Review paper

Unearthing the role of biological diversity in soil health

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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.

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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
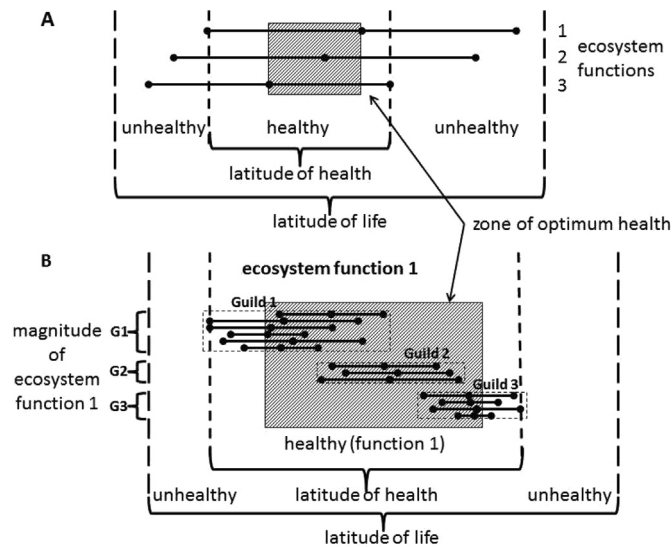
Fig. 1. A. Species diversity within functional classes determines the latitude of health of the system as a whole. **B.** Diversity of species within guilds and of guilds within a functional class are determinants of the latitude of health for that function. The magnitude of the function may vary when 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., 1998; 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., 1998). 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

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

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).

2.2. Measures of abundance

Among the challenges of assessing diversity is the selection of a measure of "abundance" appropriate for the questions at hand. Abundance might be measured as number of individuals, biomass of individuals, or as some measure of the functional activity of individuals. Clearly, interpretations of diversity may differ depending upon the abundance measures used because individuals of different species may differ substantially in size and impact on resources. In assessing ecosystem function, biomass of individuals is probably more informative than their numbers but reflects accurately neither the rate at which size is acquired, nor the rate at which a resource is utilized, unless repeated assessments are made. An alternative is to measure abundance as the metabolic footprint of species in an attempt to quantify the amount of C utilized in production and respiration averaged over the life course of the individuals (Ferris, 2010).

To illustrate the importance of an appropriate measure of abundance in terms of resource requirements, resource provision and ecosystem function, we calculated the true diversity, at a global rather than microhabitat resolution, of 735 species of predator nematodes (and guilds within that functional class) and the equivalent data for their target/potential prey, 765 herbivore species. The calculations are based on abundances measured as equal numbers of individuals of each species or as equal metabolic footprints of each species (using data assembled in http://plpnemweb.ucdavis.edu/Nemaplex). When all 736 species of predator nematodes have the same number of individuals their species diversity is 736 but the species diversity is quite low when based on the metabolic footprints of that constant number of individuals (Fig. 2A, left hand columns). When the species are equally represented in terms of metabolic footprints, their species diversity based on the numbers of individuals equivalent to the metabolic footprints is much lower (Fig. 2A right-hand columns). Differences in diversity assessment based on measure of abundance as numbers of individuals or metabolic footprints are similarly demonstrated for herbivore nematodes (Fig. 2B). Clearly, interpretation of prey availability to meet requirements of the predator assemblage will be quite different depending on the measure used for abundance.

2.3. Resolution and scale

2.3.1. Patch size

An important decision in measuring diversity is the choice of sample unit size. Assessment of abundance may be based on samples from a single point, within a quadrat, or on composite samples of various sizes from multiple points. It may be based on quantifying the individuals actually present at each location or on the number aggregated at an attractant. Clearly, the single point and quadrat measures come closer to assessing the species richness and abundance in a patch than the composite sample and attractant methods, but how large is the patch in which individual species are either interacting or contributing to an ecosystem service in a complementary manner? To illustrate the issue, we use data from Sánchez-Moreno et al. (2009) to determine species richness and true diversity of bacterial-feeding and fungal-feeding nematodes as means from 40 soil samples of either single 100 g cores, composites of three cores, or composites of nine cores (Fig. 3). Estimates of both species richness (representing actual number of species) and true diversity (representing effective number of species) increased with sample unit size, dampening to an apparent upper asymptote with the rate of increase in richness greater than that in diversity. The inferred ecosystem function of the nematode assemblages is that of nutrient mineralization during the decomposition of root exudates
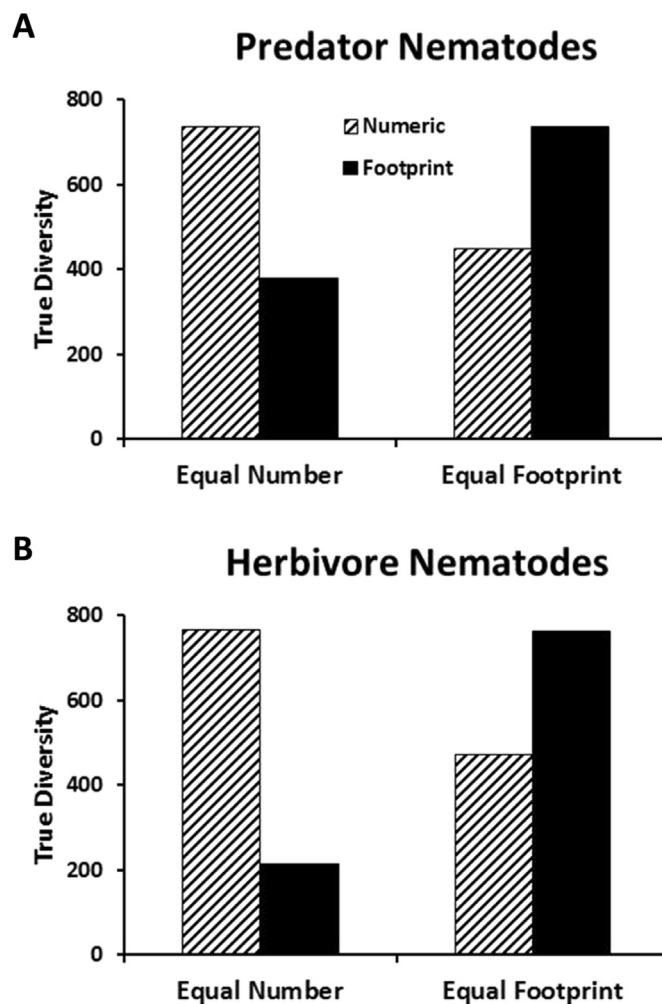
Fig. 2. True diversity (effective number of species) of 735 species of nematodes with inferred predatory habits (panel A) and 765 species with herbivore habits (panel B). Diversity is calculated for equal abundance of each species, whether measured as numbers of individuals or metabolic footprints, for numbers of individuals where metabolic footprint is held constant for each species or for metabolic footprint where number of individuals is held constant for each species.

and organic residues. If diversity is an important component of effective utilization of resources and the complementary contribution of species to ecosystem function, as we suggest in Fig. 1, then the effective number of species in single core samples indicates complementarity of function on a microhabitat scale, in three-core samples on a local scale and in nine-core samples on a field scale.

2.3.2. Trophic and life history characteristics

Species diversity within functional classes of organisms may be examined at different levels of functional resolution. At one level, probably with greatest practical applicability, the diversity of all the species that contribute to the same function may be calculated. At a higher level of resolution, species within a functional class may be separated into guilds based on their life history strategies and feeding habits. In the case of soil nematodes, the life history component of guild classification is based on grouping into five life history categories that range from rapidly growing and reproducing r-selected opportunists to slow-growing K-selected taxa (Bongers, 1990; Bongers et al., 1991; Bongers and Bongers, 1998; Ferris and Bongers, 2009; Ferris, 2010). The feeding habits of guilds are determined by observation of behavior or inferred from the
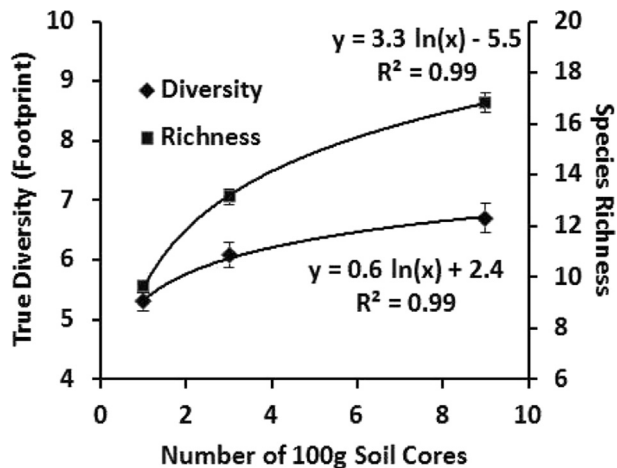
Fig. 3. Actual and effective number of species (i.e., species richness and true species diversity, respectively) of bacterial- and fungal-feeding nematodes contributing to the ecosystem service of N-mineralization in soil samples representing areas of three different sizes. Each measurement is a mean of 40 observations of soil samples of 100, 300, and 900 g soil, with metabolic footprints used as the measure of species abundance. Data from Sánchez-Moreno et al. (2009).

configuration of the stoma and other feeding structures (Yeates et al., 1993). Any of the five life-history categories may include nematodes with different feeding habits, resulting in a matrix of functional guilds (Ferris et al., 2001). When species diversity within a functional class is calculated, R in eq. (1) or (2) refers to the number of species. When guild diversity within a functional class is calculated, R refers to the number of guilds.

2.4. Model application to nematode assemblages

2.4.1. Ecosystem function: nutrient mineralization and soil fertility

Bacterivore and fungivore nematodes contribute significantly to N-mineralization in soil by excreting, in mineral form, N assimilated in excess of their body needs (Ingham et al., 1985; Ferris et al., 1997; Chen and Ferris, 1999; Okada and Ferris, 2001). The guilds of this functional class include both the first responders to resource enrichment and those important in a successional context in continuing the function after the most labile resources have been depleted (Bongers and Ferris, 1999; Ferris et al., 2001; Ferris and Matute, 2003).

Using data from Sánchez-Moreno et al. (2009), we illustrate the contributions to the ecosystem service of nutrient mineralization of the number of individuals in a functional class and the diversity of species in the class (Fig. 4). During the first four sampling periods in that study, diversity in the functional class, based on metabolic footprints of individuals, was greater in the organic plots with conservation tillage than in the conventional plots with standard tillage. In the same time range, abundance of individuals was not as great as in the later sampling periods when it was distinctly greater in the organic plots than in the conventional plots. However, in the later periods, species diversity was similar in the two sets of plots. The increase in abundance of individuals in this functional class was largely due to increases in abundance of the bacterivore genus *Acrobeloides* and the fungivore genera *Aphelenchoides* and *Aphelenchus*. Those increases in abundance reduced the effective number of species, and hence reduced true diversity. We suggest that these data indicate greater ecosystem service in the organic plots during the early part of the series due to the high diversity and consequent complementarity of access to resources by taxa adapted to different conditions. In the latter part of the series, magnitude of the ecosystem service would be attributed to greater
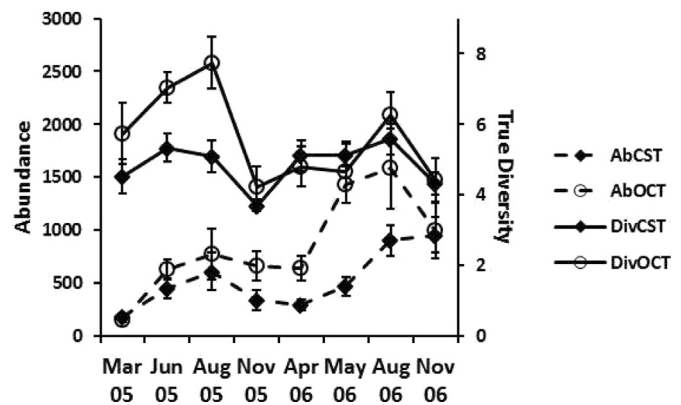

Fig. 4. Total abundance of individuals contributing to the nutrient mineralization function in field plots subjected to conventional agricultural practices with standard tillage (AbCST) or organic practices with conservation tillage (AbOST) and species diversity (effective number of species), based on abundance measured as metabolic footprints, in the same plots (DivCST and DivOST). Data from Sánchez-Moreno et al. (2009).

abundance and metabolic footprints of individuals even though resources may not have been fully exploited in all microhabitats (Figs. 1 and 4). Thus, by definition, the data indicate greater soil health in the organic conservation tillage plots than in the conventional standard tillage plots throughout the period of observation.

2.4.2. Management of species abundance and diversity

From an applied perspective, Ferris et al. (2012) separated nematode prey into the amplifiable prey (bacterivores and fungivores), which can be augmented by organic amendment without enhancing potential damage to plants, and target prey (herbivore species), which might be suppressed by a greater abundance of predators. In that context, subdivision of prey diversity into amplifiable and target components is of interest. Analysis of the ecosystem function of the regulation of opportunistic species, and soil suppressiveness to pest species, may require assessment of the species diversity and abundances of individuals of guilds in two functional classes. One functional class consists of species of specialist and generalist predators of other nematodes. The other class consists of species that constitute prey for the predators; it includes guilds of herbivore, bacterivore and fungivore species, and perhaps others. To understand the dynamics of these interactions, two sets of abundance and diversity calculations are appropriate — one for the predators and one for their prey resources.

In banana plantations in Costa Rica (data from Ferris et al., 2012), species richness and true diversity of species within functional classes and guilds within functional classes were greater for herbivores, microbivores and predators in organic production systems than in conventional systems (Fig. 5A). In addition, the biomass of each functional class was much greater in the organic than the conventional system (Fig. 5B), from which we infer that the magnitude of ecosystem services, and the range of conditions under which they are provided, are greater in the organic system. Therefore, the two conditions of greater abundance of individuals contributing to each function and greater diversity within each functional class resulting in greater complementarity of function among microhabitats satisfy the definition of soil health.

2.5. Model application to other organism assemblages

Many groups of organisms contribute to soil ecosystem services. For example, the protozoa are important contributors to nutrient
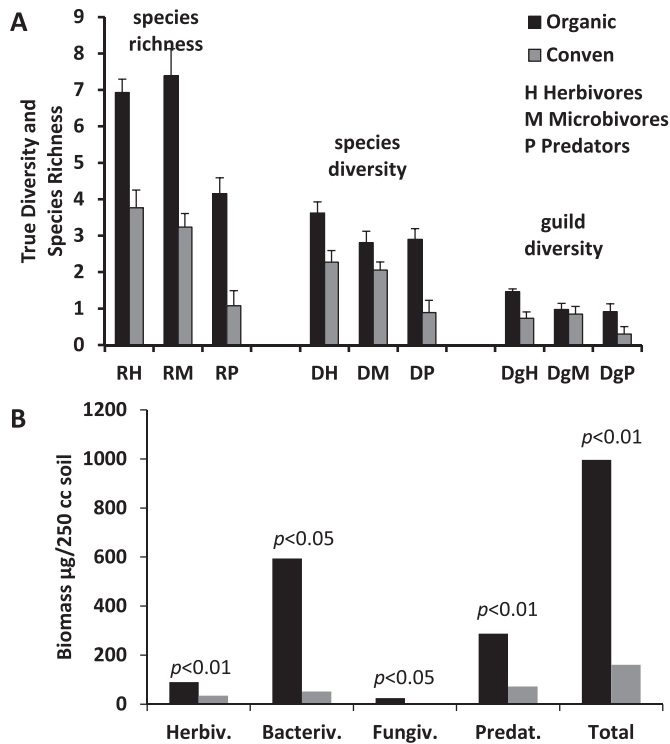
Fig. 5. A. Species richness and true diversity, based on numbers of individuals, of soil nematode assemblages in functional classes and in guilds within functional classes in organic and conventional banana production systems in Costa Rica. **B**. Biomass of the different functional classes of nematodes in the two management systems.

mineralization (Clarholm, 1985; Griffiths, 1994). Thus, species diversity of protozoa might be partitioned into functional guilds with abundances determined by most probable number techniques (Adams and Welham, 1995) and based on numbers of individuals, biomass of individuals, or an assessment of the physiological activity of individuals determined by growth or activity rates. A range of experimental constructs is possible, including measure of the ecosystem service at different levels of diversity but at similar levels of resource availability. A broader-spectrum analysis of the relationship between nutrient mineralization and organism diversity would include guilds of both nematodes and protozoa in the diversity assessment. In fact, all organisms in the soil ecosystem, through their excretion functions, contribute to nutrient mineralization. However, current identification constraints probably preclude timely assessment of diversity at that magnitude and such whole system approaches underscore the potential of evolving molecular procedures.

Among other applications to ecosystem function are the diversity of engineers of soil structure and of organisms that have beneficial symbiotic relationships with plants. For example, mycorrhizal fungi may constitute more than 10% of soil microbial biomass and conceivably the effectiveness of their access and transfer to plants of nitrogen, phosphorus and other minerals will be related to species diversity (Johnson et al., 2006; Fitter et al., 2011). Such questions, involving both mycorrhizal fungi and fungal endophytes, might be addressed at the individual plant species or at the plant community level. Again, some measure of abundance of individual species or functional types is required, for example, colony-forming units, spore abundance, proportional root colonization or fungal biomass. The basic hypothesis tested here would be that both abundance and diversity contribute to the magnitude and resilience of the function and consequent impact on growth of a plant or plant community.

A potential application of the relationship of ecosystem function to abundance and diversity at the microbial level is to base the assessment on functional groups determined by the range of organic substrates that are degraded (Degens and Harris, 1997; Degens et al., 2001; Liu et al., 2008). The assessment of catabolic richness and catabolic diversity of soil organisms by such biochemical analyses provides functional substitutes for species abundance, richness and diversity.

In this paper, we have suggested that the abundance and diversity of generalist and specialist predatory nematode species has a regulatory impact on abundance of their prey (Fig. 5). However, suppressiveness of soil to pathogens or parasites of plants may be a function of the abundances and diversity of many functional groups, including fungi and microarthropods (Nordbring-Hertz et al., 2006; Read et al., 2006). These organisms vary in their ability to exploit different microhabitats and in their mechanisms of predation. Inclusion of a greater spectrum of regulators or agents of suppression in diversity assessments will surely provide greater insights into the suppressiveness or regulatory function. Again, the potential for molecular profiles of organisms of similar function is evident. However, as important as such methods may become, we stress the need for observation and experimentation at an organismal level to provide the basis for partitioning into functional groups and to guilds within functional groups.

3. Discussion

3.1. The importance of diversity

The examples presented herein underscore the importance of considering multiple metrics of indicator species of soil health and its component ecosystem services. They also provide a reminder that the abundance and diversity of organisms, again measured on a functional basis, are important determinants of the magnitude of ecosystem services. High diversity among species of a functional class may increase the probability that one or more taxa within a functional guild will be adapted to exploit differences in changes in the availability of resources. Some microcosm experiments support that hypothesis (Wagg et al., 2014); others do not (Wardle et al., 1997). High abundance of species within a functional class may offset a lack of diversity but will not support exploitation of resources in all microhabitats. In the examples provided, by expressing abundance of organisms in terms of their metabolic footprints, or biomass as a proxy for metabolic activity, and assessing their diversity, we incorporate the three components (biomass, activity and diversity) of biological assessment of soil condition.

In experiments to determine the influence of functional composition and functional diversity on ecosystem processes, Tilman et al. (1997) varied diversity as the number of plant species per plot, functional diversity as the number of functional groups per plot and functional composition as the types of functional groups in a plot. Functional groups were based on intrinsic physiological and morphological differences of plants reflected in their phenology and life history characteristics. Here we apply similar structure to functional classes of the nematode assemblage that perform various ecosystems services but the approach is similarly applicable to other taxa of organisms or to combinations of taxa.

The partitioning of diversity within functional classes recognizes that the magnitude and latitude of ecosystem services may differ among guilds (Fig. 1B). The life history or other characteristics of species in one guild of a functional class may be quite different from those in another; one guild may consist of opportunistic species while those in another guild have more conservative life history characteristics. If the only organisms present are those in

the first guild, the function may be performed very rapidly but, for the function to persist, organisms of other guilds must be present (Fig. 1B). Average within-guild diversity may provide a measure of functional complementarity, the integral contribution of organisms differing slightly in their specialties and adaptations but with the same general life course trajectories. The effective number of functional guilds (i.e., the diversity of guilds within a functional class) may provide a measure of continuity of the complementarity; that is, the successional contribution of different guilds to the same ecosystem service.

3.2. Maximum diversity, diversity thresholds and designed diversity

If, as we suggest, diversity is important for the complementarity of function of soil and other ecosystms, the question becomes: how much diversity is relevant? As common in biological systems, the relationship between the magnitude of ecosystem service and diversity is probably one of diminishing returns. That is, at some level, the additive contribution of diversity to an ecosystem service becomes minimal. The measures that we have applied to functional classes do not have open-ended scales in the soil, at least not in the short term, as soils are less subject to sudden invasions or extinctions than above ground or aquatic habitats. Consequently, we can assume a finite number of species within the cadre of organisms contributing to each function. For example, a maximum of 16 taxa of bacterivore and fungivore nematodes was recorded in samples from the organic and conventional plots under different soil tillage regimes (Fig. 4). If all those taxa were equally abundant in all plots at all sampling periods, either numerically or as metabolic footprints, then, per definition, the maximum possible true species diversity of nematodes contributing to nutrient mineralization would have been 16. Therefore, we have a measure of the upper limits of diversity of the functional class for these plots and can use that as a measure of how close the systems are to their maxima. Of course, given the oscillations in species abundance likely to occur in soil micropatches (De Ruiter et al., 1998; Georgieva et al., 2005; Zelenev et al., 2006), true diversity will seldom be at a maximum. A maximum diversity of 7.8 for the functional class was observed in the organic conservation tillage plots, approximately 50% of the theoretical maximum diversity (Fig. 4). Such assessments might provide a framework for stewardship of the systems with the goal of enhancing functional complementarity across soil microhabitats in both spatial and successional contexts.

However, ecosystem services may not be maximized at maximum diversity. For example, if the desired service is the mineralization of nutrients in a system where labile organic materials are supplied regularly, say monthly, the importance of successional changes to guilds of organisms that exploit more recalcitrant materials is reduced and the effective number of functional guilds at which the service is provided might be low. In this example, high species diversity concentrated in guilds of enrichment opportunists, and consequently low guild diversity, would offset the immobilization effect of exploitative pulses in microbial biomass. If, on the other hand, the system is amended with more complex organic materials and at a lower frequency, a greater diversity of guilds might be desired so that successional complementarity would continue the service; that is, the guild diversity threshold would be higher. Similarly, if regulation of opportunistic species by higher-order predators was a goal, a high diversity threshold of prey taxa would be important so that a range of resources of different size and activity are provided to sustain the higher-order guilds.

In the studies of Tilman et al. (1997), functional composition and diversity of functional groups were the principal determinants of the ecosystem service. Those authors concluded that overall

function of the ecosystem is strongly affected by change in species composition resulting from invasions, and by changes in nutrient enrichment and management practices. In other plant diversity studies, Finn et al. (2011) and Díaz and Cabido (2001) determined that greater diversity of plants representing different functional and temporal traits increased complementarity in resource use and productivity. There are many examples of ecosystem engineering of agricultural production systems via the use of crop rotation and the mixtures of cultivars employed in soil-building cover crops (Altieri, 1999; Ferris et al., 2004; Lin, 2011).

3.3. Functional magnitude

Clearly, the magnitude of an ecosystem service is a function of both the diversity of species performing the function, as proposed herein, and of their abundance. In simple terms, ten species of nematodes with a total metabolic footprint of 1000 will more effectively access available resources and be active over a wider range of conditions than a single species with the same total metabolic footprint. We propose diversity-weighted abundance (θ), the product of the relevant diversity and abundance parameters for the ecosystem function of interest, as a means of comparing functional magnitude among guilds performing the same function in different assemblages of like species.

$$\theta = (^qD)^b \cdot \sum_{i=1}^{R} A_i \tag{3}$$

where ^qD is the true diversity and A_i is the numerical, biomass, or metabolic footprint abundance of the R species in the functional class of interest, or of guilds within the functional class, and b is a coefficient of average dissimilarity among the species (0—1 range) in functionally important traits such as feeding or behavior. The parameter b allows consideration of the fact that some species are functionally more similar than others, and that species diversity can be expected to increase the functional magnitude of an assemblage to a greater degree when the species are functionally more dissimilar.

To illustrate the diversity-weighted abundance concept we use hypothetical data for four herbivore species inhabiting a fixed area of landscape (Fig. 6). For this example, for no other reason than to demonstrate use of Equation (2), we set q = 2 and arbitrarily provide greater weight to more abundant species in the diversity calculation. We set b at 1, giving equal importance to both diversity and abundance. When each species is present at equal biomass, true diversity is equal to species richness; when different numbers of species are present at unequal biomasses, true diversity is less than species richness (Fig. 6A). From Fig. 6A, we calculate the arbitrary units of plant carbon mineralized at 100-unit biomass increments for each species diversity level. That allows calculation of θ at each biomass and diversity level and the corresponding magnitude of the mineralization function (Fig. 6B).

We concluded that in the Costa Rica banana study (Fig. 5) greater abundance of individuals contributing to each function and greater diversity within each functional class result in greater complementarity of function among microhabitats. We use the data to calculate θ for each functional class of nematodes as indicators of the relative soil health of the organic and conventional production systems (Table 1). The functional magnitude of all functional classes is greater in the organic than the conventional system. Of the two decomposition channels, that driven by bacterivores is much more active than that driven by fungivores in both systems. We infer that the function of regulation of opportunistic species by predation is greater in the organic system even
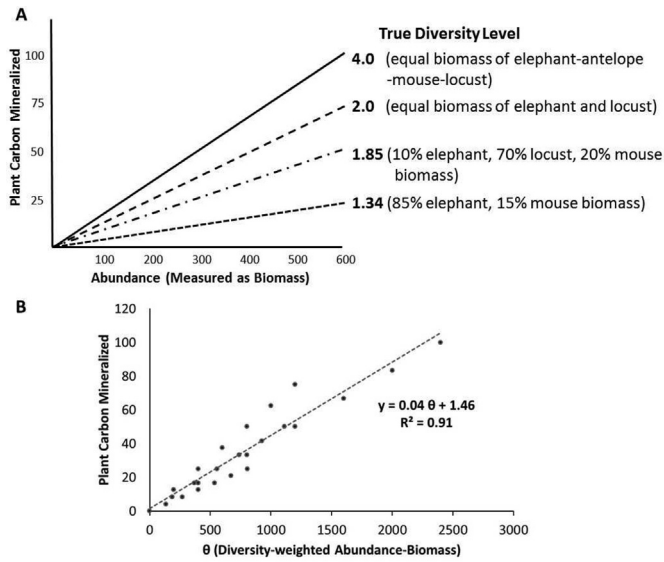
Fig. 6. Hypothetical data to illustrate the concept and a potential application of diversity-weighted abundance (θ). The mineralization of plant-bound carbon from a constant amount of plant biomass by above-ground herbivore assemblages at different abundance and species diversity (**A**) and its relationship with diversity weighted-abundance calculated at 100 unit increments in biomass for each herbivore assemblage (**B**).

though the relatively small flow through the herbivory channel is greater in the conventional system. In the latter system, herbivore nematodes are regulated not by predation but by three to four applications of nematicides each year.

Data do not currently exist for extensive testing of the hypothesis that diversity-weighted abundance of nematodes or other soil organisms, where abundance is measured in terms of biomass or physiological activity, is a reliable indicator of ecosystem function. Validation of the hypothesis will require future experimentation with collection of appropriate data on abundance, species diversity and associated measures of ecosystem function. However, as an illustration of concept, we present data from field experiments in which mineral N in soil samples was measured in relation to the biomass of species of bacterial-feeding nematodes where abundance had been manipulated by the use of cover crops and different frequencies of irrigation (Ferris et al., 2004) (Fig. 7A). In this example, there is no improvement of goodness-of-fit provided by use of diversity-weighted abundance (Fig. 7C) rather than unweighted abundance (Fig. 7B) as the independent variable. However, we consider that the rationale of the underlying principles (Fig. 1) warrant further exploration of the concept. Regarding the variability within this and similar datasets, it is useful to reflect that (1) nematodes are not the only contributors to N-mineralization; they are also indicators of the presence, abundance and activity of other organisms that participate in the function (Yeates et al., 2009), and (2) these data are derived from field studies with associated environmental variability and sampling constraints affecting both dependent and independent variables.

3.4. Biological assessment of soil health

There is a variety of biological indicators proposed for assessment of soil health (Dick, 1997; Van Straalen, 1998; Van Bruggen and Semenov, 2000; Bending et al., 2004; Kools et al., 2005). The quantification of species diversity within functional classes can be added to that list. Another useful nematode-based component of soil health assessment is a faunal analysis, which provides a
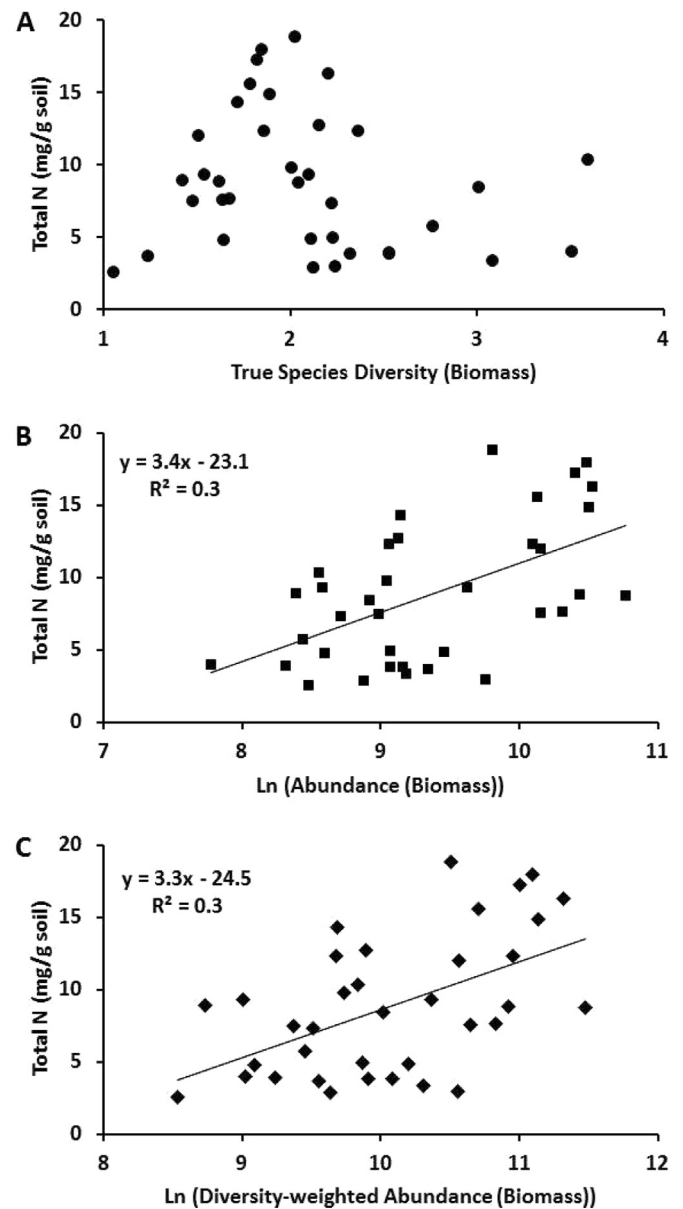

Fig. 7. The relationship between mineral N levels and diversity (**A**), abundance (**B**) and diversity-weighted abundance (θ) (**C**) of bacterial-feeding nematode species in field plots subjected to different irrigation and cover crop frequencies. In each case, abundance is measured as nematode biomass. Data from Ferris et al. (2004).

measure of habitat quality, soil food web condition, and the nature of ecosystem services available (Ferris et al., 2001). Additionally, metabolic footprints provide assessment of the magnitude of the ecosystem services based on the life course, behavioral and metabolic profiles of species assigned to a range of functional guilds (Ferris, 2010). Similar abundance, diversity and activity measures could be used for other indicator organisms. Quantification of

Table 1
Diversity-weighted abundance (θ) for functional classes of soil nematode assemblages in organic and conventional banana production systems in Costa Rica. Means and standard errors are based on 13 samples for each production system.

	Bacterivores		Fungivores		Predators		Herbivores	
	Organ.	Conv.	Organ.	Conv.	Organ.	Conv.	Organ.	Conv.
θ mean	1067	108	33	1.1	874	50	350	85
Std. error	323	30	16	0.4	152	22	111	16

various biological components of soil health will be further facilitated by current and evolving methods via DNA and metabolic profiles (Helder et al., 2004; Gans et al., 2005; Holterman et al., 2008).

4. Conclusions and emergent hypotheses

1. Species diversity and species abundance in functional classes of organisms that provide ecosystem services are important measures of the biological component of soil health.
2. High species diversity combined with high species abundance within functional classes facilitates exploitation of resources, and greater contribution of organisms to ecosystem services, in a spatially diverse habitat.
3. High diversity and abundance among guilds within functional classes promotes successional complementarity of ecosystem services.
4. While species diversity assessments indicate the potential for exploitation of resources and the complementarity of contributions to ecosystem services, assessment of the magnitude of the services requires determination of biomass and metabolic activity of the participant organisms.
5. Diversity-weighted abundance (θ) provides an integral indicator of the functional magnitude of ecosystem services in different assemblage combinations of similar species.

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