.	Low degree of specialized equipment required.	Time consuming, lower throughput than pyrosequencing methods, cloning biases.
Small subunit (SSU) rDNA/rRNA pyrosequencing			Low cost per base pair of sequence. SSU rRNA universally found, and contains conserved regions that allow for phylogenetic discrimination.	rDNA generally fails to distinguish between microbes actively growing, dead, or in stasis. High equipment costs. Bias with DNA/RNA extraction methods and SSU rDNA/rRNA amplification.
Metagenomics			Provides insight into metabolic pathways of entire microbial community. Can result in complete sequencing of previously unidentified and uncultured microbial species. No reliance on known sequences.	Costly to achieve high coverage rates of microbial community. Does not indicate which species are active or in stasis. Data analysis is complex, computer intensive, and time consuming.
Metatranscriptomics			Provides information on gene expression profiles of bacterial community at time of sampling, indicating potential responses to environmental cues. As with metagenomics, sequence can be unknown beforehand.	In bacteria, rRNA accounts for 95% of total RNA, bacterial rRNA removal difficult and introduces biases. Based on assumptions that RNA will be translated into protein and subsequently activity.

Table 3 Continued

Table 3 continued

Method	Notes	Benefits to soil production	Advantages	Disadvantages
Sequence-based methods (continued)				
Microarrays			Can be used for analysis of DNA or RNA. A large amount of information placed on a single array.	Nonspecific hybridization, time consuming array construction requires expensive equipment, target genes/organisms determined a priori.
quantitative polymerase chain reaction (qPCR) (DNA)/ reverse transcriptase polymerase chain reaction (qRT-PCR) (RNA)			Rapid, reproducible, cost effective, high sensitivity. Primer sets can be of narrow or broad specificity, each microbial gene can serve as a target for study.	Primer bias, fluorescent probe options limit analysis to a few targets per assay, targets based only on known sequences.
Other methods				
Culturing	Provide biomarker (e.g., PLFA, FISH) or biochemical data (e.g., community-level physiological profile [CLPP]) of select microbial species or whole communities. Not high throughput in nature, and some require sophisticated equipment for analysis of samples (e.g., FISH).	Metabolically active soil microbes (except PLFA). Can study specific organismal interactions (e.g., FISH) and preference for carbon substrates (e.g., CLPP). PLFA have data foundation for comparative studies between ecosystems.	Isolated microbes are available for additional analysis and characterization.	Low throughput, difficult or impossible to grow many soil microbes.
Community level physiological profiling			Moderate throughput; insights into heterotrophic substrate usage; new, improved platforms are available	Lower discriminatory power; often bias toward faster growing microbes, particularly Biolog.
Fluorescent in situ hybridization (FISH)			Multiple probes can be used simultaneously. Highly sensitive, detect single cell in complex environments.	Traditional methodology is not quantitative. Some probes may not effectively penetrate certain cells.
Phospholipid fatty acid (PLFA)			Biomass, community structure.	Coarse resolution; lower throughput, improved with microplate format.

is, in part, due to (1) relatively quick generation times, which allow for adaptation to environmental variation; (2) ability for many microbes to carry out conjugation and the passage of plasmid-borne genes and elements among individuals; and (3) genetic competence, which enables horizontal gene transfer across different genera and facilitates uptake and genomic integration of exogenous DNA. As a result, the distribution of many functional traits across unrelated taxa creates questions as to the accuracy of using microbial community phylogenetic (structural) data to infer functional changes within a particular community. But, true in situ functional measurements of specific soil microbial activities are quite elusive, as the act of making a measurement or collecting a sample alters microbial activities.

Despite these challenges, the relationship between soil microbial community structure and function and whether they respond in unison to their local environment determines the best approaches to gauge management effects on the collective function of soil microbial communities. Ecological hypotheses regarding the biogeography of soil microorganisms and the potential for endemic soil microbial populations have been used to examine community structure-function relationships and evaluate functional redundancy. A combination of high throughput DNA sequencing and enzyme activity were applied to soil fungal communities in a study that spanned local and continental scales (Talbot et al. 2014). These researchers found that some fungi were endemic (unique) to certain locales, while overall community function was similar across all the sites. Wholesale quantification of soil microbial allele frequency (gDNA) and transcript abundance (mRNA)—an inventory of genetic potential and activity generally known as "metagenomics"—has also been used to address this same question. In contrast to the findings of the previous study, these researchers found strong correspondence between functional and structural diversity in soil microbial communities from globally distributed sites (Fierer et al. 2012). In a separate metagenomic study of prairie soil bacterial communities, a single phylum, Verrucomicrobia, was responsible for much of the biogeographical variation observed and provided evidence in opposition to functional redundancy (Fierer et al. 2013). The extent of microbial species endemism and functional redundancy are central to measurement of soil health and resilience, particularly in relation to biodiversity (Griffiths and Philippot 2013).

The ability to sequence environmental DNA to the depth currently available has changed the questions that can be posed when exploring the soil microbial ecosystem. Soil nuclear metagenomes are being explored as snapshots of varied environments, but there are few examples of replicated sites with a priori agricultural

management treatments being tested. This limits evaluations of the environmental or agricultural management drivers responsible for functional changes within with the soil microbial community. In a recent breakthrough, microarray approaches were used to measure functional gene abundances in replicated field plot soils under high input (i.e., conventional) versus low input (conservation) agricultural management (Xue et al. 2013). These authors made two notable findings: (a) the abundance of functional genes for N transformations (denitrification and ammonification) was closely linked with independent measures of soil N pools and fluxes; and (b) functional gene diversity was significantly higher in the low input production system compared to the high input production system.

USING EMERGING KNOWLEDGE AND ANALYTICAL TOOLS TO IMPROVE SOIL HEALTH AND RESILIENCE

Ultimately, soil health and resilience will rely on maintaining functionally diverse, robust soil biological communities that support high levels of critical services, simply by carrying out their life-sustaining processes. Experimentally, soil biodiversity has been strongly associated with key ecosystem functions such as decomposition and nutrient cycling (Wagg et al. 2014). Some agricultural management practices can have negative effects on soil health, while other practices are more conducive to soil biological health (figure 3). Much of the data that supports existing soil health assessments of agricultural management practices is based on bulk soil measures like biomass, respiration, or enzyme activity. In a relatively few cases, specialized organisms such as the obligate biotropic arbuscular mycorrhizal fungi (AMF) have been used to demonstrate positive effects of conservation agricultural practices like cover cropping on soil health (Lehman et al. 2012). However, limited knowledge of AMF ecology, fluid taxonomic assignments, and inadequate analysis tools currently restrict application of this specific approach in numerous field applications. Similarly, there is inadequate knowledge concerning the soil microbial consortia responsible for weed (Kremer and Li 2003) and pathogen (Mendes et al. 2013) suppressive soils, or the ecology of plant growth promoting rhizobacteria (Zahir and Frankenberger 2004) to take advantage of these biological services.

Figure 3

Agricultural management practices and general effects on soil health (Altieri 1999; Jansa et al. 2006; Moonen and Barberi 2008; Dias et al. 2014).

Tend to Reduce Soil Health	Tend to Promote Soil Health
Aggressive tillage	No-till or conservation tillage
Annual/seasonal fallow	Cover crops; Relay crops
Mono-cropping	Diverse crop rotations
Annual crops	Perennial crops
Excessive inorganic fertilizer use	Organic fertilizer use (manures)
Excessive crop residue removal	Crop residue retention
Broad spectrum fumigants/pesticides	Integrated pest management
Broad spectrum herbicides	Weed control by mulching, cultivation

The challenge at hand is to use the emerging basic knowledge of soil microbial diversity and modern analytical tools in the testing of relevant ecological hypotheses (e.g., endemism and functional redundancy) under differing agricultural management practices. Since soil type, climate, and vegetation, and local management practices are known to influence soil microbial communities and vary regionally, research must be performed at regionally distributed sites by multidisciplinary teams. The known seasonality effects on soil microbiological dynamics must be accounted for with temporally dense sampling schemes. The outcome of this science will serve as the basis to answer the following questions that are central to promoting soil health and resiliency:

1. What are the most useful measures of soil health?
2. How is soil health linked to management decisions, including the use of biological amendments?
3. What benefits does soil health have for the individual producer/rancher?

Answering these questions in a scientifically defensible manner will promote agricultural practices that take full advantage of the services provided by soil biota while maintaining or improving soil health and resilience.

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