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Review Paper

Searching for unifying principles in soil ecology

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ABSTRACT

The field of soil ecology has relatively few fundamental unifying principles that can be used to explain and predict patterns and processes in belowground ecosystems. Here we propose that a first step towards developing a more comprehensive set of unifying principles in soil ecology is to identify and understand the characteristics shared by a wide range of soils, the common mechanisms driving soil biogeochemical processes, and the biogeochemical constraints imposed on soil biota regardless of soil type. Very often, soil ecologists focus on the differences between soils when, in fact, many soils share a common set of ecological mechanisms that govern biogeochemical processes. Here we explore evidence for the existence of unifying principles in soil ecology, highlighting some of the similarities in carbon dynamics and soil communities across widely different soil types and examining the various mechanisms that may drive these similarities. Given that soils are extremely complex environments that exhibit substantial spatial and temporal heterogeneity, defining overarching principles is, arguably, more challenging in soil ecology than in other disciplines. However, recent methodological advances hold great promise for testing and formulating unifying principles, particularly when such methods are used consistently, in concert with other interdisciplinary approaches, and across a range of sites. Soils are not identical, but they do exhibit consistent patterns and processes that, if explored more intensively, will affirm the existence of unifying principles in soil ecology.

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1. Introduction

As soil ecologists, we tend to focus on the differences between soils, the biotic and abiotic factors driving these differences, and why these differences may be important. This is a valuable approach as it allows us to characterize the variability in soil properties and processes across space and time and to evaluate the effects of human activities on soil functions. Many key advances in understanding the potential effects of invasive species, climate change, elevated atmospheric CO₂ concentrations, chemical contaminants, and agricultural production on belowground ecosystems have been based on studies where the effects of specific treatments or disturbances on soil properties are examined. Such studies are particularly valuable for informing land managers and

policy makers of the potential changes in environmental quality and ecosystem productivity that may accompany changes in soil management. However, in our quest to identify differences between soils, we often overlook the characteristics shared by a wide range of soils, the common mechanisms governing soil processes, and the biogeochemical constraints imposed on soil biota regardless of soil type.

Here we argue that it is equally valuable for researchers to recognize that many soil properties and processes are remarkably predictable given the diversity of biotic and abiotic factors that influence the belowground ecosystem. Even where disturbances such as agricultural conversion or plant invasions have altered soil properties, the underlying processes often remain remarkably similar (Haas et al., 1957; Mann, 1986; Lauber et al., 2008). The same is true with regards to soil processes in temperate and tropical ecosystems. Biological processes and reaction rates are often faster in the tropics with the pools of C and other nutrients reflecting these rates, however, soil communities and their chemical and physical controls are often qualitatively similar (Jenkinson, 1971; Six et al., 2002).

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Our objectives for this review are to encourage further development of the rich heritage of research in soil ecology by highlighting the similarities between soils and the mechanisms that may underlie these similarities. We are not arguing that all soils are identical, nor are we arguing that there are no key differences between soils that affect how they function or should be managed. Rather, by highlighting the similarities and consistent patterns, instead of the differences, we hope to encourage future work refining 'unifying principles' that can be used to identify and understand the fundamental processes controlling soil biota and soil biogeochemical processes across time and space. The discipline of soil ecology is at a unique point in its history; the emergence of new methods to characterize soil communities and soil organic matter (SOM) dynamics (e.g. environmental genomics, automated tracer techniques, and improvements in spectroscopic methods for analyzing SOM), coupled with an increasing awareness that soils are key players in ecosystem responses to global change have accelerated research into the broad ecological patterns exhibited by soil biota and their associated processes. We will use these advances to highlight the evidence that such 'unifying principles' must exist and outline specific strategies that would encourage research on identifying fundamental patterns and processes in soil ecology.

2. A historical perspective

There are a wide variety of conceptual developments that have led to important advances in the field of soil ecology. We cannot adequately cover all of the relevant literature but we can provide a few references to selected reviews and textbooks that will hopefully prompt the reader to examine this history in a modern context. For example, Waksman's soil microbiology text (1952 and earlier editions) highlighted advances in the study of decomposition, plant–microbe interactions, and nutrient cycling research related to soil fertility. Soil fauna and their contributions to decomposition processes, which have been described since the late 19th century (Darwin, 1881), have been summarized in many works, including those by Coleman et al. (2004), Swift et al. (1979), and Lavelle and Spain (2001). The development of isotopic tracer techniques in the mid-20th century (Coleman and Fry, 1991; Boutton and Yamasaki, 1996) allowed for the quantification of decomposition processes and nutrient cycling rates that subsequently led to the development of more advanced models. This work has been further expanded with conceptual perspectives on soil heterogeneity and the linkages between soil carbon dynamics and biotic and abiotic soil processes (Sollins et al., 1996; Killham, 1994; Beare et al., 1995; Lavelle and Spain, 2001). More recent reviews (Wall et al., 2005; Schimel, 2007) and textbooks (Bardgett, 2005; Paul, 2007a) have shown that soil biota no longer need to be viewed as a 'black box' and provide interdisciplinary perspectives on key conceptual issues within the field of soil ecology. Paul (2007b) provides a more detailed historical overview of conceptual developments within the field of soil ecology and demonstrates how the field of soil ecology has, over time, evolved from a field primarily focused on soil fauna to one that is far more integrative, incorporating soil microbiology, biogeochemistry, soil faunal research, and pedology.

Clearly, there is a rich history of research and concept development in soil ecology and these advances have put us in a position to develop a more comprehensive set of unifying principles that effectively integrate the numerous disciplines within the field of soil ecology. Most scientific disciplines are built upon fundamental principles that can be used to explain and predict how systems work, regardless of the specific system in question (Margalef, 1963; Lawton, 1999). In these fields, considerable attention is devoted to

advancing fundamental theories or developing new ones (Kuhn, 1962). Although there are some fundamental concepts in the field of soil ecology (e.g. concepts related to stoichiometry, food web dynamics, and carbon storage), soil ecology has relatively few basic principles that can be used to explain soil nutrient cycling, decomposition dynamics, and soil community structure. This has been noted previously (Wardle and Giller, 1996; Andr n et al., 2008) and is supported by Barot et al. (2007) who concluded from an analysis of 23,000 studies that modeling and theoretical approaches are not used frequently by soil ecologists and that "soil ecologists tend to present their results in such a way that they are poorly linked to general theories of ecology...".

This disparity may be partly related to the fact that soil ecology is a relatively young, highly interdisciplinary field; however, other interdisciplinary fields have made more progress, or at least efforts toward progress, in this arena. As just one example, consider the field of plant ecology and the extensive efforts that have gone into developing general theories regarding the local, regional, and global structuring of plant diversity and plant community dynamics (e.g. Grime, 1977; Tilman, 1994; Hubbell, 2001). Similarly, in aquatic ecology there have been many efforts to develop fundamental principles, including trophic cascade theory (e.g. Carpenter et al., 1985) and ecological stoichiometry (e.g. Elser et al., 2000). These and other theories not only provide a framework for subsequent research within the discipline but also provide opportunities to link ecology with other scientific disciplines.

One could easily attribute the slow rate of theory development in soil ecology to the overwhelming complexity of the soil system, the high degree of spatiotemporal variability, and the multiple interacting factors that can influence soil biogeochemical processes. Likewise, there are many methodological challenges inherent to soil studies, particularly the challenges associated with surveying the diversity of soil communities and measuring *in situ* soil biological processes (Coleman, 1985; Fitter, 2005). Other possible reasons for the paucity of general theories include the historical links between soil ecology and applied scientific fields, which may put less emphasis on general theory development, or a lack of well designed cross-site studies with corresponding efforts at synthesis. We contend that there are, in fact, many reasons for soil ecologists to be optimistic. Methodological limitations are being overcome, the use of meta-analysis and biogeographical data to analyze and observe patterns across sites is increasing (e.g. Tonitto et al., 2006; Fierer et al., 2007; van Groenigen et al., 2007; Attwood et al., 2008) and more scientists are using interdisciplinary approaches to understand soil ecology and biogeochemistry than ever before.

The field of soil ecology is not entirely bereft of qualitative and quantitative theories that have helped encourage soil ecologists to think of soil ecology as a more predictive science. In one of the best known examples, Dokuchaev (1880), followed later by Jenny (1941), outlined and attempted to quantify the unifying roles of climate, organisms, parent material, landscape, and time on soil formation. These roles established the causal interactions between soil forming processes and are used today in many soil classification schemes and ecosystem models. Likewise, many integrative models have been developed to predict terrestrial carbon, nitrogen, and phosphorus dynamics across space and time (e.g. Walker and Syers, 1976; Parton et al., 1987). Despite this progress, we still hold that the field of soil ecology could benefit from more research seeking to identify and test fundamental principles in soil ecology. If we look into the future, we believe that the field of soil ecology is poised at a pivotal intersection where individual advances in soil biology, physics, and chemistry can be synthesized to expand our understanding of the below-ground ecosystem.

3. Consistency in soil biogeochemistry and biota

Although soils are variable and there is no such thing as an 'average' soil, there are numerous lines of evidence suggesting that a variety of 'unifying principles' must exist in the discipline of soil ecology given the notable consistencies in soil biological characteristics and processes. What follows is not intended as a comprehensive review of the evidence for such consistencies; rather, we have selected a handful of examples to highlight some of these consistencies, focusing primarily on those similarities in soil organic carbon (SOC) dynamics and soil biota across ecosystems. Although one can easily criticize these individual lines of evidence on conceptual or methodological grounds, they do suggest that there exist common soil characteristics and patterns across a broad range of soil types that motivate the exploration of fundamental principles in soil ecology.

The similarities in the chemical composition of SOM across soils under different vegetation types provide one line of evidence for consistent biogeochemical processes. For example, the C:N ratio of SOM is often dependent on the proportion of particulate organic matter present and converges on a ratio of 14:1 in less disturbed systems (Cleveland and Liptzin, 2007) and 10:1 in cultivated soils (Stevenson, 1994). The amino acid composition of a wide range of soils is also remarkably similar (Sowden et al., 1977), as one would suspect from the similarities in proteins and enzymes in both plants and microorganisms. A range of chemical methods have been used to show that changes in vegetation alter SOM chemistry and that different native vegetation on the same soil type also influences SOM chemistry (Nierop et al., 2001a,b; Quideau et al., 2001; Filley et al., 2008). However, the direct effects of vegetation on SOM are often strongest in particulate or light fractions, which typically reflect the composition of vegetative inputs (Hannam et al., 2004; Filley et al., 2008). In silt plus clay fractions (<53 μm) and other older, more decomposed SOM pools, there is typically a higher abundance of aliphatics, carbohydrates, and N-containing compounds that are microbially derived (Kiem and Kögel-Knabner, 2003; Kleber et al., 2007). Indeed, older, more processed SOM fractions from different ecosystems often share more in common with each other than differently aged pools within an ecosystem (Grandy et al., 2007), reflecting the sharp changes in SOM that occur as it is processed by soil communities. Likewise, with depth through the soil profile, there is a predictable decrease in SOC content accompanied by consistent increases in the mean residence time of the SOC pools (Gaudinski et al., 2000; Fontaine et al., 2007) and increases in alkyl C content (Lorenz et al., 2007). Carbon to N ratios decrease with depth as does the proportion of non-hydrolyzable C, even as the turnover times of SOC pools increase to thousands of years (Trumbore and Harden, 1997; Paul et al., 2001).

Many soil microbial communities are remarkably similar in their phenotypic and genotypic characteristics. Nearly all soils are dominated by a select few bacterial phyla (Janssen, 2006); the relative abundances of these taxa are not necessarily constant, but soil bacterial communities are relatively similar to one another if we compare soil bacterial communities to those communities found in other microbial habitats (Lozupone and Knight, 2007). Likewise, archaeal:bacterial ratios are fairly constant in soil, with archaeal abundances rarely exceeding 10% of the bacterial abundances in most of the soils that have been examined to date (Buckley et al., 1998; Leininger et al., 2006; Roesch et al., 2007). Although fungal:bacterial ratios can be highly variable across soil types (Bailey et al., 2002; Ananyeva et al., 2006; Joergensen and Wichern, 2008), the C:N:P ratio of soil microbial biomass is surprisingly well-constrained across ecosystems (Cleveland and Liptzin, 2007) and microbial communities with very different fungal:bacterial ratios can have very similar growth yield

efficiencies (Six et al., 2006; Thiet et al., 2006). We might expect changes in plant communities to have important influences on belowground biota, but several studies have found minimal direct effects of plant species identity on soil microbial community characteristics (Groffman et al., 1996; Maly et al., 2000; Bezemer et al., 2006; Kielak et al., 2008).

When significant variability in soil microbial or faunal characteristics is observed, this variability is often predictable. For example, across a broad range of soil and ecosystem types, both extracellular enzyme activities and bacterial community composition can be predicted remarkably well from a single edaphic variable, soil pH (Fierer and Jackson, 2006; Sinsabaugh et al., 2008). In addition, the size of the microbial biomass pool is often predictable, being closely related to the size of the total soil organic carbon pool and relatively constant with biomass C often 1–3% of SOC (Anderson and Domsch, 1989; Wardle, 1992). Although a range of 1–3% may represent a two hundred-fold difference from an organisms' viewpoint, it represents a fairly narrow range when considering microbial biomass as a percentage of SOM and a possible nutrient pool. Recent work has shown that the abundance of soil invertebrates across ecosystems can also be predicted reasonably well with a simple model based on body size, temperature, net primary production, and trophic level (Meehan, 2006). Of course, there are many exceptions to these patterns and trends (and these exceptions are noteworthy), but these examples, and many others described in current soil ecology texts (e.g. Lavelle and Spain, 2001; Coleman et al., 2004; Bardgett, 2005), do suggest that there are often readily predictable patterns exhibited by faunal and microbial communities across space and time.

4. Processes underlying consistency in soil biogeochemistry

If we assume that there may be some degree of consistency, or at least fundamental predictability, in soil biological processes across soil types, we must then ask why such consistencies exist. What makes soil soil? Or, more specifically, why are soil decomposer communities and soil carbon dynamics often so predictable across a wide range of soil types? The mechanistic constraints are likely to fall into two basic categories: constraints on biotic processes and constraints imposed by the physiochemical characteristics of the soil environment.

4.1. Biotic processes

Stoichiometric and metabolic constraints on soil communities are major factors underlying the predictable patterns that soil C cycling and biota exhibit. Just as travel between New Jersey and Manhattan in the eastern U.S. is largely constrained to a limited set of tunnels and bridges, all compounds that get metabolized in soil must pass through the same physiological 'funnel' that constrains decomposition to a shared set of biochemical pathways (McGill, 2007). The existence of such a 'funnel' may partially explain why parameters such as litter C:N ratio and lignin:N ratio can often predict decomposition rates across a range of ecosystem types, why low quality litter will be perceived as low quality litter regardless of the decomposer community in question, and why distinct decomposer communities often yield similar patterns of decomposition on a common substrate (Parton et al., 2007).

Some microbial taxa may be better at degrading certain carbon types than other taxa and the overall rates of decomposition can vary dramatically across soil and ecosystem types. Decomposition processes, however, are fundamentally constrained by nutrient stoichiometry and the energetics of metabolism (Schimel and Weintraub, 2003). Not all decomposers have the same nutrient requirements, but the consistency in C:N:P ratios of soil microbial

biomass (Cleveland and Liptzin, 2007) suggests that soil microbes, like many aquatic organisms (Redfield, 1958), must abide by general stoichiometric rules. Likewise, all decomposer organisms require energy for survival and in unsaturated surface soils the majority of this ATP-energy is likely to be derived from aerobic respiration of organic compounds. Thus, at some fundamental level, most decomposition processes lead to the eventual conversion of the organic compounds, in whole or in part, to only a handful of possible intermediate metabolic products (e.g. pyruvate, acetyl-CoA, and the various compounds that make up the tricarboxylic acid cycle). These biochemical constraints are also evident in the initial stages of catabolism. For example, there is a shared set of extracellular enzymes that carry out some of the more important, rate-limiting steps in organic matter decomposition, regardless of the soil type or decomposer community in question (Sinsabaugh, 1994; Moorhead and Sinsabaugh, 2000).

The existence of constraints that influence microbial processes regardless of the specific taxonomic group in question could contribute, in part, to distinct taxa having physiological attributes that are qualitatively similar. Changes in decomposer communities often elicit only minor changes in decomposition rates, even when those communities are phylogenetically distinct from one another. For example, in a recent study Kemmitt et al. (2008) found that the rate of SOM decomposition was largely unaffected by changes in the size of the microbial biomass pool size or by changes in microbial community composition. Strickland et al. (2009) measured decomposition on a common set of litter substrates and found that decomposition rates only varied by as much as 20%, even when decomposition was carried out by very distinct microbial communities. Functional redundancy is also exhibited by soil invertebrate communities and is often linked to physiological traits such as body size, mode of movement and gut enzyme composition (Siepel and Maaskamp, 1994; Wolters, 2001; Berg et al., 2004). Many studies demonstrate that the presence of soil fauna and the diversity of faunal functional groups can significantly influence rates of decomposition and nutrient cycling (Bardgett and Chan, 1999; Kandeler et al., 1999b; Bradford et al., 2007). Evidence suggests, however, that at larger scales the effects of different faunal communities on decomposition rates may be relatively small. For example, Wall et al. (2008) found that rates of decomposition of a common substrate in a range of biomes were significantly influenced by the presence of soil fauna, but information on soil faunal abundance only improved models of decomposition rate by 7% over models that solely considered abiotic factors.

4.2. Abiotic processes

The decomposer 'funnel' is one key factor regulating soil C dynamics, but in order to understand the fundamental constraints on SOM dynamics we also need to consider abiotic conditions in the soil. Strong evidence for the importance of abiotic factors comes from the ability to predict soil nutrient dynamics across different soil types, management practices, and climate regimes using primarily abiotic parameters (Parton et al., 1987). Litter decomposition can also be reasonably well predicted using abiotic parameters alone (Parton et al., 2007).

Once plant carbon inputs are processed through the decomposer 'funnel', there are a suite of predictable physical and chemical mechanisms or phenomena that can affect the soil organic C pools. To phrase this another way, there is a discrete set of abiotic factors including environmental soil conditions (e.g. temperature, moisture, and pH) and edaphic soil properties (e.g. texture and mineralogy) that regulate the turnover rates of soil carbon pools (Sollins et al., 1996; Six et al., 2002; Mikutta et al., 2006; Kögel-Knabner et al., 2008). Soil organic matter has long been known to be derived

primarily from plant constituents that are processed by microbes (Gleixner et al., 2002; Horwath, 2007). There is a substantive literature based on humic fractionation, NMR and pyrolysis showing that the original building blocks of plant residues and microbial constituents are further transformed in soil by secondary chemical reactions (Baldock et al., 1997; Gleixner et al., 2002; Simpson et al., 2007) leading to the formation of novel compounds (Stevenson, 1994; Horwath, 2007).

If the decomposer 'funnel' were the overriding control over SOM dynamics, we would expect that the biochemical complexity of SOM would be a good predictor of SOM turnover time. However, studies using compound-specific isotope values and other chemical methods have found that relationships between initial structure and stability are rarely straightforward (Gleixner et al., 2002). For example, the silt- and clay-associated C pools, which often have turnover times several orders of magnitude greater than the particulate (>53 μm) fractions, contain polysaccharides, N-containing compounds, alkyl aromatics and aliphatics (Kiem and Kögel-Knabner, 2003; Grandy et al., 2007; Kleber et al., 2007). Based on biochemical structure alone, many compounds in these groups should have high turnover rates. That some of these structures may persist for hundreds to thousands of years in soil is due to association with minerals providing long-term protection from microbial attack (Paul et al., 1997; Six et al., 2002; Kleber et al., 2007). Particulate SOM may be protected to a degree by soil structure formation (e.g. aggregation) and the high concentrations of lignocellulose; however, the most stable C pools are the ones bound to mineral surfaces, and these are typically structures produced through interactions between decomposition products and physiochemical processes (Six et al., 2002; Kleber et al., 2007).

If biological processes were the overriding control over SOM dynamics we would also expect that soil mineralogy and texture would have little direct effect on total soil C concentrations but relationships between silt plus clay content and C concentration are well established (Feller and Beare, 1997; Hassink, 1997). Six et al. (2002) found that the amount of soil in the 0–20 μm size fraction explained between 41 and 55% of the variability in silt plus clay-associated C. They also found that differences in clay mineralogy influenced the relationship between silt plus clay proportion and silt plus clay-associated C. Other studies have similarly found strong relationships between texture and SOM content in different ecosystems and recent research suggests that soils have a finite capacity for sequestering C, based largely on the quantity and properties of clay and silt in the soil (Six et al., 2002; Stewart et al., 2007, 2008).

5. How do we identify 'unifying principles'?

If there are predictable constraints on soil biota and soil biological processes, how do we go about identifying and understanding these constraints? In a general sense, any study that attempts to develop unifying principles in soil ecology needs to be structured so the questions and methodological approaches capture widely-applicable knowledge and smooth out the 'noise' between sites. Spatial and temporal heterogeneity will always be one of the greatest challenges to developing unifying theories in soil biogeochemistry. Soil biota and microbial extracellular enzymes are not evenly distributed across microhabitats (Kandeler et al., 1999a; Hansen, 2000; Blackwood and Paul, 2003; Ettema and Yeates, 2003) and variation in SOM can be measured at scales below 50 nm (Lehmann et al., 2008). Although this heterogeneity is pervasive and can occur at scales that are difficult to adequately assess using current methodologies, it should not necessarily be considered an insurmountable problem. Predicting some fundamental processes may require characterizing this variability, but for

many biogeochemical processes, soil heterogeneity should be a repeatable outcome of similar overall averages from heterogeneous microsites (e.g. Schimel and Bennett, 2004; Balser et al., 2006). Below, we have outlined broad recommendations for research approaches that will lead to the development of new unifying theories in soil biogeochemistry.

5.1. Changes in epistemology

We have focused on SOM dynamics and soil biota as evidence for general patterns in soil ecology but believe that there are likely to be other consistent patterns, processes, and responses across soil types. However, identifying these consistencies is not trivial. One reason for this is that our statistical approaches are best-suited for identifying differences between soils; we often have only qualitative evidence that soils are similar given the range of possible characteristics and responses. For example, it is far easier to argue that C:N ratios differ across soil types, since soil C:N ratios typically range from 8:1 to 20:1 (Cleveland and Liptzin, 2007), than it is to convince a skeptical audience that C:N ratios are remarkably similar given the range of possible ratios that could exist. Likewise, when similarities are observed (particularly those similarities in soil carbon chemistry or microbial community composition), it is far too easy to discount the observed similarities by criticizing our methods or techniques for having insufficient resolution to resolve the differences. Moreover, due to the well-recognized bias against the publication of studies that report negative (or no) results (Knight, 2003; Kotze et al., 2004), more manuscripts are published that demonstrate differences in measured processes or characteristics than similarities. Furthermore, studies that employ similar methodologies and come to similar results as previous studies, but on a different soil type under different climatic conditions, are deemed to be not novel and are less likely to be published, hindering generalization across soil types. In short, we are quite good at describing differences between soils, but we are not very good at determining when these differences may or may not be relevant and generalizable.

5.2. Consistency in methods

In most cases, the extrapolation and comparison of soil biological characteristics measured in individual studies occurs post facto, in the discussion sections of individual papers and in comprehensive 'review-type' papers. However, since methods in soil biology and soil ecology are rarely standardized across research groups, the quantitative comparison of research findings across sites is often difficult, if not impossible. As an example, consider studies characterizing SOM chemistry where the differences in methodological approaches prevent robust comparisons between studies. NMR spectroscopy provides useful insights into functional groups and can be used with isotopes but it provides little information about the specific molecular constituents of SOM (Preston, 1996; Mathers et al., 2000). For this reason, it may be difficult to correlate NMR results with microbial processes. Pyrolysis-mass spectroscopy and variations on the technique provide information about small molecules and thus may correlate strongly with soil microbiological properties (Grandy et al., 2007, in press; Leinweber et al., 2008). However, these methods do not provide information on macromolecular structure and have other limitations including the potential production of novel compounds and inconsistent recovery of some chemical groups (Samukawa, 1996). Other methods, including those using various chemical extraction techniques, also have a range of benefits and drawbacks that can make them difficult to compare (Preston, 1996; Mathers et al., 2000). Likewise, when fingerprinting methods (e.g. DGGE or T-RFLP) are

used to assess the composition of soil microbial communities, the results cannot be directly compared between studies and the re-analysis of published data by outside parties is essentially impossible (Kirk et al., 2004; Thies, 2007). When sequence-based approaches are used to survey microbial communities and the DNA sequence information is deposited in accessible databases (like GenBank), the survey results can be directly compared between studies and the results reanalyzed when new questions arise or as taxonomic schemes change. Collection and extraction techniques for soil fauna also vary greatly in efficiency and the technique employed depends not only upon the taxa of interest but also on the characteristics of the substrate from which the taxa will be extracted (André et al., 2002).

We are not recommending that researchers should settle on a given methodological approach when more appropriate methods are available, this would be a mistake considering that many of the methods available to soil ecologists are rapidly improving. Rather, we are suggesting that researchers should carefully consider whether the data obtained with a given methodological approach will allow the results to be directly compared to previously published or future studies on the research topic. Further, there should be more effort made to collate results using different methods so that researchers can more easily compare studies. One way to do this is to have many research groups analyze the same soils using their preferred techniques (e.g. Beck et al., 1997). This type of analytical round-robin would provide insights into the strengths and weaknesses of specific methods and uncover the biases associated with these methods.

5.3. Collection of integrated datasets

Few individual research labs can collect all the data that may be relevant from a given soil. With different groups analyzing the same set of samples from different research perspectives, we are more likely to gain an integrated understanding of the soils being studied. For example, if information on microbial and faunal community composition, soil carbon chemistry and dynamics, extracellular enzyme activities, nutrient cycling rates, and edaphic characteristics are all measured on the same set of samples, the resulting dataset will do far more to improve our understanding of the belowground ecosystem than datasets consisting of just a handful of these measurements and analyses. Soils within established research sites have often been well-characterized by soil physicists, chemists, and biologists, but there are few examples of cases where identical samples have been studied by an interdisciplinary group of researchers. Because of this, the spatial and temporal variability in soil properties at a given site may obscure the direct integration of the various datasets. Such coordination is not easy, but the pay-off for individual groups can be large as it will be far easier to place the results from a specific study or set of analyses into a broader context.

5.4. Cross-site studies

The ability to identify unifying principles in soil ecology will increase exponentially with the number of soil samples examined. This includes experiments or manipulations conducted in the same manner across multiple sites to determine how different soils may respond to the same treatments. Consider studies such as LIDET (Gholz et al., 2000), GLIDE (Wall et al., 2008), and the extensive European soil translocation transects (Bottner et al., 2000) which have greatly improved our understanding of the biotic and abiotic controls on soil processes simply because they used standardized protocols to examine soil processes and characteristics across a range of ecosystem types.

The value of cross-site studies becomes increasingly relevant if we want to understand and predict soil ecological responses to global change factors. For example, the effects of nitrogen fertilization on microbial decomposition have been explored in many individual studies reporting a wide range of responses (Fog, 1988; Knorr et al., 2005). However there are surprisingly few comprehensive cross-ecosystem comparisons of nitrogen effects on decomposition rates and soil communities, wherein the same experimental treatments are imposed on all soils with decomposition rates and soil characteristics measured in the exact same manner across widely different ecosystems (however see Berg and Matzner (1997)). This failure to conceive, implement, and acquire funding for such cross-site experiments limits our ability to predict responses of decomposition rates to nitrogen fertilization and understand the factors mediating the nature of these responses. The development of soil classification and soil maps on a global basis, such as the FAO UNESCO, has required extensive data comparison and data synthesis and demonstrates the potential success of global collaboration to understand different sites. Further, these maps have already proven useful for understanding global patterns in soil biology and nutrient cycling and will be invaluable resources for future efforts to develop fundamental theories in soil ecology.

Adoption of these approaches, or a subset of these approaches, may well come at the cost of some understanding of soil biology at individual sites. For example, the larger the number of sites, the fewer the number of replicates that can be studied from an individual site (given the ever-present budgetary constraints). Likewise, methods that have been refined for an individual soil type have not necessarily been optimized for research at other sites. Nevertheless, if we want to achieve a comprehensive understanding of soil ecology and begin to identify broad patterns, we must strike a balance between research depth and breadth to broaden the focus of our research programs.

6. Concluding thoughts

Soil ecology is, almost by definition, an interdisciplinary field. The diversity and scope of accomplishments in soil ecology reflect its multi-faceted nature and some of the most important advances in agronomy, ecosystem ecology, microbiology, and environmental science can be linked to research examining the interactions between soil organisms and their environment. Further, the emergence of global climate change, biodiversity loss, and agricultural sustainability as global issues has put soil ecology in the spotlight. As the field gains prominence and more recognition for its contributions to society, it is important for soil ecologists to ask where the field stands relative to other scientific disciplines. If recent papers are any indication (Barot et al., 2007; Andr en et al., 2008) there is a growing demand for a better understanding of fundamental theories in soil ecology.

We broadly agree with this sentiment and have outlined several lines of evidence suggesting that unifying principles in soil ecology are more common than we may think. This evidence includes consistency in microbial communities and soil organic matter dynamics across widely different ecosystems. In large part, this consistency is driven by constraints over the physiology and metabolic activity of soil communities. As organic matter, mostly plant material, passes through the microbial 'funnel' it undergoes transformations that reduce variations in chemical structure. This consistency is also due in part to the effects of physical and chemical processes in the soils and their overriding effects on organic matter stabilization.

Obviously, not all soils are identical and some of the observed changes in soil biota and biological processes across time and space

will not be readily predictable. However, soil ecologists now have a set of tools available for studying microbial communities, organic matter dynamics, and nutrient cycling that could provide critical new insights. If these tools are correctly used, future work focused on identifying 'unifying principles' in soil ecology will invariably lead to quantitative and conceptual developments in the field (Wall et al., 2005; Filley and Boutton, 2006). Instead of piecing together results from studies that may not be directly comparable to one another, we could build on concepts in soil ecology to develop an integrated set of hypotheses to understand soil biological and biogeochemical processes across time and space.

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