Soil Biology & Biochemistry 103 (2016) 320–326

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Review Paper

Too much or not enough: Reflection on two contrasting perspectives on soil biodiversity

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ARTICLE INFO

Article history:
Received 7 July 2016
Received in revised form
9 September 2016
Accepted 13 September 2016

ABSTRACT

Soil biodiversity has become a major area of research over the last decade, and the literature on the topic has expanded tremendously in recent years, so much so that a huge number of publications now deal with soil biodiversity every year. This article does not attempt the formidable task of drawing a general picture of where the field is at the moment, but it zeroes in instead on two perspectives that seem to have gathered momentum over time and raise concern about future progress. The first perspective involves the implicit assumption that to make sense of either the species-, genetic-, or functional biodiversity of soils, it is not necessary to consider in detail the features of (micro)habitats provided by soils to organisms, and that analysis of the information provided by extracted DNA or RNA suffices. The second perspective is associated with research on the effect of the physical and chemical characteristics of microhabitats on the activity of microorganisms. It basically hypothesizes that all microorganisms behave similarly, and therefore that observations made mostly with bacteria can be extended readily to all organisms, ignoring taxonomic biodiversity. To illustrate both perspectives, we provide a number of illustrative examples from the relevant literature and analyze them briefly. We argue that these two perspectives, if they spread, will hinder progress in our understanding of soil biodiversity at any level, and especially of its impact on soil processes. In order to return to a more fruitful middle ground, where both a variety of organisms and the characteristics of the microhabitats where they reside are carefully considered, several routes can be envisaged, but our experience suggests that an emphasis on genuinely interdisciplinary research is crucial.

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1. Introduction

Over the last few years, biodiversity has become the object of great interest in the public at large. Soil biodiversity has ridden on the coattails of this surge of attention. Articles in newspapers or in magazines targeting wide audiences frequently mention the billion

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http://dx.doi.org/10.1016/j.soilbio.2016.09.008

or so organisms, including many thousands of bacterial and fungal species, that one can find in a single spoonful of soil (e.g., Carson et al., 2010; Delmont et al., 2014), or the fact that there is supposedly more diversity in a gram of soil than above ground in the whole of the Amazon basin. In terms of research, soil biodiversity has become a major area of activity, at different levels: taxonomic, genetic or functional. Among researchers, soil biodiversity has been advocated by some as a critical factor controlling the vast array of microbial processes that are crucial to the proper functioning of soils (Bradford et al., 2014a,b; Byrnes et al., 2014; Bardgett and van der Putten, 2014; Orgiazzi et al., 2015), regulate their ability to provide services to human populations (Nannipieri et al., 2003), and stabilize global life conditions on earth (Ferris and Tuomisto, 2015). The number of scientific articles devoted to soil biodiversity in soil-, microbiology-, or ecology journals is increasing exponentially, with close to 5000 articles published on the topic just in the last 5 years in the journals indexed in the Web of Science, and the number (1170) of articles devoted to it in 2015 in these same journals representing a 21% increase relative to 2014. At frequent intervals, workshops and conferences are focused on this area all over the world.

The shear mass of publications on soil biodiversity makes the topic very difficult to review in detail. Nevertheless, in broad terms, it is clear that this intense activity has led to important breakthroughs in a number of areas, especially since the development and adoption by soil scientists of a very sophisticated molecular toolbox, including high-throughput sequencing (HTS) technologies. As pointed out by Dini-Andreote and van Elsas (2013), these tools have made it possible to access thousands to millions of microbial phylotypes at relatively low cost and effort. As a result, some aspects of the taxonomic and genetic diversity of rhizosphere and soil microbial communities have progressed appreciably in the last few years (Gattinger et al., 2002; Kondorosi et al., 2013; Grattepanche et al., 2014). Our understanding of the relationship between diversity and functions has also improved markedly, for example with regard to interactions among bacteria (Lupatini et al., 2014) or the symbiotic activity of mycorhizae (Kisa et al., 2007; Martin et al., 2008). In other respects, advances have been appreciable as well but somewhat slower, e.g., on the relationship between biodiversity and fate of soil organic matter under changing environmental conditions, or in terms of understanding how the hydric regime of soils influences their microbial ecology as well as a number of microbial processes, like greenhouse gas release (Blagodatsky and Smith, 2012; Rabot et al., 2014).

Given this recent progress, it would be reasonable to expect that, in the years ahead, there will be a dramatic increase in our ability to characterize the taxonomic-, genetic-, or functional diversity of soil microorganisms, and in our collective understanding of their practical relevance for a wide range of processes about which major questions remain. However, two perspectives that, at least to us, seem to have gained increasing numbers of adherents in recent years, raise concern about the speed with which one can expect this further insight to emerge, and about whether it will be such as to enable researchers to resolve some of the pending issues.

In this context, the key objective of this short review is to identify and describe these two perspectives, as well as to illustrate them with recent publications. Whereas a single illustrative publication would probably have sufficed, we have instead selected two publications for the first perspective, and four for the second, in part to avoid giving the (mistaken) impression that we are singling out a particular publication, which would be unfair to the authors. The book and articles that we have chosen are all very well written and easy to read, with the consequence that it is straightforward to grasp the viewpoint adopted by their authors. After an analysis of these examples, we outline and discuss what we think is needed in order to avoid the potential pitfalls associated with the two perspectives, and to point out what we are convinced is a more fruitful middle ground.

2. Diverse, but it matters where they live

The first perspective is associated with research that is so focused on biodiversity that most other aspects of soils, and in particular the characteristics of the microscale environments in which soil organisms live, recede into the distant background, when they are mentioned at all. Increasing numbers of articles concentrate on extracting DNA or RNA from soils, and on applying to the extracts a battery of ever more sophisticated molecular biology techniques to characterize the biodiversity of soils (Jeffery et al., 2010; Maron et al., 2011; Ranjard et al., 2013; Morin et al., 2013; Myrold et al., 2014; Mendes et al., 2015).

To get published, these articles most often have to provide some information about the soils used, e.g., their location, their name in one soil classification system or another, as well as selected macroscopic parameters like their particle size distribution, cation exchange capacity, organic matter parameters, or pH. However, generally little if anything is done with this information, treated as if it were merely anecdotal. Clearly, the main preoccupation lies with characterizing the DNA or RNA extracts. Some of this work could be criticized on the grounds that detailed descriptions obtained with novel analytical methods are often excessively glorified, that the observations they provide are often misinterpreted or interpreted with limited applicability to the actual habitat of microorganisms, and that due consideration is not given to known microbial ecology principles. One could also argue that, in most cases, observations are not driven by a scientific hypothesis, whether on soil processes or on the parameters that influence them. But the main aspect of this research that interests us here is that it is completely disconnected from information about the habitats that soils provide to organisms.

An organism-centered approach is of course far from devoid of interest, since the information it generates could be of value for example to find bacterial or fungal species able to produce novel antibiotics or various types of biomolecules that may have commercial potential, e.g., in terms of plant growth promotion or for the treatment of raw materials, wastes, or drinking water. However, beyond this specific purpose, it is unclear to what extent, in and of itself, this information on soil biodiversity is useful, let alone reliable. First of all, as some authors have shown, the extraction of DNA or RNA from soils in many cases manages to get at only a fraction of the total amount of these molecules that are present (e.g., Baveye, 2009b; Terrat et al., 2012; Knauth et al., 2013; Dlott et al., 2015; Wagner et al., 2015). Furthermore, issues associated with sample size (generally <0.5 g per sample) and sample collection protocols (in terms, e.g., of replication) adopted to obtain DNA over large and heterogeneous field area raise questions about claims that are made, e.g., by Leff et al. (2015), concerning the representativeness of DNA analysis results. In this respect, the eye-opening recent article by Penton et al. (2016) shows how crucial the sample size is in the analysis not only of the overall bacterial and fungal community structure, but also of the number of operational taxonomic units (OTUs) in soils, as well as of the richness, evenness and diversity of their microbial population.

Quantitative information about the effectiveness and representativeness of extraction protocols in specific soils is improving (e.g., Huang et al., 2016) yet generally remains very scanty. Nevertheless, since this extraction appears to be affected by the nature of solid constituents and the physicochemical properties of soils (e.g., Crecchio and Stotzky, 1998), it would seem important to know something about the characteristics of the microenvironments in