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Review Paper

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

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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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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 which microorganisms reside before one can have any confidence that the sample of DNA or RNA extracted is representative of the whole. In particular, it would be useful to know if the physicochemical characteristics of the soils at the microscale (in particular the surface chemistries of soil constituents) are such that significant amounts of extracellular DNA could be preserved intact in soils for extended periods of time (Pedersen et al., 2015). Therefore, one could argue that without a solid understanding of how the properties of microhabitats could affect the extraction of RNA or DNA, the perspective on soil biodiversity (at any level) that one obtains in the end may be very biased and misleading.

Aside from these technical problems, it is striking that this perspective, centered exclusively on the organisms, clashes with almost 60 years of experimental evidence accumulated by soil microbiologists on the functions fulfilled by soil microoganisms and on the processes that they influence. Ever since the work of Rovira and Greacen (1957), it has been clear to soil microbiologists that the activity of microorganisms in soils could not be studied independently of the microenvironments in which these microorganisms are located. Alexander (1964) summarized this eloquently already half a century ago: “microorganisms apparently in the same habitat are, in fact, often exposed to entirely different environmental influences and population pressures. To understand the forces actually affecting the organisms, a microenvironmental concept rather than the gross macroscopic view of interactions must be adopted.” This message has been frequently reiterated since 1964 (e.g., Hattori, 1973; Stotzky, 1986; Chenu and Stotzky, 2002; Attard et al., 2011; Vos et al., 2013; Uroz et al., 2015; Xun et al., 2015; Falconer et al., 2015; Baveye, 2015; Barcenas-Moreno et al., 2016) and a sizeable amount of experimental data clearly indicates that one cannot infer much from the mere presence of specific organisms in soils if one knows nothing of the geometry and connectivity of the pore space in which soil organisms evolve, or about the composition, physicochemical features, and spatial heterogeneity of the soil constituents and nutrients with which soil organisms are in contact.

This message has been particularly clear in the past in the context of nitrogen cycling. Various authors, starting more than 30 years ago (e.g., Parkin, 1987), have indeed shown that denitrification can easily occur in microsites in soils, even if macroscopic measurements of redox potential or pH indicate that in principle this process should not unfold. Experience shows that nitrification and denitrification can occur under an extremely wide range of soil conditions. Therefore, to be able to predict the extent of either of these processes in a given soil, traditional macroscopic measurements of soil characteristics may not be relevant at all, and other types of measurements are needed to assess if organisms can find, or create, in a specific soil the type of microenvironments they need. Reaching a similar conclusion, albeit for different reasons, Dini-Andreote and van Elsas (2013) argue that high-throughput sequencing (HTS) strategies are not adequate to obtain detailed insights into organismal ecology and physiology (reflecting the behavior of populations of cells) within the community in the rhizosphere, and they call for a paradigm shift away from HTS.

In the 60s, when Alexander (1964) wrote the aforementioned conclusion, soil microbiologists could not be faulted for not following up on it. Indeed, little could be done experimentally at the time to characterize microhabitats in soils. The situation had improved a little, but not tremendously, by the late 80s, with the advent of scanning- and transmission electron microscopes (Foster, 1988). Fortunately, phenomenal technological advances in the last decade have made readily available to scientists an array of tools, including, e.g., dedicated stations at various synchrotron facilities around the world, widespread benchtop X-ray computed tomography scanners, and NanoSIMS machines, which are now making it possible to probe and characterize quantitatively the environment of microorganisms in soils. Thus, what once constituted a major obstacle to probing microhabitats in soils has been alleviated in recent years, and there is no real excuse anymore not to attempt to do so on a regular basis.

Regardless of how one views this first, organisms-centered perspective, two publications seem most appropriate to showcase it. The remarkably illustrated “European atlas of soil biodiversity” (Jeffery et al., 2010), proposing a number of attractive soil biodiversity maps of Europe, has drawn considerable attention since it came out, and many soil scientists either have a copy of it or have had a chance to at least peruse it. In this Atlas, which provides an overview of the literature, with a strong emphasis on the role of soil flora and fauna on the delivery of ecosystem services by soils, there are sections on “Soil as a habitat” and “Soil structure and soil biota”, amounting to 4 pages (out of 128 in total), but curiously in the text, there is barely any mention of clay or oxide minerals, of local pH or redox conditions that may influence microbial growth, or of the existence of niches or microhabitats. Nor is there very much at all on the geometry, connectivity, and tortuosity of pores in which soil organisms proliferate.

In part because its publication in PNAS is likely to give it increased visibility, several aspects of the recent article by Wagg et al. (2014) make it another logical choice to illustrate the approach we associate with this first perspective. In their account of efforts to find out whether reductions of biodiversity in soil communities have consequences for the overall performance of an ecosystem, the authors point out that “in soils below ground […] the functioning of biodiversity is not well understood.” The rest of the text makes it clear that the authors consider that further understanding of this functioning of biodiversity will come entirely from consideration of the organisms in presence, and not from a closer look at soils and habitats conditions at different scales. Indeed, the soil they used in their experiments is described in the text as a “standard sterile soil”, with no explanation of what this “standard” qualifier might mean. Supplemental information provided with the article mentions that the soil was collected from grassland in Switzerland, and was sieved through a 5 mm mesh. Values are provided for pH, the amounts of available N, P, K, in the soil, as well as the concentrations of Ca, P, K, and Mg extractable with ammonium acetate-EDTA, but other than that, no information of any kind is reported about the microscale environments that the soil provided to the organisms it hosted.

3. Forgetting fungi, archaea, protists, and all the others

The second perspective we identify in the literature, in which soil biodiversity is not paid sufficient attention, goes exactly in the opposite direction. Articles associated with this perspective typically deal with processes that either are influenced in some way by soil organisms, or directly influence their activity. In either case, the articles envisage only one type of soil organism, e.g., specific bacterial or fungal species. That, in itself, is not a problem as long as the conclusions reached are restricted to the organism(s) involved, under the conditions of the experiments, and are not considered generally applicable to soils, which contain a multitude of other organisms beside the targeted one(s). However, some articles commonly make a huge leap of faith in this respect and extend their conclusions to the organism in question in the presence of others, or even more broadly, generalize the findings to all organisms. This not only ignores entirely the enormous taxonomic and functional diversity of soils but also in many cases invalidates whatever explanation is being proposed.

A first example of this second perspective is provided by a group of articles (Tiedje et al., 2001; Treves et al., 2003; Carson et al., 2010) that link soil bacterial diversity with the fact that in unsaturated soils, the bulk aqueous phase (excluding very thin films that cover all surfaces) is spatially discontinuous and therefore could physically isolate groups of cells in separate portions of the pore space. In unsaturated soils containing only non-filamentous bacteria, it may indeed be the case that the thin films connecting the "pendular" water bodies represent an insurmountable obstacle to movement, at least as long as there is no major change in water content, such as after a rain. This may also be the case for protists, who feed on bacteria and fungi. Being aquatic organisms, they prefer wet conditions in soils (e.g., Stefan et al., 2014).

By contrast, the propagation of fungi, and also of filamentous bacteria, in the pore space tends to be hindered if too many of the pores are filled with water (Otten et al., 1999, 2001; Falconer et al., 2012, 2015; Kaisermann et al., 2015). This feature may affect the distribution of bacteria in soils where they cohabit, since the growth of fungal hyphae in partly desaturated pores may actually make it possible for bacteria to hop from one pendular water pocket to another, through a process often referred to as "fungal highway" (Kohlmeier et al., 2005; Warmink et al., 2011; Ellegaard-Jensen et al., 2014). It is very plausible that mesofaunal and macrofaunal activity in soils, also commonly ignored (e.g., Briones, 2014), may lead to the same outcome.

These observations do not mean that physical separation of hydrated volumes in an unsaturated soil has no influence on the biodiversity of soil organisms. But it is clear that other explanations need to be invoked as well, like the adaptation by organisms of the physicochemical characteristics of microhabitats in which they reside (Foster, 1988), the production of antibiotics (Abrudan et al., 2015), or the spatial segregation pressures due to predation (Ronn et al., 2012; Jiang et al., 2015), and competition among organisms.

A parallel story is told in our other example of the second trend. In this article, Manzoni and Katul (2014) deal with experimental observations, made by a number of authors (e.g., Greaves and Carter, 1920; Orchard and Cook, 1983), that soil microbial respiration ceases below water potentials around −15 MPa, much lower than the water potential range (from about −0.1 to −1 MPa) in which the connectivity of the water-filled pore space in the selected soils decreases sharply. Since the connectivity of the water phase is essential for the movement of bacterial cells toward food sources, these observations were viewed as conflictive by Manzoni and Katul (2014), who came up with an imaginative solution to resolve it. They hypothesized that bacterial cells interacting with a small volume of soil may still experience a hydraulically connected environment even below the critical or threshold matric potential at which the average connectivity drops significantly. By and large, their calculations suggest that this hypothesis may be valid. However, one might argue that its premise is dubious. Indeed, it assumes that bacteria are the only organisms present in an unsaturated soil in experiments such as those of Orchard and Cook (1983), as illustrated in Fig. 1a. Unless special precautions are taken to eliminate fungi entirely, one could probably safely assume that fungi are present under most circumstances, and that Fig. 1b is therefore probably a better depiction of life in soil pores, at least at a scale too small to represent all the other meso- and macro-organisms that are also present. Since there is plenty of experimental evidence demonstrating that fungal hyphae and filamentous bacteria are able to proliferate in unsaturated soils and metabolize organic matter at matric potentials significantly below the hydraulic connectivity threshold (e.g., Wolf et al., 2013), the persistence of respiration at matric potentials below that threshold should not really be a surprise, and there is no need, in order to account for it, to develop a physical model like that of Manzoni and Katul (2014), as appealing as this model may be on theoretical grounds.

These different examples of neglect of biodiversity are far from isolated cases. In fact, in this respect as well, the literature on microbial influences on the nitrogen cycle in soils is replete with articles that, although nominally dealing with "microorganisms", only refer to bacteria (e.g., Zhu et al., 2013). The occasional inclusion of archaea (e.g., Tatti et al., 2014) is often based not on direct evidence of their role, but on the circumstantial evidence that a part of the genes believed to code in bacteria for specific transformations of nitrogenous compounds, are also common in archaea. Fungi tend to be entirely ignored in much of this literature, even though research has shown that N_2O production could be reduced by 80% upon addition of a fungicide to some soils (Laughlin and Stevens, 2002; Yanai et al., 2007; Crenshaw et al., 2008), whereas exclusion of ectomycorrhizal mycelia has the opposite effect in other soils (Emfors et al., 2011).

4. Removing disciplinary blinders

Whether they correspond to situations where the physicochemical characteristics of soils are ignored (first perspective) or where only a subset of organisms present in soils are considered (second perspective), the extreme simplifications of a complex reality, to which the above examples amount, can no doubt be rationalized in a number of different ways, for example by invoking the need to start with simple descriptions of systems, which can later be made more realistic. One of the reviewers of this article has rightfully asked in this context whether progress could not be achieved through "rigorous disciplinary work with associated integrative synthesis papers." This approach seems appealing in more ways than one, in particular since it would allow most researchers to remain in the comfort zone of the discipline in which they have been trained and have carried out their work until now. From our experience, however, this approach leads most often to a situation described many centuries ago already, in the celebrated and often recanted Jain parable of the six blind men and the

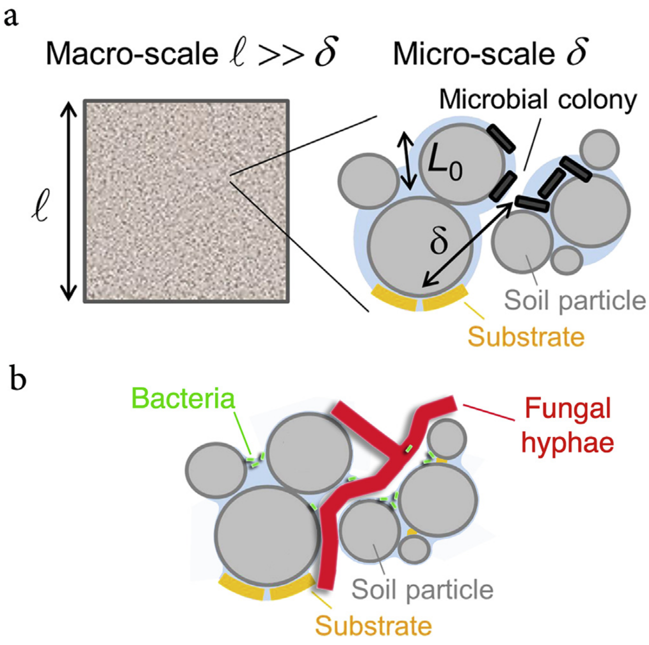

Fig. 1. (a) Schematic illustration of biomass distribution in an unsaturated soil, as depicted by Manzoni and Katul (2014), (b) similar illustration but with bacteria not necessarily located in microcolonies. Fungal hyphae are present, bridging between pores that are filled with water, and potentially carrying bacteria.

elephant (see, e.g., en. wikipedia.org/wiki/Blind_men_and_an_elephant). Perhaps the 19th century poet John Godfrey Saxe summarizes best our impression of what typically results from the juxtaposition of individual disciplinary perspectives: "So oft in theologic war, The disputants, I ween, Rail on in utter ignorance, Of what each other mean, And prate about an Elephant, Not one of them has seen!" Certainly, sound "integrative synthesis" articles, to which the reviewer alluded, could serve the purpose of providing a picture of soils in all their daunting complexity. But who will have enough of a global vision to write such "integrative" articles, if everyone remains within the confines of his/her narrow discipline?

In many ways, we believe that it is more fruitful to simply look at the two perspectives on biodiversity described above as the result of an engrained reluctance to cross traditional disciplinary divides. The solution may be the development of interdisciplinary research programs. It is tempting to think that if soil microbiologists and zoologists were routinely working in interdisciplinary-, or even just multidisciplinary teams with soil physicists or physical chemists, they would be sensitive to the importance of the features of microscale environments that soil organisms inhabit, and they would be less intimidated than they currently are by the various physical and mathematical tools used by physicists to describe these microenvironments. Conversely, if soil physicists were collaborating more closely with soil biologists, they would be unlikely to believe that what they think is true for some bacteria under very special conditions, applies to them generally in soils, or even to all soil organisms. In this respect, we entirely agree with Blagodatsky and Smith (2012) who, in their in-depth review of the literature on predictions of greenhouse gas emissions from soils, point out the extreme need for a "junction between soil physics and soil biology" and for the development of "ideal models" that are half-way between these two disciplines.

Of course, this is easier said than done. Multiple reasons conspire to hinder interdisciplinary efforts (Baveye, 2009a, 2013; Baveye et al., 2014). Our experience over the years suggests that funding agencies pay lip service to the idea of interdisciplinarity but do precious little to promote it. Likewise, we feel that reward systems in universities and research centers effectively discourage interdisciplinarity, and even the way we publish our research (including the importance that is assigned to bibliometric indicators like the *h*-index) put those who engage in interdisciplinary research at a disadvantage. In addition, given how little time each individual researcher has to read even the literature published in his/her narrow field of expertise (Baveye, 2014), it is not surprising that very few are at leisure to develop the kind of common understanding and language that come from reading the literature extensively and are prerequisites to effective interdisciplinary communication.

5. How do we get to the middle-ground?

Regardless of the specific reasons that have caused interdisciplinarity to be short-changed so far in the examples described earlier, and of what could/should have been done to enable the disciplinary divide to be effectively bridged, we believe that if the two perspectives we have identified continue to attract adherents, we shall end up with masses of experimental information and theories about soil biodiversity that are so fragmentary and incomplete as to be difficult to use for any practical purpose. In that respect, we feel that researchers who operate from one of these perspectives should be strongly encouraged to meet somewhere halfway between them, i.e., to consider in their research *both* the biodiversity of soils and the physicochemical complexity of the habitats that soils offer to living organisms.

What form this encouragement ought to take should be discussed. Perhaps a way to achieve results is for reviewers of articles submitted to the top journals in the field to systematically help authors make their research less one-sided and more encompassing. Editors could ensure this by trying to select either individual reviewers who have a good track record in interdisciplinary research, or a mix of reviewers who are associated with different disciplines, and by eventually asking authors to revise their manuscripts in ways that include information relevant to different perspectives. The same approach could be adopted to review proposals submitted for funding.

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