Abstract

Our interests in soil change are moving away from soil properties and increasingly towards changes in the processes and functioning of soils. Soil organisms are fundamental to dynamics and change in soils through their fundamental role in soil processes [1]. However it is only with recent technical and theoretical advances that we have started to establish quantitative relationships between soil biology and soil change (c.f. [2]). It is this predictive understanding that will enable us to fully integrate soil biology into the effective monitoring and sustainable management of soils. This paper outlines some of the recent advances in soil biology and discusses their relevance to monitoring and management.

1. Introduction

We can now ‘see’ the world below our feet in high definition thanks to progressive advances in genetic, imaging and biochemical techniques that are coupled with use of ever more powerful computational techniques. This combination is shedding new light on our understanding of the complexities of the soil ecosystem and its contribution to wealth creation, recreation and environmental sustainability [3]. With the development of genetic tools, we can extract DNA and RNA directly from soil and have far less reliance on isolating or culturing soil organisms to identify or count them. The application of genetic tools to soils around the world has demonstrated that soil ecosystems are amongst the most diverse and biologically active in the entire world, as illustrated in table 1. Estimates of the number of individual bacterial cells in a gram of soil are upwards of 10 billion, more than the number of people on earth [4]. The field of soil biology is being revolutionised with the rate of discovery of new species at weekly for bacteria and monthly for fungi [5]. This rate of discovery is likely to continue as DNA approaches are applied to less well-characterised groups (e.g. protozoa, acari, collembola) and to the multitude of diverse and rare soils and habitats around the world. There are now maps of the soil bacterial taxa of many soils of the world and we know which taxa are amongst the most abundant and which typically represent the rarer forms (e.g. www.earthmicrobiome.com). This type of information is required for the other soil biota groups and is being undertaken through the Global Soil Biodiversity Initiative (http://www.globalsoilbiodiversity.org).

Our understanding of the diversity of soil biology is rapidly extending beyond this classical taxonomic approach and is increasingly focussed on the characterisation and quantification of the functional
Table 1. Summary of the biological diversity associated with the major soil-dwelling organisms.

| Group/taxon (size) | Species described | Completely sequenced genomes | Species estimates |
|-------------------|-------------------|------------------------------|-------------------|
| Viruses (nm)      | 1,832             | 3954\(^1\)                  | >>4,000,000       |
| Bacteria (µm)     | 11,082            | 4520\(^1\)                  | >4,000,000        |
| Archaea (µm)      | 453               | 272\(^1\)                   | >>10,000          |
| Fungi (µm-mm)     | 24,645            | 587\(^1\)                   | 1,500,000         |
| Protozoa (µm-mm)  | 114,109           | 1\(^2\)                     | 200,000           |
| Nematodes (µm-mm) | 15,000            | 963\(^3\)                   | 20,000            |
| Collembola (µm-mm)| 6,500             | 0\(^4\)                     | 15,000            |
| Acari (mm)        | 20,000            | 5\(^4\)                     | 80,000            |
| Isoptera (mm)     | 2,600             | 0\(^4\)                     | 10,000            |
| Oligochaeta (mm)  | 3,650             | ?                            | 8,000             |

\(^1\) as described in [5] \[https://www.sanger.ac.uk/resources/downloads/protozoa\] \(^2\) as described in [www.nematodes.org]\[^3\] as described in [http://www.arthropodgenomes.org/wiki]

diversity of soil organisms. This is not straightforward since one species can have multiple roles across different soil processes (e.g. both the production and oxidation of methane can be carried out by the same soil microbes) and many species or organisms can carry out the same process (e.g. degradation of complex organic compounds). This principle is known as ‘functional redundancy’ and it is this feature that gives soils an enormous capacity to resist, recover and adapt to change. The ability to define and ultimately predict the implications of a change in soil biodiversity for a loss or the improvement in soil processes still remains the “holy grail” in soil biological research. We need to unravel the idiosyncratic relationships between soil biodiversity and function as recently illustrated by Neilson et al [6]. This may require revision of the more classical approach to functional soil biodiversity, which has been heavily reliant on the allocation of conventional knowledge of taxa to the assignment of function. It will require a revision of the role of soil organisms in (bio) geochemical and (bio) physical processes, of the models that represent these processes (e.g. [7]) and how environmental change alters these dynamics (e.g. [8]). The UK NERC Soil Biodiversity and Function Programme, implemented on a Scottish upland farm, developed several methodological approaches to explore these relationships [1].

DNA-based methods continue to develop at a rapid pace to identify and estimate the role of soil organisms in multiple soil processes including the mineralisation of nutrients, the control of pathogens and the remediation of pollutants. DNA cloning techniques have enabled detailed studies on the distribution of important functional groups of soil microbes. In Scotland, these have been used to explore the occurrence and distribution of ammonia oxidising bacteria across different land uses and soils [9]. More intensive use of DNA approaches takes us into the territory of quantitative PCR (qPCR) [10] and microarray methods [11] which can show the presence, and estimate the abundance, of a whole range of genes associated with different processes of interest. The application of qPCR methods have been used in Australia to survey the distribution and abundance of genes associated with N-mineralisation and fixation across three major Victorian soil types demonstrates the utility of this approach [12]. Further technological advances in four areas - metagenomics [13, 14, 15], metatranscriptomics [16], metabolomics [17] and proteomics [18] - have opened up exciting new ways
to assess the function of soil biology. These methods enable the simultaneous investigation of multiple processes performed by a particular soil biological population at fixed point in time and space. And now we have the ability to link genetic methods with isotopic tools to directly link organism to function (e.g. NanoSIP, [19]). The increasing challenge is synthesising and interpreting the immense amount of data that these techniques generate.

2. Soil biology – what’s where and why?
The structure and activity of soil biological communities is reflected in their biogeography. A key challenge is to be able to predict why particular organisms and functional groups of organisms occur, or do not occur, in particular locations. This is the foundation of being able to utilise soil biology in monitoring or management. In the case of bacteria, it has been proposed that this biogeography is controlled primarily by the edaphic features of an ecosystem [20]. This means that everything is not everywhere but instead is defined by the physico-chemical features across a range of scales from the soil pore/aggregate (µm of) the landscape (km). In Australia, there is significant investment in measuring the soil microbial diversity associated with regional grain production systems (e.g. www.soilquality.org.au) and more broadly across the major terrestrial biomes (e.g. www.bioplatforms.com.au/special-initiatives/environment/soil-biodiversity). Preliminary data from Australian soil biodiversity surveys suggests strong correlations between soil type, regional rainfall distribution patterns and land-use. A regulator of soil community diversity is soil pH. For example, we see higher abundance of the bacterial phylum Acidobacteria in the low pH Ferrosols compared to the high pH Calcarosols of the Mallee [21]. This agrees with trends observed in soil biodiversity surveys elsewhere [20]. In the UK, there has been a similar investment in exploring the biogeography of soil biology. The Defra funded SQID project investigated the structure and function of soil organisms in typical land uses across the British mainland [22]. This study demonstrated the overwhelming influence of land use on the structure and activity of soil biota (other than soil bacteria) with an underlying influence of other factors including soil chemistry and plant community structure. This research has moved on to establishing characteristic soil biological communities for different land uses, to establish a monitoring framework, and in quantifying the impact of drivers of change such as nitrogen deposition from point sources (e.g. [23]) and management systems [24] as a precursor to defining indicators of change. Thus, with new techniques available for assessing soil biodiversity, questions related to the impacts of land use, management, pollution and climate change can be assessed. Given that biodiversity expresses a biogeography, it is becoming apparent that change in soil biodiversity needs to be measured and interpreted within a regional context to ensure that pro-active management, remedial or protective actions are relevant and hence effective. What these studies have demonstrated is that soil biology cannot be investigated in isolation of other soil properties, soil processes and wider environmental factors.

3. Why bother with soil biology?
With increasing emphasis on recognising and quantifying the value of soils to society [25], the “value” of soil biology has been considered in various ways. Ultimately, it is recognised that soil biology, with its vital role in key soil processes, is valuable to food, water and energy security. All are reliant upon the role of soil biology in nutrient release, pest and disease regulation and retention and in the stability / erodibility of soils, amongst other key ecosystem services. Soil biology also has a vital role in regulating our climate, as it is the key in the turnover of soil organic matter and release of greenhouse gases [26]. Our habitats that are valued for their conservation status often rely upon soil organisms (e.g. symbionts) for their characteristic flora and fauna while many important pharmaceutical products have been developed from soil derived biological compounds. However can we really put an economic value on soil biology? In 1997, Pimentel and co-authors estimated that the global value of soil biodiversity exceeded 1.5 trillion dollars. Although this figure demonstrates the importance of soil biology to a wide range of ecosystem services, the economic values are difficult to relate to management within specific regions or for particular land uses. At a national level, Glenk and
collaborators [27] explored the value of soil biology to the Scottish economy. Ultimately, this study demonstrated that the ability to value the contribution of soil biology to food, water, energy, conservation and other services is severely limited by local scale data and defined relationships between soil biology and these services.

There are a few examples globally where we can truly appreciate and realise the value of soil biology, which can be illustrated by examples from Australia. Here, soil is viewed as a resource for sustaining and improving agricultural production and profitability. There are two major drivers for investment in Soil Biology. The first relates to the mounting concern regarding the continued degradation of the soil resource (State of the Environment and National Soils RDE Strategy) and the second the escalating input costs of production and the perception that soil biology can offset these. Investment in soil biology is largely industry based with $45M invested by the Grains Research and Development Corporation (GRDC) since 1992 [28]. This has served to focus research activity on applied outcomes related to demonstrating and quantifying the agronomic significance and developing management strategies (and products) that promote and enhance beneficial processes for productivity gains. Increasing energy costs that are driving up input (fertiliser N/P, lime, biocides) costs, and a general concern that soils are degrading further with increasing levels of salinity, acidity and disease and declining or low levels of carbon are considered by a growing stakeholder group to represent the major constraints to sustainable profitability [29, 30]. Grains Research and Development Corporation (GRDC) is the major funder of soil biology research in Australia investing more than $16M in two initiatives from 2002-2007 and 2009-2014. An economic evaluation based on judgements of the possible levels of adoption and benefits in areas relating to nutrient balance, disease control (including inoculants) and inoculants (yield increasing) indicate a net present value of $32 million and a benefit/cost ratio of the order of 4. The time lag from 2002 to the break-even point is of the order of 20 years. Sensitivity analyses aiming to capture the possible range of adoption and benefits indicated a range from break-even to a net present (2009) value of $120 million [31]. The time lapse between the investment and the return, coupled with the considerable effort in integrating information into a regional context represent the two major challenges for ongoing investment in this area.

4. Where are we at now and what are some of the remaining challenges?

There has been a revolution in knowledge regarding soil biodiversity with the development of molecular and imaging techniques. An analysis of the history of technology shows that technological change is exponential. So, at the present rate, in the context of soil biology, we are on the upslope and will experience something like 100’s of years of progress in 10 year (http://www.kurzweilai.net, 2001). Keeping the speed of advances in mind, the critical features of studying and, ultimately, utilising soil biology must be that they have a focus (a question), a scale (a time frame and spatial context), a multi-disciplinary approach and a pathway to adoption that is meaningful to multiple end-users. It is crucial that soil biology is integrated fully with soil assessments to gain a holistic appreciation of soil change in both space and time.

Examples of some big (and difficult) questions are those posed by Handelsman and co-workers [32] for microbial communities which can be expanded to soil biology in general:

- How resilient are soil biological communities in the face of rapid global change?
- Can soil biological communities help to buffer and mediate key elemental cycles which are now undergoing rapid shifts?
- Can changes in soil biological communities serve as sensors and early-alarm systems of environmental change?
- To what extent can we manage soil biological communities to modulate the effects of human activities on natural elemental cycles sensibly and deliberately?

We are advancing slowly towards some answers with massive genetic datasets being generated and analysed that will fill some of the knowledge gaps in defining species and function of soil biology across the soils of the world. There are also many outstanding challenges. A significant technical challenge is requirement for sophisticated informatics approaches that can process enormous amounts
of data and statistical techniques to explore the non-linearity in relationships between soil biology and its environment. Similarly a significant social challenge is transforming the way we think about and investigate soil biology. This requires a greater attention to systems and non-linear thinking. In practical terms, this means increasing use of metadata, often described as the ‘halo of data’, which includes soil chemical, physical and historical agronomic/land-use data that enables an accurate description of the soil as a habitat for biological functions. This, in turn, requires cooperation across a range of skill-sets from the soil biologist, soil scientists to experiential skills of land-holders. A noteworthy model of such a coordinated systems-based approach is provided by the human microbiome project [33] which shares a central tenet with soil biodiversity; the absolute reliance on a diverse microbial community to sustain a healthy system, whether a human body or a soil. No doubt these are exciting times for mapping the biogeography of soil biology and the changes in functionality as a result of human interventions. This will not only challenge some long held ecological concepts borrowed from above-ground systems but will generate indisputable evidence of soil biology as an asset worth protecting.

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