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Review

Microbial communities and their relevance for ecosystem models: Decomposition as a case study

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ABSTRACT

Soil microbial communities are so vastly diverse that complex interactions, which alter ecosystem functions, may occur among microbial species and functional groups. In this review, we explore the empirical evidence for situations when shifts in the community structure of microbes would elicit a change in ecosystem process rates, specifically decomposition, even when microbial biomass remains constant. In particular, we are interested in a subset of these scenarios in which knowledge of microbial community structure would improve model predictions for ecosystem functions. Results from microcosm and field studies indicate that microbial species diversity, functional group diversity, and community composition can all influence ecosystem process rates. The underlying mechanisms that may elicit changes in ecosystem functions from shifts in microbial community structure include evolutionary constraints on microbial trait adaptation, trait correlations, dispersal limitation, and species interactions. The extent of microbial diversity in soils is not known, so it is presently not possible to model all scenarios of microbial community structure shifts. However, by incorporating documented patterns in functional groups that are relevant for a particular ecosystem process and potential relationships between microbial phylogeny and function, the predictive power of process models will be significantly improved. The inclusion of this information into process models is critical for predicting and understanding how ecosystem functions may shift in response to global change.

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1. Introduction

Bacteria and fungi play a significant role in global C and N cycling and are responsible for about 90% of all organic matter decomposition (Swift et al., 1979). Soil microbial communities are many times more diverse than their associated plant and animal communities (Whitman et al., 1998; Hawksworth, 2001), and less than 5% of all microbes have been identified and described (Schleifer, 2004). While it is broadly recognized that microbes are critical for driving soil nutrient cycling, the role of microbial community structure in determining ecosystem process rates is not well characterized.

In ecosystem models, microbial diversity is often considered a 'black box' (Andren and Balandreau, 1999) with rate equations that model inputs and outputs to various pools (e.g., different soil organic matter pools). The community structure of microbes inside the black box is omitted in most process models. These biogeochemical models can be adequate for predicting large-scale cycling of

nutrients such as C and N under stable conditions (Bolker et al., 1998; Schimel et al., 2004; Manzoni and Porporato, 2009). However, future predictions of biosphere-atmosphere fluxes and feedbacks under global change scenarios can differ by magnitudes (Friedlingstein et al., 2006). Part of these discrepancies may lie in the fact that in many instances the diversity of microbial species, functional groups, or both may be important in determining the rates of ecosystem functions, particularly in non-stable environmental conditions. If so, then knowledge of the content of the microbial 'black box' is required for current and future predictions of ecosystem function.

For any given ecosystem, a certain set of taxa can potentially colonize the area via dispersal, migration, or germination. This pool of "potential biota" (θ) is one of the five state factors identified by Jenny as strongly and consistently influencing ecosystem function (Jenny, 1941; Amundson and Jenny, 1997; Fig. 1). The other state factors are climate (cl), topography (r), parent material (p), and time (t). It is important to note that θ is distinct from the community structure of organisms that are actively functioning within an ecosystem. Potential biota, therefore, are not the biota that inhabit an ecosystem at any given time point, but are the biota from the surrounding areas able to colonize the ecosystem. The biota which survive in the ecosystem depends on the other

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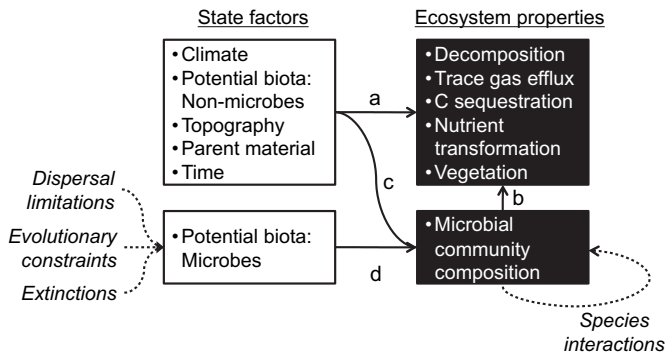


Fig. 1. Conceptual framework for how ecosystem process models should reconsider microbial community structure in order to better predict soil nutrient dynamics. In some cases, microbial community structure does not matter for predicting ecosystem processes (a), and the state factors alone (excluding microbial biota) are sufficient. However, in many other scenarios, microbial community structure must be taken into account (c). To create models with greater predictive power, information from empirical studies needs to be considered regarding when other state factors control microbial communities (b) and how ecological and evolutionary processes constrain microbial communities (d).

properties of the ecosystem (Amundson and Jenny, 1997), analogous to the concept of ‘habitat filtering’ (Keddy, 1992). The role of potential biota has been investigated primarily with respect to plants and animals, and less with microbes (θ_{mic}). In Jenny’s model, ‘community structure’ is an ecosystem property that is determined by θ in combination with other state factors. In other words, cl , r , p , or t serve as environmental filters that determine which of the potential biota occupy an ecosystem.

Using Jenny’s framework, if microbial community structure does not strongly influence other ecosystem properties, then nutrient dynamics could be predicted solely as a function of cl , r , p , t , and potential non-microbial biota (Scenario a, Fig. 1). Hypothetically, this situation could occur if individual microbes were generalists capable of conducting a very large array of critical transformations of nutrients required to maintain ecosystem function across a broad range of environmental conditions (Schimel, 1995). This functional redundancy would alleviate the effect of species shifts. However, physiological trade-offs likely preclude the possibility of such ‘super-organisms’. In addition, robust empirical evidence indicates that key nutrient transformations such as nitrification and nitrogen fixation are conducted by only a subset of microbes using specialized physiological pathways (Yanagi and Yamasato, 1993; de Boer and Kowalchuk, 2001). These transformations are termed ‘narrow’ processes (Schimel, 1995). Thus, it is likely that microbial community structure influences other ecosystem properties under many circumstances (Scenario b, Fig. 1).

Another possibility is that θ_{mic} is expansive, encompassing most microbes—or most functional genes of microbes—within a region or the globe. In this case, microbial community structure could be predicted from cl , θ_{non} (potential non-microbial biota), r , p , and t (Scenario c, Fig. 1), assuming that microbial function does not vary within microbial species across environments (an oversimplification for the purpose of the null hypothesis). Under this scenario, if relationships between microbial community structure and other ecosystem properties (Scenario b) were well understood, then ecosystem models could theoretically predict ecosystem function without explicitly incorporating microbial community structure. This circumstance would be analogous to the paradigm of ‘everything is everywhere, but the environment selects’ first written by Baas-Becking (1934).

If this is not the case, then θ_{mic} could be an important constraint on microbial community structure (Scenario d, Fig. 1). A few mechanisms could limit the extent of θ_{mic} , including dispersal limitations, evolutionary constraints, and local extinctions. In addition, interactions

among taxa within communities could elicit non-linear relationships between microbial community structure and other ecosystem properties.

Under global change scenarios, complex modeling that incorporates parameters for microbial community structure may be needed for predicting some ecosystem functions. However, most process-based models that incorporate microbes are based on simple microbial parameters or functions (McGill et al., 1981; Bosatta and Berendse, 1984), and the percentage of variables in biogeochemical models that incorporate microbial pools has not substantially increased since the 1970s (Manzoni and Porporato, 2009). Thus, a pressing question for global change research and soil biology is: when should models incorporate more complex parameters for microbial community structure? In this review, we address the mechanisms by which θ_{mic} and microbial community structure can influence ecosystem function. In particular, we identify the circumstances under which cl , θ_{non} , r , p , and t are insufficient to predict a subset of key ecosystem properties. Our goal is to facilitate modeling of terrestrial ecosystems so that when the community structure of microbes is relevant, we can improve mechanistic predictions of ecosystem function under global change. Additionally, we provide this review for heuristic purposes so that microbial ecologists can focus on experiments that not only advance the field of soil microbial science, but that can also be useful for integration with modeling efforts. While we recognize that important patterns and processes also occur in marine and aquatic microbial communities (Fuhrman, 2009), here we focus on soil microbes.

A number of reviews have assessed the relationship between soil biodiversity and ecosystem function, exemplifying the broad interest in this subject (Andren and Balandreau, 1999). Several of these reviews highlight the relevance of this topic for humans such as understanding the relationship between soil biodiversity and sustainability in agriculture (Kennedy and Smith, 1995; Giller et al., 1997) and global change (Balsler et al., 2006). Other reviews document patterns across trophic levels in soil food webs (Brussaard et al., 1997; Mikola and Setälä, 1998) and provide assessments of techniques for measuring microbial diversity in soil (Kent and Triplett, 2002). Our review builds upon previous papers to outline both empirically and theoretically when the community structure of microbes is useful in predicting function in ecosystem process models. We do not review all theoretical models (for a recent comprehensive review see (Manzoni and Porporato, 2009)), but rather we highlight models and experimental data that have made significant advancements in our understanding of specific ecosystem processes. We focus on soil microbes, specifically bacteria and fungi. While archaea (Torsvik et al., 2002; Prosser and Nicol, 2008) and soil viruses could be important components to the structure-function relationship (Kimura et al., 2008; Srinivasiah et al., 2008), too few studies exist to incorporate these groups into an extensive review. We also discuss the role of microbial ‘functional groups’, which we broadly define as microbes that perform similar transfers of energy and nutrients. These distinctions can be an exercise in semantics, and we recognize that the delineation of microbes into functional groups depends on the scale of the study being conducted and the nature of the question that is being asked. To illustrate the relevance of microbial community structure in process models, we focus on the specific ecosystem function of decomposition.

2. Review

2.1. Links between ecosystem processes, models, and microbial community structure

2.1.1. Decomposition

Decomposition, which is primarily driven by bacteria and fungi, is second only to photosynthesis in driving the quantity of C that is

cycled through ecosystems. The complexities involved in the transfer of soil organic matter into its inorganic constituents and living biomass has rendered it one of the most difficult processes to model and simulate, despite the fact that the predominant factors controlling decomposition were identified in 1929 (Tenney and Waksman, 1929). These factors, including substrate chemical composition, nitrogen availability for decomposer microorganisms, the community structure of decomposer organisms, and abiotic environmental conditions, are still applicable to decomposition studies today, but despite sophisticated modeling efforts, uncertainties in parameter calibrations and underlying assumptions persist.

A major challenge for modeling decomposition is deciding which microbial parameters and mechanisms are important for predicting soil nutrient fluxes. Most models of decomposition are process-based, using first order kinetics to describe large-scale flows of C through the various trophic pathways (Yadav and Malanson, 2007). The first attempt to model decomposition of organic matter with explicit consideration of the microbial community assumed that decomposition rate was proportional to the growth rate of the decomposers (Parnas, 1975). Microbial biomass has continued to be an important component in decomposition models, and about 70% of contemporary models include at least one microbial biomass parameter (Manzoni and Porporato, 2009).

However, microbial biomass alone may not always accurately predict fluxes of nutrients from plant litter decay, as experimental evidence indicates that the community structure of the microbes comprising the biomass may also be important. For example, using reciprocal transplants of soil cores between grasslands and conifer ecosystems, Balsler and Firestone (2005) showed that microbial community structure was correlated to N-mineralization and CO₂ production, but that microbial biomass and environmental variables were not the driving factors in functional differences. Another scenario in which microbial community structure may be more important than microbial biomass in decomposition is in ectomycorrhizal-dominated forest communities. Ectomycorrhizal fungi can comprise the majority of total microbial biomass in some forests (Wallander et al., 2001), and decomposition is often slowed when ectomycorrhizal abundance increases (Singer and Araujo, 1979; Read, 1991; Read and Perez-Moreno, 2003). Ectomycorrhizal fungi could drive this pattern because they receive most of their C from their host tree, negating the need to breakdown C-rich compounds. In fact, ectomycorrhizal fungi may suppress other heterotrophic decomposers (Gadgil and Gadgil, 1971, 1975), although support for this mechanism has been primarily obtained in the laboratory (Olsson et al., 1996; Lindahl et al., 1999). Since heath and boreal forests (Read et al., 2004), many temperate forests (Read, 1991), and some tropical forests are dominated by ectomycorrhizal trees (Alexander et al., 1992; Torti et al., 2001; Henkel et al., 2002), understanding the precise mechanisms for slowed decomposition in these forests and incorporating this information into models may be globally relevant.

Empirical data also suggest that bacterial and fungal species richness may be important for predicting decomposition, although these parameters have not been incorporated into contemporary modeling efforts. In one study, the progressive reduction in microbial diversity from filtration and serial dilutions of forest soil caused parallel reductions in metabolic activity (Salonius, 1981). In controlled microcosm experiments rates of respiration and decomposition tend to rise as microbial species richness increases. However, this relationship often plateaus at the higher end of the richness continuum. For example, in a study in which richness of bacteria varied between 1 and 72 species, respiration rates accelerated with increasing richness, but more subtly after the addition of 18 species (Bell et al., 2005). Similarly, cellulose decomposition increased linearly as numbers of cellulolytic bacterial species increased from one to four, but not from four to eight (Wohl et al., 2004). In another experiment using

a diversity gradient of 1–43 saprotrophic fungi isolated from humus, the same pattern emerged: respiration increased with increasing fungal species, but only at the species poor end (Setälä and McLean, 2004). These results imply that there may be functional redundancy in the decomposition of some plant-derived substrates at higher levels of species richness, but that consideration of microbial community structure is critical for process rates at the species poor end of the richness continuum. An alternative interpretation is that in these controlled microcosm experiments the species pools were so drastically reduced, that the microbes responsible for the further breakdown of litter were not present. Further empirical work needs to resolve these uncertainties before implementation into models occurs, but these data suggest that in some cases species richness, rather than just biomass, matters for decomposition.

The most comprehensive model of decomposition that incorporates microbes is that of Moorhead and Sinsabaugh (2006). In this model, three guilds of microbial decomposers are separately modeled, based on their suites of target compounds (i.e., labile, moderate, or recalcitrant), and external constraints on their process rates are incorporated. For instance, the guild that targets labile compounds is stimulated by N availability, whereas the guild targeting recalcitrant compounds is inhibited. The incorporation of microbial guilds had only a moderate influence on predicted rates of decomposition. It was challenging however, to parameterize traits of microbial guilds, such as C uptake rate and substrate use efficiency. Likewise, validation was difficult because shifts in these microbial guilds have rarely been measured concurrently with decomposition rate (Moorhead and Sinsabaugh, 2006). Ultimately, parameterization and validation of this model will require field-based measurements of the abundance of the three guilds during decomposition, as well as the N-sensitivity of those guilds.

2.2. Directions for future research: closing the gaps

Which decomposition processes would be better modeled through incorporation of microbial community structure? This approach may be particularly important when predicting turnover of more recalcitrant compounds, such as at later stages of decomposition or during breakdown of soil organic matter (Table 1). The enzymes involved in the breakdown of the more recalcitrant compounds, such as polyphenoloxidase and peroxidases, are restricted to certain groups of microbes such as white- and soft-rot fungi (Berg and McClaugherty, 2003). In other words, decomposition of recalcitrant compounds constitutes a 'narrow process', which should be sensitive to community structure (sensu Schimel, 1995). Specifically, the rate-limiting variables for recalcitrant C

Table 1

Three main phases of decomposition have frequently been identified in relation to the dominant organic compounds present. As a result of the varying levels of recalcitrance, the main microbial decomposers are different for each decomposition phase. The prediction is that the importance of microbial community structure will increase as decomposition progresses, since fewer microbes possess enzymes for the degradation of the more recalcitrant organic compounds.

Decomposition phase	Dominant organic components	Main microbial decomposers	Predicted importance of microbial community structure
Early	soluble sugars	Many species of fungi and bacteria	small
Mid	cellulose, hemicellulose	Fungi (brown-rot, soft-rot, some white-rot); some bacterial species	important, but some functional redundancy
Late	lignin	Fungi (white-rot, soft-rot); few bacteria	very important

pools may be the enzymatic capabilities of the resident microbial community (Fontaine and Barot, 2005).

In contrast, microbial community structure may be less important for turnover of more labile materials such as soluble sugars and amino acids. A broad phylogeny of taxa are capable of taking up and metabolizing simpler compounds. For instance, most microbes are capable of degrading glucose via glycolysis (Berg and McLaugherty, 2003). Rates of turnover for some labile substrates such as amino acids do not vary greatly across ecosystems, even though microbial communities are likely to differ (Jones et al., 2009a). Moreover, a significant portion of soluble sugars can be leached from plant litter, a process which is not microbially-mediated (Berg and McLaugherty, 2003).

If microbial community structure is more important for predicting dynamics of recalcitrant compounds than labile compounds, then this information could be used to focus modeling efforts. The use of multiple C pools was made popular in the well-known CENTURY model, which distinguished among “active”, “slow” and “passive” soil organic matter (Parton et al., 1987). Similar frameworks have been incorporated in subsequent models with organic carbon pools differentiated by age or recalcitrance (Potter et al., 1993; Gignoux et al., 2001; Bruun et al., 2004). These pools correspond to stages of decomposition: 1) early stages, during which fast-growing microbes consume soluble sugars with significant leaching occurring simultaneously; 2) mid-stages with partly decomposed litter, in which cellulose and hemicellulose form the main organic matter constituents; and 3) near-humus, later stages when recalcitrant compounds like lignin predominate. The pools of soil C that dominate the various stages of organic matter decomposition range widely in their chemical composition, recalcitrance, and residence times (Berg and McLaugherty, 2003). Some soil C is cycled within hours and days, whereas other soil C can persist for more than 1000 years (Paul et al., 2001). Within these frameworks, microbial community structure could be incorporated into the “slow” or “passive” pools as appropriate.

2.3. Testing the underlying mechanisms that may alter θ_{mic}

Current models of biogeochemical cycling have the ability to simulate large-scale fluxes of nutrients under relatively stable conditions (Lawrence et al., 2009; Manzoni and Porporato, 2009). The current challenge is applying these models to shifting state factors, particularly under scenarios of global change. One major limitation in accomplishing this task is that we do not fully understand the mechanisms underlying these large-scale nutrient fluxes and in particular, under what circumstances microbial community structure is important. Only when the mechanisms are sufficiently evaluated and able to be generalized can we begin to incorporate them into soil process models. Here, we review several mechanisms that may elicit patterns linking microbial community structure with ecosystem function.

When altered microbial community structure results in a decrease in ecosystem function, there is an implication that a potential niche has not been filled. What mechanisms would lead to this circumstance? One mechanism that may be responsible is evolutionary constraints on trait adaptation. In other words, in a community of microbes in which an important functional group has been lost, the remaining microbes may be genetically unable to adapt to perform the missing function. Genes that are functionally related tend to be clustered in the genome, particularly in prokaryotes (Overbeek et al., 1999; Ling et al., 2009). Therefore, microbes may not be able to fill a new niche and compensate for a lost ecosystem function, because their own gene clusters are constrained to maintain different functions. This mechanism may be especially relevant for situations in which narrow processes have been lost. There is a major gap in knowledge between the sequences of microbial genomes and

gene functions, so it is still unclear to what extent functional genes involved in most ecosystem functions are correlated. This is clearly demonstrated in *Aspergillus nidulans*, which is predicted to have 9451 open reading frames (regions that can code for proteins), but less than 10% of these coding regions have been assigned a function (David et al., 2008). Thus, an important direction for future research is determining the identity of functional genes, assessing which functional processes are evolutionarily constrained (Koonin and Wolf, 2008), and which traits are correlated. This information will inform mechanistic models attempting to predict when diversity effects will be observed with microbial community structure shifts.

Another mechanism that may elicit microbial community structure-ecosystem function effects in field conditions is dispersal limitation of microbes. If a particular functional group of microbes becomes extinct in a system, then they should be quickly replaced if dispersal limitation does not constrain their recolonization. However, it is not fully known which microbes are dispersal-limited and which are ubiquitous (Martiny et al., 2006; Taylor et al., 2006; Jenkins et al., 2007). Negative interactions among microbial taxa could also result in diversity effects on ecosystem function. In classical competition theory, when organisms have similar ecological traits, competition for one resource either results in the maintenance of diversity via niche differentiation or a loss in diversity through extinction of the inferior competitor (Gause, 1934). There is a large body of research demonstrating competition among microbes. These competitive interactions could alter ecosystem process rates because the superior competitor is not always the most efficient metabolizer. Exploitation competition, where one microbe takes up a resource faster than another, rendering it unavailable to other microbes, could result in incomplete exploitation of a second resource. Microbes that participate in allelopathy could also suppress the faster and more efficient microbes, or they could suppress microbes that are also important in different nutrient transformations. For example, ‘cheater’ microbes, which do not produce their own enzymes, but instead intercept the products produced by extracellular enzymes of other microorganisms, could suppress proliferation of enzyme-producers (Allison, 2005). Competition between decomposer fungi can be altered by water availability (Griffith and Boddy, 1991; Lee and Magan, 1999), temperature (Schoeman et al., 1996), and elevated CO₂ (Boddy, 2000), which indicates that the effects of global changes on ecosystems may be mediated through the alteration of negative species interactions.

Competitive interactions between bacteria and fungi are also important (Moller et al., 1999; de Boer et al., 2005; de Boer and Van der Wal, 2008). Bacteria and fungi can compete for chemical compounds in soils, and they can exude inhibitory compounds targeted at each other (de Boer and Van der Wal, 2008). The success of fungi or bacteria in accessing nutrients seems to depend on a variety of environmental variables such as soil nutrient status, moisture, pH, and disturbance (de Vries et al., 2006). These interactions are imperative to understand in predicting nutrient cycling, as the relative abundance of bacteria versus fungi can affect the quantity and quality of C that is produced (Fischer et al., 2006). Pathways of nutrient flows are also different for fungi and bacteria (Moore et al., 1988), and there is some evidence from modeling that when disturbance shifts the balance from fungi to bacteria (or vice versa), ecosystem processes are significantly modified (Moore et al., 2005).

In other instances, positive species interactions such as mutualism and facilitation may lead to non-additive increases in nutrient transformations. A classic example of this scenario occurs during the decomposition of plant matter. Certain groups of fungi and bacteria can only persist when simple compounds are liberated by other groups of microbes targeting recalcitrant compounds such as lignin (Frankland, 1969; Wardle, 2006). Without this cross-feeding, decomposition would be significantly slowed. Synergistic interactions between mycorrhizal fungi and bacterial species also play

important roles in the establishment and functioning of the mycorrhizal mutualism. ‘Helper bacteria’ often facilitate fungal colonization of the plant root (Garbaye, 1994) and germination of mycorrhizal fungal spores (Ali and Jackson, 1989). Similarly, facilitation of nodulation, mycorrhizal colonization, and plant production has been observed as a result of interactions among AM fungi, *Rhizobium* nitrogen-fixing bacteria, and diazotroph bacteria (Biró et al., 2000). Positive interactions have also been found between different types of mycorrhizal fungi. *Eucalyptus* trees, which can be colonized by both AM and EM fungi, can produce more biomass when both groups of fungi colonize their roots (Chen et al., 2000). Together, these studies indicate that positive interactions between microbial species and different functional groups can significantly affect process rates, and should be looked at further in both experimental and theoretical explorations of soil nutrient dynamics.

2.3.1. Experimental approaches, challenges, and directions for future research

Compared to microcosm experiments, field studies that manipulate microbial community structure are more difficult to implement and interpret due to the enormous complexity of soils. Several studies highlight correlations between shifts in microbial community structure and ecosystem function (Waldrop et al., 2000; Snajdr et al., 2008; Hsu and Buckley, 2009), but few are able to directly control for species numbers, microbial abundance, or functional groups.

Nonetheless, several field studies have used creative methods to control for community structure. One is the use of biocides and selective inhibitors to determine effects of excluding specific microbial groups on process rates. In one study, bacteria, fungi, and microarthropods were each selectively inhibited, and they were found to contribute to different aspects of ecosystem functioning (Beare et al., 1992). Fungi contributed more to decomposition of surface litter, bacteria to decomposition of buried litter, and microarthropods to N dynamics on surface litter. Thus, interactions across trophic groups altered plant litter decomposition and N dynamics (Beare et al., 1992). Another study that used selective inhibition to exclude nitrifiers found that C cycling and N dynamics in vegetation and soil were dramatically altered (Austin et al., 2006). These techniques of selective inhibition have great potential for elucidating the effects of altering microbial community structure in situ, although only larger functional groups of microbes can be targeted.

When species diversity of the general microbial community is destructively reduced (without targets) by fumigation or serial dilutions, the patterns are difficult to interpret. In one study, a reduction in soil biodiversity resulted in differential effects on ecosystem function (Griffiths et al., 2000). Some functions such as nitrification, denitrification, and methane oxidation decreased with loss of soil diversity, but other functions such as decomposition of plant residues increased with decreasing diversity. Another fumigation experiment also found that alteration of microbial community structure (including bacteria and fungi) resulted in complex patterns (Degens, 1998). Fumigated soils had reduced capacity to break down amino acids and carbohydrates, but increased potential to degrade organic acids. Despite our inability to understand all of the mechanisms involved in altered microbial structure and function by non-targeted destruction, this technique may be a more realistic approximation of the consequences associated with global change. Coupled with more controlled laboratory studies, destructive field studies may be a valuable tool for predicting microbial resilience to disturbances.

3. Conclusions

The equations for many models of biogeochemical cycling fit empirical data with a certain degree of accuracy for large-scale fluxes,

but often with parsimonious functions where microbial community structure is either implicit or highly simplified. It is evident from the literature that there are many scenarios that require consideration of microbial community structure in predicting ecosystem process rates. We are just beginning to characterize the overwhelming diversity of soil microbes by using DNA sequencing, so our abilities to link all components of community structure to function are not presently possible (Jones et al., 2009b). However, results from field and microcosm manipulations indicate that microbial species diversity, functional diversity, and abundance can all influence soil nutrient dynamics. Iterations of models at smaller scales with more detailed microbial mechanisms may be essential for predicting decomposition dynamics and other ecosystem processes in changing environments, but have rarely been tested (Lawrence et al., 2009).

Many studies document shifts in microbial community structure in response to global changes such as soil warming (Zogg et al., 1997; Allison and Treseder, 2008), N amendment (Allison et al., 2007; Treseder, 2008), and elevated concentrations of greenhouse gases (Treseder, 2004; Carney et al., 2007). However, many uncertainties remain regarding microbe–climate feedbacks (Bardgett et al., 2008; Pendall et al., 2008), as few experiments have examined the interactions of multiple climate drivers on microbial functional responses. The importance of understanding how microbial community structure changes will affect functions such as decomposition cannot be overestimated. Whether or not C is stored or respired under multifactor global changes may determine whether or not microbial–climate feedbacks are positive or negative (Davidson and Janssens, 2006). Disentangling the role of extrinsic state factors and microbial mechanisms in driving soil nutrient fluxes is imperative for predicting ecosystem processes under future global change scenarios. While microcosm studies may miss important interactions and non-additive effects present in field settings, they provide valuable mechanistic information for potential patterns and processes under controlled conditions. In order to better inform process-based models, we recommend the development of more highly controlled field experiments in which microbial community composition can be directly and precisely manipulated. We suggest that for processes where mechanisms can be understood and experimentally explored, modeling efforts should be coupled with our empirical understanding of the mechanisms. For broad processes, such as CO₂ efflux from soil where separating root and microbial contributions is extremely challenging (Hanson et al., 2000), microbial structure may be less important.

References

- Alexander, I., Ahmad, N., Lee, S.S., 1992. The role of mycorrhizas in the regeneration of some Malaysian forest trees. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 335, 379–388.
- Ali, N.A., Jackson, R.M., 1989. Stimulation of germination of spores of some ectomycorrhizal fungi by other microorganisms. *Mycological Research* 93, 182–186.
- Allison, S.D., 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters* 8, 626–635.
- Allison, S.D., Hanson, C.A., Treseder, K.K., 2007. Nitrogen fertilization reduces diversity and alters community structure of active fungi in boreal ecosystems. *Soil Biology and Biochemistry* 39, 1878–1887.
- Allison, S.D., Treseder, K.K., 2008. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology* 14, 2898–2909.
- Amundson, R., Jenny, H., 1997. On a state factor model of ecosystems. *Bioscience* 47, 536–543.
- Andren, O., Balandreau, J., 1999. Biodiversity and soil functioning – from black box to can of worms? *Applied Soil Ecology* 13, 105–108.
- Austin, A.T., Sala, O.E., Jackson, R.B., 2006. Inhibition of nitrification alters carbon turnover in the Patagonian steppe. *Ecosystems* 9, 1257–1265.
- Baas-Becking, L.G.M., 1934. *Geobiologie of Inleiding Tot de Milieukunde*. Van Stockkum & Zoon, The Hague, 263 pp.
- Balser, T.C., McMahon, K.D., Bart, D., Bronson, D., Coyle, D.R., Craig, N., Flores-Mangual, M.L., Forshay, K., Jones, S.E., Kent, A.E., Shade, A.L., 2006. Bridging the

- gap between micro – and macro-scale perspectives on the role of microbial communities in global change ecology. *Plant and Soil* 289, 59–70.
- Balser, T.C., Firestone, M.K., 2005. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. *Biogeochemistry* 73, 395–415.
- Bardgett, R.D., Freeman, C., Ostle, N.J., 2008. Microbial contributions to climate change through carbon cycle feedbacks. *Isme Journal* 2, 805–814.
- Beare, M.H., Parmelee, R.W., Hendrix, P.F., Cheng, W., Coleman, D.C., Crossley, D.A., 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecological Monographs* 62, 569–591.
- Bell, T., Newman, J.A., Silverman, B.W., Turner, S.L., Lilley, A.K., 2005. The contribution of species richness and composition to bacterial services. *Nature* 436, 1157–1160.
- Berg, B., McClaugherty, C., 2003. *Plant Litter Decomposition, Humus Formation, Carbon Sequestration*. Springer-Verlag, Germany, 286 pp.
- Biró, B., Koves-Pechy, K., Voros, I., Takacs, T., Eggenberger, P., Strasser, R.J., 2000. Interrelations between *Azospirillum* and *Rhizobium* nitrogen-fixers and arbuscular mycorrhizal fungi in the rhizosphere of alfalfa in sterile, AMF-free or normal soil conditions. *Applied Soil Ecology* 15, 159–168.
- Boddy, L., 2000. Interspecific combative interactions between wood-decaying basidiomycetes. *Fems Microbiology Ecology* 31, 185–194.
- de Boer, W., Folman, L.B., Summerbell, R.C., Boddy, L., 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. *Fems Microbiology Reviews* 29, 795–811.
- de Boer, W., Kowalchuk, G.A., 2001. Nitrification in acid soils: micro-organisms and mechanisms. *Soil Biology and Biochemistry* 33, 853–866.
- de Boer, W., Van der Wal, A., 2008. Interactions between saprotrophic basidiomycetes and bacteria. In: Boddy, L., Frankland, J.C., Van West, P. (Eds.), *Ecology of Saprotrophic Basidiomycetes*. Elsevier Ltd., Oxford, UK, pp. 143–153.
- Bolker, B.M., Pacala, S.W., Parton, W.J., 1998. Linear analysis of soil decomposition: insights from the century model. *Ecological Applications* 8, 425–439.
- Bosatta, E., Berendse, F., 1984. Energy or nutrient regulation of decomposition: implications for the mineralization-immobilization response to perturbations. *Soil Biology and Biochemistry* 16, 63–67.
- Brussaard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P., Fragoso, C., Freckman, D.W., Gupta, V., Hattori, T., Hawksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Rusek, J., Soderstrom, B., Tiedje, J.M., Virginia, R.A., 1997. Biodiversity and ecosystem functioning in soil. *Ambio* 26, 563–570.
- Bruun, S., Six, J., Jensen, L.S., 2004. Estimating vital statistics and age distributions of measurable soil organic carbon fractions based on their pathway of formation and radiocarbon content. *Journal of Theoretical Biology* 230, 241–250.
- Carney, K.M., Hungate, B.A., Drake, B.G., Megonigal, J.P., 2007. Altered soil microbial community at elevated CO₂ leads to loss of soil carbon. *Proceedings of the National Academy of Sciences of the United States of America* 104, 4990–4995.
- Chen, Y.L., Brundrett, M.C., Dell, B., 2000. Effects of ectomycorrhizas and vesicular-arbuscular mycorrhizas, alone or in competition, on root colonization and growth of *Eucalyptus globulus* and *E. urophylla*. *New Phytologist* 146, 545–556.
- David, H., Ozelik, I.S., Hofmann, G., Nielsen, J., 2008. Analysis of *Aspergillus nidulans* metabolism at the genome-scale. *Bmc Genomics* 9, 15.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173.
- Degens, B.P., 1998. Decreases in microbial functional diversity do not result in corresponding changes in decomposition under different moisture conditions. *Soil Biology and Biochemistry* 30, 1989–2000.
- Fischer, H., Mille-Lindblom, C., Zwirrmann, E., Tranvik, L.J., 2006. Contribution of fungi and bacteria to the formation of dissolved organic carbon from decaying common reed (*Phragmites australis*). *Archiv Fur Hydrobiologie* 166, 79–97.
- Fontaine, S., Barot, S., 2005. Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecology Letters* 8, 1075–1087.
- Frankland, J.C., 1969. Fungal decomposition of bracken petioles. *Journal of Ecology* 57, 25–36.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., Zeng, N., 2006. Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *Journal of Climate* 19, 3337–3353.
- Fuhrman, J.A., 2009. Microbial community structure and its functional implications. *Nature* 459, 193–199.
- Gadgil, R.L., Gadgil, G.D., 1971. Mycorrhiza and litter decomposition. *Nature* 233, 133.
- Gadgil, R.L., Gadgil, P.D., 1975. Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. *New Zealand Journal of Forest Science* 5, 35–41.
- Garbaye, J., 1994. Helper bacteria – a new dimension to the mycorrhizal symbiosis. *New Phytologist* 128, 197–210.
- Gause, G.F., 1934. *The struggle for existence*. The Williams & Wilkins company, Baltimore, 176 pp.
- Gignoux, J., House, J., Hall, D., Masse, D., Nacro, H.B., Abbadie, L., 2001. Design and test of a generic cohort model of soil organic matter decomposition: the SOMKO model. *Global Ecology and Biogeography* 10, 639–660.
- Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M.N., Swift, M.J., 1997. Agricultural intensification, soil biodiversity and agroecosystem function. *Applied Soil Ecology* 6, 3–16.
- Griffith, G.S., Boddy, L., 1991. Fungal decomposition of attached angiosperm twigs. IV. Effect of water potential on interactions between fungi on agar and in wood. *New Phytologist* 117, 633–641.
- Griffiths, B.S., Ritz, K., Bardgett, R.D., Cook, R., Christensen, S., Ekelund, F., Sorensen, S.J., Baath, E., Bloem, J., de Ruiter, P.C., Dolfing, J., Nicolardot, B., 2000. Ecosystem response of pasture soil communities to fumigation-induced microbial diversity reductions: an examination of the biodiversity-ecosystem function relationship. *Oikos* 90, 279–294.
- Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48, 115–146.
- Hawksworth, D.L., 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. *Mycological Research* 105, 1422–1432.
- Henkel, T.W., Terborgh, J., Vilgalys, R.J., 2002. Ectomycorrhizal fungi and their leguminous hosts in the Pakaraima Mountains of Guyana. *Mycological Research* 106, 515–531.
- Hsu, S.F., Buckley, D.H., 2009. Evidence for the functional significance of diazotroph community structure in soil. *Isme Journal* 3, 124–136.
- Jenkins, D.G., Brescacin, C.R., Duxbury, C.V., Elliott, J.A., Evans, J.A., Grablow, K.R., Hillegass, M., Lyono, B.N., Metzger, G.A., Olandese, M.L., Pepe, D., Silvers, G.A., Suresch, H.N., Thompson, T.N., Trexler, C.M., Williams, G.E., Williams, N.C., Williams, S.E., 2007. Does size matter for dispersal distance? *Global Ecology and Biogeography* 16, 415–425.
- Jenny, H., 1941. *Factors of Soil Formation*. McGraw-Hill, New York, 281 pp.
- Jones, D.L., Kielland, K., Sinclair, F.L., Dahlgren, R.A., Newsham, K.K., Farrar, J.F., Murphy, D.V., 2009a. Soil organic nitrogen mineralization across a global latitudinal gradient. *Global Biogeochemical Cycles* 23, 5.
- Jones, R.T., Robeson, M.S., Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009b. A comprehensive survey of soil acidobacterial diversity using pyrosequencing and clone library analyses. *Isme Journal* 3, 442–453.
- Keddy, P.A., 1992. Assembly and response rules – 2 goals for predictive community ecology. *Journal of Vegetation Science* 3, 157–164.
- Kennedy, A., Smith, K., 1995. Soil microbial diversity and the sustainability of agricultural soils. *Plant and Soil* 170, 75–86.
- Kent, A.D., Triplett, E.W., 2002. Microbial communities and their interactions in soil and rhizosphere ecosystems. *Annual Review of Microbiology* 56, 211.
- Kimura, M., Jia, Z.J., Nakayama, N., Asakawa, S., 2008. Ecology of viruses in soils: past, present and future perspectives. *Soil Science and Plant Nutrition* 54, 1–32.
- Koonin, E.V., Wolf, Y.I., 2008. Genomics of bacteria and archaea: the emerging dynamic view of the prokaryotic world. *Nucleic Acids Research* 36, 6688–6719.
- Lawrence, C.R., Neff, J.C., Schimel, D.P., 2009. Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. *Soil Biology and Biochemistry*. doi:10.1016/j.soilbio.2009.06.016.
- Lee, H.B., Magan, N., 1999. Environmental factors and nutritional utilization patterns affect niche overlap indices between *Aspergillus ochraceus* and other spoilage fungi. *Letters in Applied Microbiology* 28, 300–304.
- Lindahl, B., Stenlid, J., Olsson, S., Finlay, R., 1999. Translocation of P-32 between interacting mycelia of a wood-decomposing fungus and ectomycorrhizal fungi in microcosm systems. *New Phytologist* 144, 183–193.
- Ling, X., He, X., Xin, D., 2009. Detecting gene clusters under evolutionary constraint in a large number of genomes. *Bioinformatics* 25, 571–577.
- Manzoni, S., Porporato, A., 2009. Soil carbon and nitrogen mineralization: theory and models across scales. *Soil Biology and Biochemistry* 41, 1355–1379.
- Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., Horner-Devine, M.C., Kane, M., Krumhins, J.A., Kuske, C.R., Morin, P.J., Naeem, S., Ovreas, L., Reysenbach, A.L., Smith, V.H., Staley, J.T., 2006. Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology* 4, 102–112.
- McGill, W.B., Hunt, H.W., Woodmansee, R.G., Reuss, J.O., 1981. A model of the dynamics of carbon and nitrogen in grassland soils. In: Clark, F.E., Rosswall, T.H. (Eds.), *Terrestrial Nitrogen Cycles*. Ecological Bulletin, Stockholm, pp. 49–116.
- Mikola, J., Setälä, H., 1998. Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. *Oikos* 83, 180–194.
- Moller, J., Miller, M., Kjoller, A., 1999. Fungal-bacterial interaction on beech leaves: influence on decomposition and dissolved organic carbon quality. *Soil Biology and Biochemistry* 31, 367–374.
- Moore, J.C., Walter, D.E., Hunt, H.W., 1988. Arthropod regulation of microbiota and mesobiota in belowground detrital food webs. *Annual Review of Entomology* 33, 419–439.
- Moore, J.C., McCann, K., de Ruiter, P.C., 2005. Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. *Pedobiologia* 49, 499–510.
- Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. *Ecological Monographs* 76, 151–174.
- Olsson, P.A., Chalot, M., Baath, E., Finlay, R.D., Soderstrom, B., 1996. Ectomycorrhizal mycelia reduce bacterial activity in a sandy soil. *Fems Microbiology Ecology* 21, 77–86.
- Overbeek, R., Fonstein, M., D'Souza, M., Pusch, G.D., Maltsev, N., 1999. The use of gene clusters to infer functional coupling. *Proceedings of the National Academy of Sciences of the United States of America* 96, 2896–2901.
- Parnas, H., 1975. Model for decomposition of organic material by microorganisms. *Soil Biology and Biochemistry* 7, 161–169.

- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic-matter levels in Great-Plains grasslands. *Soil Science Society of America Journal* 51, 1173–1179.
- Paul, E.A., Collins, H.P., Leavitt, S.W., 2001. Dynamics of resistant soil carbon of midwestern agricultural soils measured by naturally occurring C-14 abundance. *Geoderma* 104, 239–256.
- Pendall, E., Rustad, L., Schimel, J., 2008. Towards a predictive understanding of belowground process responses to climate change: have we moved any closer? *Functional Ecology* 22, 937–940.
- Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A., Klooster, S.A., 1993. Terrestrial ecosystem production – a process model based on global satellite and surface data. *Global Biogeochemical Cycles* 7, 811–841.
- Prosser, J.I., Nicol, G.W., 2008. Relative contributions of archaea and bacteria to aerobic ammonia oxidation in the environment. *Environmental Microbiology* 10, 2931–2941.
- Read, D.J., 1991. Mycorrhizas in ecosystems. *Experientia* 47, 376–391.
- Read, D.J., Leake, J.R., Perez-Moreno, J., 2004. In: *Mycorrhizal Fungi as Drivers of Ecosystem Processes in Heathland and Boreal Forest Biomes*. Natl Research Council Canada, pp. 1243–1263.
- Read, D.J., Perez-Moreno, J., 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* 157, 475–492.
- Salonius, P.O., 1981. Metabolic capabilities of forest soil microbial populations with reduced species diversity. *Soil Biology and Biochemistry* 13 1–8.
- Schimel, J., 1995. Ecosystem consequences of microbial diversity and community structure. In: Chapin, F.S., Korner, C. (Eds.), *Arctic and Alpine Biodiversity: Patterns, Causes, and Ecosystem Consequences*. Springer-Verlag, Berlin, Germany.
- Schimel, J.P., Bennett, J., Fierer, N., 2004. Microbial community composition and soil N cycling: is there really a connection?. In: 2003 Annual Symposium: Soil biodiversity and function. British Ecological Society, Lancaster, UK.
- Schleifer, K.H., 2004. Microbial diversity: facts, problems and prospects. *Systematic and Applied Microbiology* 27, 3–9.
- Schoeman, M.W., Webber, J.F., Dickinson, D.J., 1996. The effect of diffusible metabolites of *Trichoderma harzianum* on *in vitro* interactions between basidiomycete isolates at two different temperature regimes. *Mycological Research* 100, 1454–1458.
- Setälä, H., McLean, M.A., 2004. Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. *Oecologia* 139, 98–107.
- Singer, R., Araujo, I.d.J.d.S., 1979. Litter decomposition and ectomycorrhizas in Amazonian forests. *Acta Amazonica* 9, 25–41.
- Snajdr, J., Valaskova, V., Merhautova, V., Herinkova, J., Cajthaml, T., Baldrian, P., 2008. Spatial variability of enzyme activities and microbial biomass in the upper layers of *Quercus petraea* forest soil. *Soil Biology and Biochemistry* 40, 2068–2075.
- Srinivasiah, S., Bhavsar, J., Thapar, K., Liles, M., Schoenfeld, T., Wommack, K.E., 2008. Phages across the biosphere: contrasts of viruses in soil and aquatic environments. *Research in Microbiology* 159, 349–357.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in terrestrial ecosystems*. Blackwell Scientific Publications, Oxford, 384 pp.
- Taylor, J.W., Turner, E., Townsend, J.P., Dettman, J.R., Jacobson, D., 2006. Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. *Philosophical Transactions of the Royal Society B-Biological Sciences* 361, 1947–1963.
- Tenney, F.G., Waksman, S.A., 1929. Composition of natural organic materials and their decomposition in the soil: IV. The nature and rapidity of decomposition of the various organic complexes in different plant materials, under aerobic conditions. *Soil Science* 28, 55–84.
- Torsvik, V., Ovreaas, L., Thingstad, T.F., 2002. Prokaryotic diversity – magnitude, dynamics, and controlling factors. *Science* 296, 1064–1066.
- Torti, S.D., Coley, P.D., Kursar, T.A., 2001. Causes and consequences of monodominance in tropical lowland forests. *The American Naturalist* 157, 141–153.
- Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164, 347–355.
- Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. *Ecology Letters* 11, 1111–1120.
- de Vries, F.T., Hoffland, E., van Eekeren, N., Brussaard, L., Bloem, J., 2006. Fungal/bacterial ratios in grasslands with contrasting nitrogen management. *Soil Biology and Biochemistry* 38, 2092–2103.
- Waldrop, M.P., Balsler, T.C., Firestone, M.K., 2000. Linking microbial community composition to function in a tropical soil. *Soil Biology and Biochemistry* 32, 1837–1846.
- Wallander, H., Nilsson, L.O., Hagerberg, D., Baath, E., 2001. Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytologist* 151, 753–760.
- Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. *Ecology Letters* 9, 870–886.
- Whitman, W.B., Coleman, D.C., Wiebe, W.J., 1998. Prokaryotes: the unseen majority. *Proceedings of the National Academy of Sciences of the United States of America* 95, 6578–6583.
- Wohl, D.L., Arora, S., Gladstone, J.R., 2004. Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. *Ecology* 85, 1534–1540.
- Yadav, V., Malanson, G., 2007. Progress in soil organic matter research: litter decomposition, modelling, monitoring and sequestration. *Progress in Physical Geography* 31, 131–154.
- Yanagi, M., Yamasato, K., 1993. Phylogenetic analysis of the family Rhizobiaceae and related bacteria by sequencing of 16S ribosomal-RNA gene using PCR and DNA sequencer. *Fems Microbiology Letters* 107, 115–120.
- Zogg, G.P., Zak, D.R., Ringelberg, D.B., MacDonald, N.W., Pregitzer, K.S., White, D.C., 1997. Compositional and functional shifts in microbial communities due to soil warming. *Soil Science Society of America Journal* 61, 475–481.