Soil Biology & Biochemistry xxx (2015) 1–9

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Review paper

Unearthing the role of biological diversity in soil health

Howard Ferris [a,*], Hanna Tuomisto [b]

[a] Department of Entomology & Nematology, University of California, Davis, CA 95616, USA
[b] Department of Biology, University of Turku, Turku FI-20014, Finland

ARTICLE INFO

Article history:
Received 8 December 2014
Received in revised form
26 January 2015
Accepted 26 February 2015
Available online xxx

Keywords:
Soil health
Ecosystem services
Functional magnitude
Diversity-weighted abundance

ABSTRACT

The soil provides a great variety of microhabitats for myriad organisms of different size, physiological activity, behavior and ecosystem function. Besides abundance of participating soil organisms, their species diversity facilitates maximum exploitation of the resources available in the different habitats. At various levels of resolution, species can be categorized into classes performing ecosystem functions and, within each functional class, into guilds of species with similar life course characteristics. Measurement of the diversity and abundance of species within a functional class provides insights into the nature of ecosystem functions and services and to the health of the soil. At higher resolution, species diversity within guilds of a functional class may infer the degree of exploitation of available resources and the complementarity of an ecosystem service; diversity among the guilds of a functional class may indicate successional complementarity of the services. A diversity of guilds within a functional class expands the range of conditions over which ecosystem services are performed while species diversity within a functional class and its guilds contributes to the magnitude of the services. Consequently, diversity of species within functional classes is a key element of the biological component of soil health. In the context of ecosystem services and soil health, the biomass or metabolic activity of species are more useful measures of their abundance than numbers of individuals. Thus, understanding of soil health and ecosystem function requires, besides knowledge of species diversity within functional classes, assessment of the range of functions currently performed in the system and the abundances of organisms by which they are performed. We propose a diversity-weighted abundance product for comparison of the functional magnitude of different assemblages of like organisms.

1. Introduction

In this paper, we introduce ideas and principles with regard to the importance of diversity as a basis for the strength and resilience of ecosystem services. To illustrate the principles we use data relating ecosystem services to nematode assemblages because those data are available to us in an appropriate format. However, the principles and approaches are applicable to any or all soil organisms, indeed to any assemblage of organisms in any ecosystem. We establish a basis for others to apply these principles to ecosystem services and organism assemblages of interest.

The provision of ecosystem services is a prominent theme among definitions of soil health. In discussing plant disease, Sorauer (1908) introduced the concept of latitude of health whereby a plant is considered healthy if its necessary physiological processes are functioning within prescribed ranges about their individual optima. If we consider the biological component of the soil as a meta-organism, the fields of oscillation of ecosystem functions constitute the "latitude of health" of the soil system. When conditions are such that one or more ecosystem functions of interest are no longer operative, the soil is in an unhealthy condition relative to that function (Fig. 1A).

The soil provides a three-dimensional matrix of differing microhabitats for a great variety of organisms and the potential for a wide range of space–trait combinations (*sensu* Lennon et al., 2012). The differences among microhabitats are determined by the particulate, porous, and stratified configuration of soil, from the disruption of its symmetry by roots, burrows and impervious zones, from the effects of physical and chemical gradients, and from diurnal, seasonal and stochastic climatic events. At the nucleus of each microhabitat is, or has been, a resource of some form that is available for exploitation by the combinations of organisms of different species and trophic habits with traits suitable for that

* Corresponding author. Tel.: +1 530 752 8432; fax: +1 530 752 5674.
E-mail address: hferris@ucdavis.edu (H. Ferris).

http://dx.doi.org/10.1016/j.soilbio.2015.02.037
0038-0717/© 2015 Published by Elsevier Ltd.

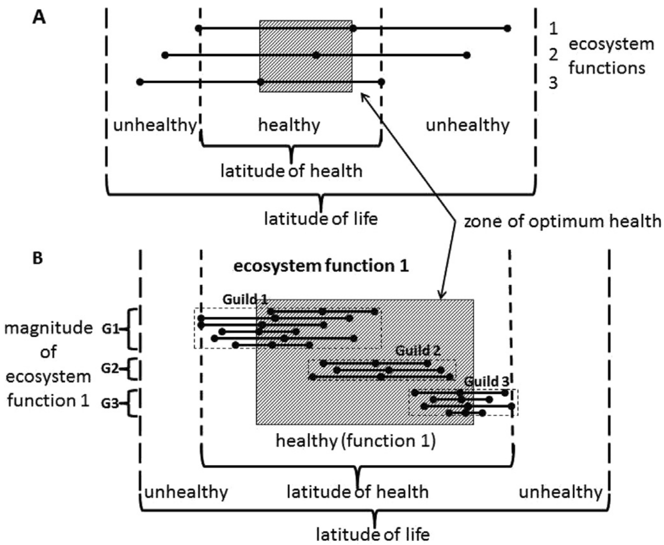

Fig. 1. **A**. Species diversity within functional classes determines the latitude of health of the system as a whole. **B**. Diversity of species within guilds and of guilds within a functional class are determinants of the latitude of health for that function. The magnitude of the function may vary when it is performed by different guilds within the functional class of species. The shaded area might be considered the zone of optimum health as it encompasses the maximum activity of all contributors to the function.

space. Consequently, bottom-up and top-down forces and ambient conditions drive waves of activity in each microhabitat (e.g., Georgieva et al., 2005; Zelenev et al., 2006). The microhabitats are linked by organism migrations, the patterns and ranges of which vary among taxa. Linkage strengths, the degrees of interactions and exchanges among microhabitat patches, are determined by patch proximity, conduits between patches provided by plant roots, fissures or burrows, and the propensity of incumbent species for interpatch movement. However, given the structural characteristics of the medium, the rate of movement between patches is likely slower than that in aerial or lotic environments.

Diversity is the condition of being comprised of different types of entities, such as species. Indices of diversity are essentially measures of the uncertainty of the outcome of repeated samples; that uncertainty is reduced as the entities are more evenly dispersed. Indices of species diversity calculated for soil organisms, including nematode assemblages, have been used to make inferences about stability and resilience of the soil ecosystem (e.g., Freckman and Ettema, 1993; Bulluck et al., 2002; Neher and Darby, 2009). However, the functional characteristics of the system may have little relationship to the species diversity of whole assemblages. Whittaker (1960, 1972) introduced the partitioning of species diversity across different spatial scales. With the rationale that the overall biological diversity of a community is greater if the species belong to different taxa, Pielou (1975) applied the partitioning of species diversity into hierarchically-nested categories that correspond to different taxonomic ranks. Following the same logic, diversity can be calculated and partitioned in relation to any relevant classification system, for example a classification of species based on their ecosystem function (Tuomisto, 2010).

Herein we draw a distinction between the trophic group and functional class of organisms. Trophic grouping reflects the source of food for a group of organisms; we use functional class to include the organisms of several trophic groups that may contribute to the same ecosystem function. Just as a diversity of response to environmental change is critical to the functional resilience of ecosystems (De Ruiter et al., 1995; Elmqvist et al., 2003; Cadotte et al., 2011), the latitude of health of the soil is extended by the range of adaptations of the species in a functional class because the function is performed by some of the species under conditions that are limiting to others (e.g., Ferris et al., 1996, 1998; De Ruiter et al., 1995). The magnitude of a function is the integral performance of all species within a functional class under prevailing resource and environmental conditions. We apply the term "species diversity of a functional class" to describe the diversity of organisms providing a specified ecosystem service. The activity of a functional class and its component guilds has greater magnitude and latitude with greater species diversity because differences in body size, behavioral attributes and physiological adaptations among species result in greater exploitation of available resources (Fig. 1B). The magnitude of a function is determined also by the abundance of individuals. When one or a few species are at greater abundance than others in a functional class, diversity is decreased but the effect of that on the magnitude of the ecosystem function may be offset by the greater activity in a proportion of the microhabitats. Herein, we explore the concept that both the biological diversity and the abundance of soil organisms are indicators of soil health. Finally, we propose diversity-weighted abundance as a measure of the functional magnitude of different assemblages of indicator organisms.

2. Model and application

2.1. Measures of diversity

Species diversity (D) takes into account both the number of species (species richness) and the degree of equality of their abundances (Macarthur, 1965; Hill, 1973; Jost, 2006, 2007; Tuomisto, 2010, 2011). Species richness (R) is the number of species present in the dataset of interest. When all R species are equally abundant, each has a proportional abundance equal to the reciprocal of the actual number of species (1/R), and the mean of their proportional abundances is also 1/R. When the species are not equally abundant, the mean of their proportional abundances can be expressed as $1/{}^qD$, where ${}^qD$ is the effective number of species (also known as true diversity or Hill number). The entity $1/{}^qD$ is calculated as the weighted generalized mean, with exponent q-1, of the proportional species abundances where the proportional abundances are used as the weights (Hill, 1973; Tuomisto, 2010, 2011). The parameter q in ${}^qD$ defines the order of the diversity. Large values of q assign greater weight to abundant species and small values of q to rare species. In effect, the parameter q determines the type of mean that is used; here we use q = 1, which defines the geometric mean and causes each species to be weighted exactly by its proportional abundance. When q = 1, ${}^1D$, is calculated with the equation

$$ {}^1D = \exp - \sum_{i=1}^{R} pi \cdot \ln(pi) \tag{1} $$

For other values of q, ${}^qD$ is calculated by the equation

$$ {}^qD = 1 \Big/ \sqrt[q-1]{\sum_{i=1}^{R} p_i p_i^{q-1}} \tag{2} $$

In these equations, R is richness (the actual number of types observed) and p_i is the proportional abundance of the ith type. Incidentally, ${}^1D$ equals the exponential of the Shannon entropy (Shannon and Weaver, 1949), an index of diversity frequently used in ecological studies (Hill, 1973; Jost, 2006; Tuomisto, 2010).

Please cite this article in press as: Ferris, H., Tuomisto, H., Unearthing the role of biological diversity in soil health, Soil Biology & Biochemistry (2015), http://dx.doi.org/10.1016/j.soilbio.2015.02.037