Soil Biology & Biochemistry 41 (2009) 2249–2256

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Review Paper

Searching for unifying principles in soil ecology

Noah Fierer[a,b,*,1], A. Stuart Grandy[c,1], Johan Six[d], Eldor A. Paul[e]

[a] Department of Ecology and Evolutionary Biology, University of Colorado, 334 UCB, CIRES, Boulder, CO 80309-0334, USA
[b] Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309, USA
[c] Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824, USA
[d] Department of Plant Sciences, University of California, Davis, CA 95616, USA
[e] Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins, CO 80523, USA

ARTICLE INFO

Article history:
Received 6 October 2008
Received in revised form
3 June 2009
Accepted 12 June 2009
Available online 3 July 2009

Keywords:
Soil ecology
Cross-site comparisons
Microbial communities
Soil carbon dynamics
Ecological principles

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.

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 CO_2 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).

* Corresponding author. Department of Ecology and Evolutionary Biology, University of Colorado, 216 UCB, CIRES, Boulder, CO 80309-0216, USA. Tel.: +1 303 492 5615.
E-mail address: noah.fierer@colorado.edu (N. Fierer).
[1] Authors contributed equally to this work.

0038-0717/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2009.06.009

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; Andrén 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 belowground ecosystem.