Chapter 11
Toward a Holistic Approach to Soils and Plant Growth

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Abstract We propose that a holistic view be taken to the study and implementation of ecological research into soils, soil organisms and plant growth. This builds upon the spatial and temporal aspects of soil physical and biological characteristics at the micro- and macroaggregate scales. This has major implications for the interactions of the soil biota and also for the possibilities of soil organic matter (SOM) dynamics, including gradual accumulation of SOM across decades and centuries. One of the key integrating factors in the role of soil biota in plant nutrition is the centrality of detrital and soil food webs in fostering nutrient cycling and ecosystem stability. We conclude with a five-dimension approach to studying key factors in soil biological interactions that affect plant nutrition and also long-term carbon balance in natural and agricultural ecosystems.

11.1 Introduction

In this second decade of the twenty-first century, a majority of the scientific world and the principal user groups (e.g., agriculturists, foresters, horticulturalists) frequently view soils as black boxes, merely providing inputs of tillage and fertilizer to them, and waiting for beneficial outcomes. The outcomes are occasionally what the users intend, but often at considerable cost compared to a more-informed

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approach. This chapter summarizes several avenues forward out of what is currently an impasse in soil biology and ecology.

As the nature and extent of soil biodiversity is more widely appreciated, particularly in the incredibly speciose area of microbial communities, there has been a temptation to focus almost exclusively on this area of soil biodiversity. As is noted in several of the chapters in this book, this basic knowledge is fascinating and important in its own right (Whitman et al. 1998). However, we suggest that a more holistic approach, including multi-trophic interactions (Havlicek and Mitchell, Chap. 2; Hazelton and Clements, Chap. 10), focusing on soils as true organizing centers of terrestrial ecosystems (Coleman et al. 1998) will pay major dividends in the future.

By emphasizing plant-soil-microbial-faunal interactions, including the increasing awareness of the key role of viruses in soils, this enables the investigator and farmer-grower to take a longer-term approach (Dighton, Chap. 1; Kimura et al. 2008; Guénola, Chap. 5). This topic is emphasized in Coleman (2011) and Van der Putten et al. (2009). We suggest that the best way to proceed successfully is to treat soils and the biota within them as an n-dimensional hypervolume, sensu Hutchinson (1957), by allowing soils to develop, biologically and pedologically, over time, including evolutionary dimensions as well.

11.2 Temporal and Spatial Dimensions of Soil Ecology

One of the recurrent themes in this book is the need to achieve a synthesis between shorter-term process studies and longer-term evolutionary studies, in a soils context. Thus whether studying phenomena at the soil micro- and macro-aggregate level, the rhizosphere, and other areas of significant activity (so-called "hot spots"), we need to study the mechanisms over short-term days to weeks, and longer-term months to years to decades in a pedological context (Coleman 2008; O'Brien and Jastrow 2013). One significant benefit of this approach is to enable soils to begin storing significant amounts of soil organic matter, which will be an important benefit gained from treating agricultural and forested soils in long-term fashion, facilitating oxygen and transport in soils. This has considerable bearing on the production and uptake processes of the major greenhouse gases (Blagodatsky and Smith 2012). This long-term approach will literally enable the soils to "work for us", sensu Elliott and Coleman (1988).

A principal reason for being concerned with the time course of micro- and macroaggregate formation is the increasing concern with the phenomenon of soil carbon saturation, in the context of global climate change (Stewart et al. 2007, 2008). Working with "nested" models should provide some useful insights into evolutionary pedology (Yoo et al. 2011; O'Brien and Jastrow 2013) develop the concept of hierarchical soil aggregates, regulating soil C and N recovery in restored perennial grasslands. They isolated particulate organic matter (POM) and silt- and clay-sized fractions from four defined locations within soil collected from an agricultural field, prairies restored for 3–33 years, and a never-cultivated remnant prairie. They then used aggregate hierarchy to define their four soil locations: non-aggregated material, free micro-aggregates, macroaggregates (excluding encapsulated microaggregates), and microaggregates within macroaggregates (Jastrow et al. 1998). They found that the duration of linear soil C and N accumulation differed among aggregate-occluded pools in relation to the combined influences of soil mass redistribution and increases in C and N concentrations. Even after several decades, silt in microaggregates isolated from within macroaggregates contributed the greatest quantities of C and N to whole soil, yet reached steady state C and N contents that were only 59 % and 56 % for C and N respectively, of those observed in the reference remnant prairie soil. O'Brien and Jastrow (2013) noted that the pools fell short of the original levels but seemed to reach steady state at the time of sampling. They postulated that several "transient steady states" could occur in some SOM pools along the way to an overall whole-soil steady state that might take centuries to achieve.

Studies of the conjoint interactions of microbes, fauna, and root and leaf litter inputs, via detrital food web models, have been very informative and productive of new insights into system-level phenomena. The importance of plants and soil biota to soil formation and processes has been understood for more than a century (Darwin 1881; Jenny 1941). Plants introduce organic substrates into soils as products of growth, senescence and death, while soil microbes and invertebrates utilize these organic substrates as an energy source and in the process contribute their own organic substrates through consumption, growth and death. For microbes the dominant constituents include microbial cell wall residues and hyphae in the case of fungi, extracellular polysaccharides, carbohydrates, and amino sugars (glucosamine, galactosamine, and muramic acid). For invertebrates the substrates include nitrogen rich fecal pellets, cell walls, chitinous exoskeletons, cytoplasm, and mucus secretions (Coleman et al. 2004).

Apart from the transformation and direct inputs of organic substrates, soil invertebrates indirectly affect the decomposition of organic substrates by enhancing the activities of soil microbes through grazing, comminution, and dissemination (Wallwork 1976; Moore et al. 1988). Moderate levels of consumption of microbes by protozoa and invertebrates can stimulate further microbial growth through the principle of optimal grazing (Hilbert et al. 1981; Clarholm 1985; Wall and Moore 1999). Assuming that microbes exhibit logistic growth tied to available resources with a carrying capacity K, microbial growth rates are maximized at population densities of K/2. Higher growth rates translate to increased utilization and transformation of organic substrates and increased production of microbial-derived organic substrates. Given that most invertebrates consume more nitrogen than they require for growth (i.e., invertebrates are net mineralizers of nitrogen), enhanced microbial growth through grazing leads to increased nitrogen availability for plants. When this process plays itself out within the rooting zone of plants, a positive feedback can occur wherein plants and the soil food web feed off one another's excess and waste. Under this scenario, plants exude excess photosynthate in the form of labile carbon substrates from their roots, which in turn are utilized by microbes and subsequently as food for microbivorous invertebrates, which release nitrogenous waste that is utilized by plants (Gupta et al. 1999; Ingham et al. 1985).

Many invertebrates feed directly on plant materials and organic substrates. The fragmentation or comminution of these materials enhances their decomposition. For plant structural materials, comminution increases the surface areas of the materials and exposes cytoplasm, thereby enabling greater access by microbes. Decomposition is further accelerated as the feeding activity often results in the translocation of nitrogen from the soil to the substrate in the form of fecal material and through fungal hyphae. Grazing by invertebrates disseminates microbes from one organic source to another as many microbes adhere to invertebrate exoskeletons and cuticles and survive passage through their digestive tracts (Coleman et al. 2012).

11.3 An Integrative Framework

A framework that links soil microbes and invertebrates as described above, directly to pedogenic processes, is beginning to emerge. Soil food webs and the differences in microbial and invertebrate life forms within them offers a starting point to connecting the components of the detrital food web to soil pedogenesis and SOM dynamics (Coleman et al. 1983, 2004). Coleman et al. (1983) identified a bacterial-based fast cycle and fungal-based slow cycle within soils. Subsequent studies revealed that these fast cycles and slow cycles were borne from the trophic interactions of detritus to bacteria and their consumers and from detritus to fungi and their consumers (Hunt et al. 1987; Moore et al. 1988; De Ruiter et al. 1996). These dominant trophic pathways, or 'energy channels', are ubiquitous across ecosystem types and grounded in the basic architecture of soil food webs and their structural stability (Moore and Hunt 1988).

These detrital food webs can be condensed into the dominant pathways beginning with pools of detritus or soil organic matter that differs in quality. These pools would serve as the primary energy sources for a suite of bacteria and fungi, each of which is consumed by a host of microbial consumers and predators. Metabolic wastes and byproducts that cycle back as energy sources and binding agents would be factored in much as C and N are in the current generation of models. This approach preserves the basic premise of material transformations that occur in the soil carbon models (Parton et al. 1987; Gijsman et al. 2002) and material transfers that occur in food web models (Hunt et al. 1987; De Ruiter et al. 1993; Fu et al. 2000) in a way that provides a common currency. Moore et al. (2003) presented a first approximation of this approach by linking the activities of organisms within the bacterial and fungal pathways to SOM dynamics and key ecosystems processes. Here, SOM is broadly defined as non-living organic material within soils, regardless of form or origin (e.g., detritus, dead roots, corpses of soil biota, traditional SOM). The balance in the activities of one pathway relative to the other is governed by the quality of SOM, with low C: N (<30) substrates favoring the bacterial pathway and high C: N (>30) substrates favoring the fungal pathway. This model allows for changes in the relative activities of the different pathways with natural seasonal variation in the phenology of plants and season succession in plant types, as well as abrupt or gradual changes that result from different land-use practices and increases in atmospheric CO_2. Fu et al. (2000) viewed the whole soil food web as a 'super-organism' and considered that organisms at different trophic levels work together to process SOM but with various strategies and turnover rates.

Global experiments and syntheses have continued to address the quantification of the role of soil fauna in ecosystem processes and in particular, have led to increased evidence for their contribution to C cycling. Global multi-site experiments show that soil fauna are key regulators of decomposition rates at biome and global scales (Wall et al. 2008; Powers et al. 2009; Makkonen et al. 2012). Garcia-Palacios et al. (2013) conducted a meta-analysis on 440 litterbag case studies across 129 sites to assess how climate, litter quality, and soil invertebrates affect decomposition. This analysis showed fauna were responsible for ~27 % average enhancement of litter decomposition across global and biome scales.

Agricultural practices affect many of the key functional and structural attributes of ecosystems in several ways: the transformation of mature ecosystems into ones that are in a managed developmental state are induced by tillage operations and other activities such as applying fertilizers and pesticides. These manipulations have the potential to shift the elemental balance of a system and decrease species diversity and alter the soil food web (Cheeke et al. 2012; Moore and de Ruiter 2012). Conventional tillage practices alter the distribution of organic material and affect the rate of formation of micro- and macro-aggregates in the soil profile. This has a profound effect on the turnover rates of organic matter that is associated with the aggregates (Elliott and Coleman 1988; Six et al. 2004; O'Brien and Jastrow 2013) as well as affecting ecosystem services (Cheeke et al. 2012). De Vries et al. (2012) showed that grassland, fungal-based, food webs were more resilient than agricultural fields with bacterial-based food webs, and provided evidence for management options that enhanced ecosystem services. Similarly, a conservation management seemed to be helpful for the development of Eucalyptus plantations in South China. The understory fern (*Dicranopteris dichotoma*) was found to contribute substantially to sustain fungal population and enhance litter decomposition in Eucalyptus plantations of south China (Wu et al. 2011; Zhao et al. 2013), although it showed less influences on the total soil microbial biomass and nematode abundance (Zhao et al. 2011).

We proposed that the biotic processes in the plant-soil biota-soil mineral system may be controlled primarily by the distribution patterns of readily favorable resources (i.e., could be used with lowest cost) among plant, soil biota and the soil minerals. One of the key characteristics of the readily favorable resources for a given biotic form is that the elemental balance (e.g., C, N, P ratio) of resource is as close as the balance of the user. The growth of plant and soil biota was then affected similarly by the difficulty of keeping the elemental balance. For instance, both plant and soil microbes need to increase the energy input when they require more nutrients, or need to deal with resource-depleted habitats. On one hand, Yi et al. (1995) found that the turnover rate of soil microbes in plantations (with low soil fertility) were usually higher than that in mature forest (with high soil fertility) in south China. This suggested that soil microbes used more energy to sustain the same level of growth in harsh environment than under favorable conditions. One the other hand, Yin et al. (2013) found that plants secrete more root exudates to stimulate soil microbes to enhance mineralization only in forest with low nutrient content in response to elevated CO_2. This may be because that plant has to activate and absorb more nutrients in response to a higher carbon fixation when CO_2 was elevated; and the extra root exudate is the cost of keeping the elemental balance. In contrast, plants could easily obtain enough nutrients in forests with high nutrient content to keep the elemental balance; as a result, less root exudate was produced in response to elevated CO_2. Soil invertebrates such as earthworms may affect the plant-microbial association by increasing the carbon and nutrient availability and, then enhance the energy utilization efficiency of both plants and soil microbes. Overall, an increased absorption of certain elements in plant or soil biota, as a consequence of the global change or human disturbance, will result in increases of other related elements; otherwise the growth of plant or soil biota may be hampered, or they would evolve to adapt a new elemental balance, i.e., changing their elemental ratios. What we need to know are which balance is optimum among plants, soil microbes and soil invertebrates and how to keep this balance, so that each component could obtain enough carbon and nutrients in time and the associated energy cost may be as low as possible.

If we recognize a well-developed natural system as the reference which is so-called “optimum balance”, the next step is to know the contribution of each major component to those key ecological processes in this reference system so that we could regulate the target system accordingly. However, it is difficult and the results may often contradict each other. As an example, here we show how earthworms contribute to net carbon sequestration in soil. Earthworms were often found to stimulate CO_2 emission, especially in short-term experiments, but they have also been reported to enhance carbon stabilization in soil aggregates in some longer-term experiments. Nevertheless, more experimental data support the view that earthworms reduce carbon sequestration due to the fact that CO_2 emission is easier to detect than carbon stabilization. As a result, a recent meta-analysis study concluded that earthworm presence will increase CO_2 emissions from soil by 33 % (Lubbers et al. 2013). In contrast, Zhang et al. (2013) found that earthworms could facilitate net carbon sequestration through unequal amplification of carbon stabilization compared with carbon mineralization. Zhang et al. proposed that neither an increase in CO_2 emission nor that in stabilized carbon would entirely reflect the earthworms’ contribution to net carbon sequestration; that is, the impacts of earthworms on the two coupled processes of carbon mineralization and carbon stabilization should be studied simultaneously. They found that, firstly, although earthworms accelerate carbon mineralization, the total amount of CO_2 that can potentially escape from the soil with earthworms differs little from soil containing no earthworms because the capacities of carbon mineralization of earthworms and soil microbiota are similar. Most previous studies did not note this and, thus, were likely to conclude that earthworms decrease carbon sequestration only because CO_2 emission was often enhanced by earthworms. Secondly, given that an increase in carbon mineralization (C_{min}) and carbon stabilization (C_{sta}) may be a natural consequence of an increased

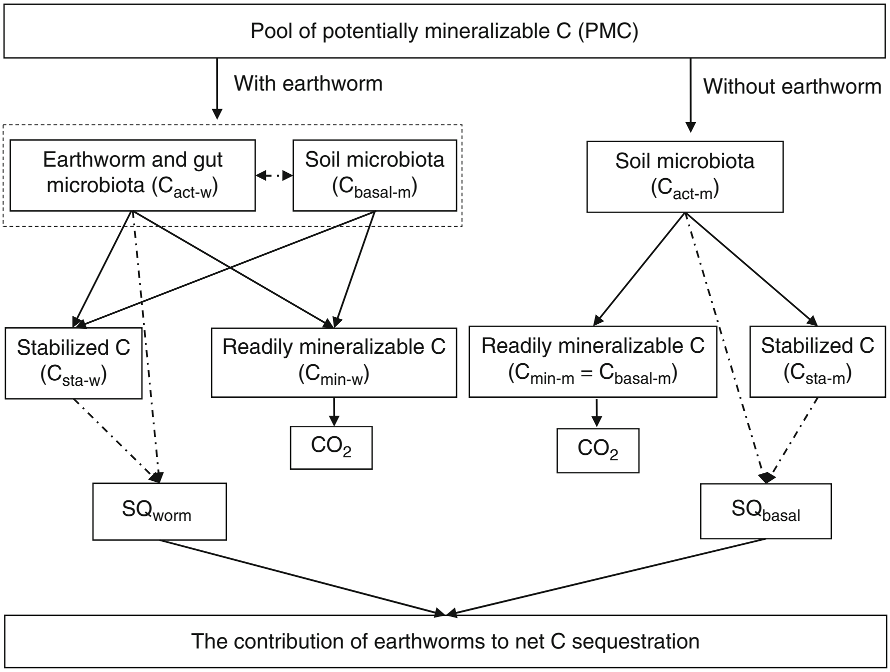

Fig. 11.1 A conceptual model of how earthworms regulate C sequestration. $C_{act\text{-}w}$ and $C_{act\text{-}m}$ refer to the earthworm-activated and soil microbiota-activated mineralizable C, respectively. $C_{min\text{-}w}$ and $C_{sta\text{-}w}$ refer to the pool of readily mineralizable C and pool of stabilized C in soil with earthworms, respectively; $C_{min\text{-}m}$ and $C_{sta\text{-}m}$ refer to the pool of readily mineralizable C and pool of stabilized C, respectively in soil without earthworms. Given that the soil microbiota-induced readily mineralizable C ($C_{min\text{-}m}$) may also be metabolized and/or stabilized by earthworms, $C_{min\text{-}m}$ is also defined as basal C ($C_{basal\text{-}m}$). Note that the value of $C_{min\text{-}m}$ ($C_{basal\text{-}m}$) in a system with and without earthworms may gradually differ as earthworm incubation proceeds. $C_{sta\text{-}w}$ and $C_{act\text{-}w}$ are the differences between C_{sta} and C_{sta} plus C_{min} between soil with and without earthworms, respectively. SQ_{worm} and SQ_{basal} refer to the C sequestration quotient in soil with and without earthworms, respectively. The *single-ended dot-dash lines* represent the major components for the calculation of SQ values. The *double-ended dotted line* indicates possible interactions (This figure was from Zhang et al. (2013))

pool of activated carbon, the pool size of the activated carbon (C_{act}) and its allocation pattern into carbon mineralization and carbon stabilization then determine the net carbon sequestration. Thus, Zhang et al. introduced the new concept of sequestration quotient (SQ, C_{sta}/C_{act}) to quantify the earthworms' impact on the balance of carbon mineralization and carbon stabilization (Fig. 11.1). The study revealed that the presence of earthworms is more likely to create a carbon sink as the carbon stabilized by earthworms outweighs that converted to CO_2 during carbon mineralization, i.e., SQ values are higher in soil with earthworms (Fig. 11.2a, b). Importantly, the patterns of CO_2 emission and net carbon sequestration are predictable by comparing SQ values between treatments with and without earthworms (Fig. 11.2c). Apparently, the concept of SQ could also be used to estimate the contributions of

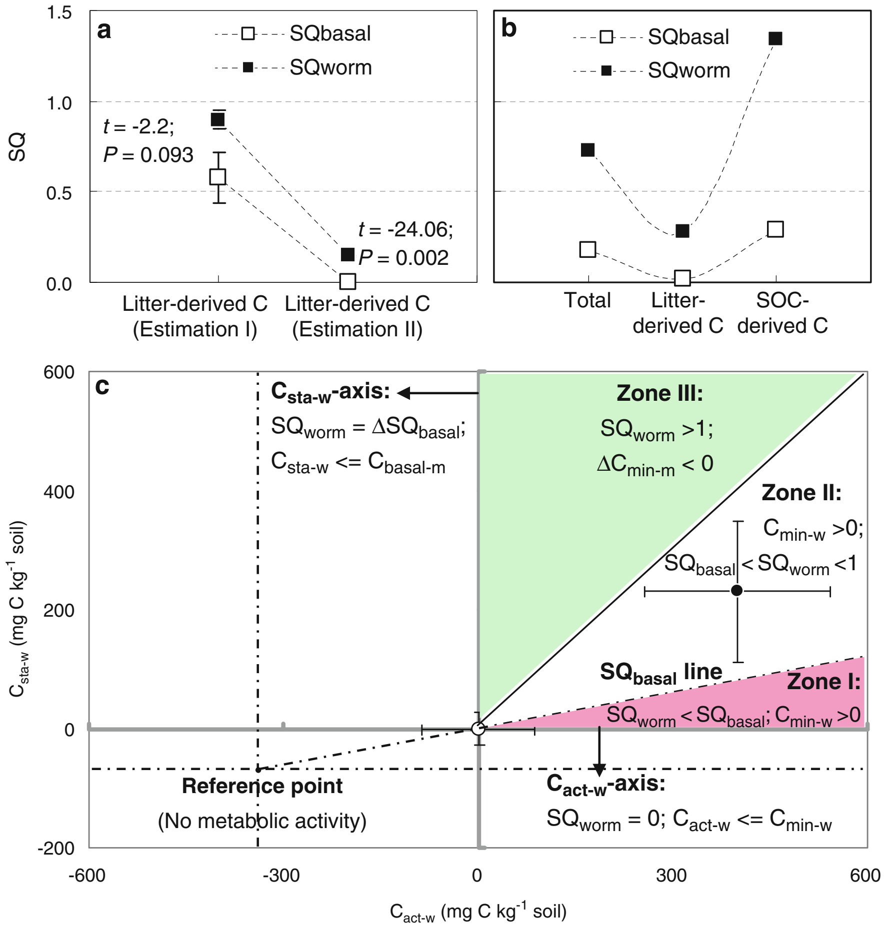

Fig. 11.2 Sequestration quotient and its connection with C sequestration. The sequestration quotient (SQ) in phase II (**a**) (mean ± s.e.m., *n* = 3) and in the literature (**b**), and the conceptual diagram (**c**) showing how to predict the impacts of earthworms on CO_2 emission and net C sequestration with SQ values. The s.e.m. is indicated by error bars. Earthworms converted the PMC into readily mineralizable C, and protected a larger proportion of readily mineralizable C. SQ_{worm} (*closed squares*) and SQ_{basal} (*open squares*) values were calculated to quantify the balances between C mineralization and C stabilization in soil with and without earthworms, respectively. Estimation I: all litter-derived C in soil aggregates were assumed to be stabilized; estimation II: about 17 % of litter-derived C in microaggregates within large macroaggregates and only 8 % of litter-derived C in microaggregates were assumed to be stabilized for soil with and without earthworms, respectively (Bossuyt et al. 2005). In (**c**) the *two dot-dash axes* represent the reference *x*-axis and *y*-axis in control soil without earthworms; the origin of the *dot-dash axes* refers to a reference point of no metabolic activity. The *two bold grey axes* represent the *x*-axis and *y*-axis in soil with earthworms, namely the net effects of earthworms on C activation (C_{act-w}-axis) and C stabilization (C_{sta-w}-axis); Zones I, II and III indicate the three major scenarios of the contribution of earthworms to C sequestration. The open white circle, i.e., the origin of the *bold grey axes* (C_{act-m}, C_{sta-m}), refers to the mean values of C_{act-m} and C_{sta-m} in control soils, i.e., the basal point. The *closed black circle* (C_{act-w}, C_{sta-w}) refers to those values in soils with earthworms. Data are the same as presented in panel (**a**) and (**b**). C_{sta-m} or C_{min-m} and C_{sta-w} or C_{min-w} refer to the soil microbiota-induced and earthworm-induced C_{sta} or C_{min}, respectively. Since part of C_{min-m} may be metabolized and/or stabilized by earthworms, C_{min-m} is also defined as basal C ($C_{basal-m}$). Note that the conversion rate from PMC to C_{min-m} and C_{sta-m} may also be affected by earthworms, thus the value of C_{min-m} ($C_{basal-m}$) in a system with and without earthworms may gradually differ as earthworm incubation proceeds (This figure was from Zhang et al. (2013))

other factors/treatments (not only earthworms) to net soil carbon sequestration and the related nutrient cycling. However, note that the net contributions of earthworms to carbon cycling at ecosystem, regional or global scale are still hard to quantify. The primary difficulty is the response and feedback of other components (e.g., plant growth) associated with earthworms' alteration of the ecosystem are scarcely known. For instance, earthworms interact with plant species and impact plant productivity of the sites, which cause feedback on carbon sequestration at the time scale of years to decades or even longer. It is thus unlikely that a short-term study can determine the actual amount of carbon being sequestered by earthworms in the field. On one hand, the earthworm-stimulated CO_2 emission may be partially offset or even overcompensated by carbon sequestration resulting from plant uptake if net primary productivity (NPP) increases in response to nutrients released by the accelerated mineralization (Edwards and Bohlen 1996). On the other hand, plant productivity may be reduced and thus results in negative feedback on the amount of carbon that earthworms can sequester if a significant proportion of the nutrients that earthworms liberate from leaf litter or SOC is leached away.

In brief, there are five major relationships in the plant-soil system: (1) one component functions as a basic condition (such as platform) which supports other components or processes but its level does not affect the magnitude of those latter components or processes. For example, the role of understory ferns in Eucalyptus plantations of south China is more likely to provide a suitable microenvironment for soil biota rather than as a food resource. (2) One component exerts ascertained impact on other components or processes either positively or negatively. For example, soil microbial biomass increase with soil fertility, while the turnover rate of soil microbes declines with soil fertility. (3) One component affects other components or processes positively through one way and negatively through other ways. For example, nematodes may reduce microbial biomass by grazing but also facilitate the dissemination of soil microbes (Fu et al. 2005); similarly, earthworms can increase carbon mineralization by enhancing carbon activation but decrease the net carbon mineralization by protecting a higher proportion of the newly activated carbon (Zhang et al. 2013). (4) One component affects other components or processes in an undetectable way. For example, as the bacterial-feeding nematode is not only affected by its prey soil bacteria but also by its predators at the same time, the correlation between bacterial-feeding nematodes and soil bacteria may be weak (Wardle and Yeates 1993); however, the contribution of bacteria to bacterial-feeding nematodes cannot be ignored. (5) One component may "trap" most of the energy and nutrient within its own loop and allow small portion of the energy and nutrients to be converted into other components. For example, as bacteria do in the ocean (Jiao and Zheng 2011), soil bacteria may capture most of the labile carbon and recycle it within the bacterial loop; this internal recycling of energy and nutrient is self-serving and not helpful to the development of the whole food web. In contrast, soil fungi are not likely to form such large internal loops but transfer more energy and nutrient to other components.

The summary of these major relationships in the plant-soil system may be a real start that we can investigate the complex system with a holistic approach.

In general, the impact of one component on other components or processes may be only in a certain range. Hence, if the change of one component or process exceeds its threshold, the related components or processes may not change accordingly if the related plant or soil biota does not necessarily evolve to adapt the new situation, or still change accordingly if the related plant or soil biota evolve successfully under such pressure/driver, or even change inversely if the related plant or soil biota cannot sustain normal metabolism. It is also notable that the high spatial and temporal heterogeneity in field soils provides a vast array of opportunity and refuge for soil biota and, thus sustain higher biodiversity and various distinct processes at different scales. Therefore, the field soil system is theoretically more stable or could recover more rapidly than microcosm soil systems in the lab, that is to say a lab microcosm study is likely to overstate the effects. This will be a major obstacle for scaling up the results from a microcosm study to field, regional and global scales. Unfortunately, given that the five major relationships occur together, the actual role of a given component in plant-soil system is hard to separate from the others, especially in field experiments. Microcosm studies in lab still provide a useful approach to quantify selected important processes which may be overridden by other processes in filed. Nevertheless, new techniques are urgently needed to overcome the intrinsic limitations of a reductionist approach. For instance, the DNA stable isotope probing (DNA-SIP) in conjunction with metagenomics is useful to link microbial identity to particular metabolic functions and ecological processes (Chen and Murrell 2010). In addition, the process synthesis-based intact approaches such as the barometric process separation (BaPS) method, which has been proposed to measure soil gross nitrification rate (Ingwersen et al. 1999), and the holistic statistical tools such as Structural Equation Modeling (SEM) (de Vries et al. 2012) are worthy of development.

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