RESEARCH ARTICLE

Testing the functional significance of microbial composition in natural communities

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Abstract

Ecologists have long studied the relationship between biotic composition and ecosystem functioning in larger organisms; however, only recently has this relationship been investigated widely in microorganisms. Recent studies are reviewed within a framework of three experimental approaches that are often used to study larger organisms: environmental treatment, common garden, and reciprocal transplant experiments. Although the composition of microorganisms cannot be easily manipulated in the field, applying these approaches to intact microbial communities can begin to tease apart the effects of microbial composition from environmental parameters on ecosystem functioning. The challenges in applying these approaches to microorganisms are highlighted and it is discussed how the experimental approach and duration affects a study’s interpretation. In general, long-term environmental treatment experiments identify correlative relationships between microbial composition and ecosystem functioning, whereas short-term common garden experiments demonstrate that microbial composition influences ecosystem functioning. Finally, reciprocal transplants simultaneously test for interactive effects of the environment and composition on functioning. The studies reviewed provide evidence that, at least in some cases, microbial composition influences ecosystem functioning. It is concluded that whole-community experiments offer a way to test whether information about microbial composition will help predict ecosystem responses to global change.

Introduction

Ecologists have long been interested in the relationship between biotic composition – the identity and diversity of organisms – and the processes that regulate material and energy flux in an ecosystem. Even Darwin (1859) discussed the relationship between species diversity and plant productivity. More recently, accelerating rates of biodiversity loss (Lawton & May, 1995) and biotic exchange (Vitousek et al., 1997) have renewed interest in this relationship (Huston, 1994; Schulze & Mooney, 1994; Loreau et al., 2002). While the nature of the relationship is not always consistent, studies on macroorganisms demonstrate that biotic composition often affects ecosystem process rates such as primary production, nitrogen cycling, and decomposition (e.g. Hector et al., 1999; Cardinale et al., 2006).

In contrast, less attention has been paid to this composition–functioning relationship within the field of microbial ecology (but see de Ruiter et al., 1995; Schimel, 1995; Schimel & Gulledge, 1998; Balser et al., 2002). Even though microbial communities have been used extensively in laboratory microcosms, these experiments are usually presented as models of macroorganism communities, rather than as direct tests of whether microbial composition itself matters to ecosystem functioning (but see van der Heijden et al., 1998; Naem et al., 2000; Bell et al., 2005).

Understanding the relationship between microbial composition and ecosystem functioning has practical implications for environmental engineering (Rowan et al., 2003; Saikaly et al., 2005) and is particularly timely and relevant in the face of rapid global change. In fact, most global change models assume that microbial composition is functionally irrelevant. Given the primary role of microorganisms in nutrient transformations, this assumption is central to predicting how ecosystems will respond to future environmental conditions.
Of course, to some extent, the composition of microorganisms (including fungi, protists, bacteria, Archaea, and viruses) matters to ecosystem functioning. If an ecosystem lost an entire functional group such as the nitrite-oxidizing bacteria, their absence would clearly impact nitrogen cycling rates. A less obvious question is whether the identity and diversity within a functional group matters to ecosystem functioning.

Numerous recent studies have revealed that compositional changes within microbial functional groups are correlated to changes in ecosystem processes (e.g. Carney et al., 2004; Waldrop & Firestone, 2004; Hawkes et al., 2005; Webster et al., 2005). While these studies are a useful starting point, as correlations, they do not demonstrate a causal relationship between microbial composition and ecosystem functioning. Indeed, because of the tight connection between microbial composition, environment variables, and ecosystem processes, one of the most difficult challenges in this area of research is testing the direct effect of microbial composition on ecosystem functioning while controlling for other environmental parameters.

For this special issue, a growing body of literature in microbial ecology that examines the composition–functioning relationship is reviewed. These studies are discussed within a larger framework of experimental approaches that have been used in classical ecology, while pointing out the challenges unique to microbial communities. For convenience, the authors use their own work as a case study to discuss the challenges of one possible approach. This paper concludes by examining the relevance of microbial composition–functioning relationships for global change predictions.

### A framework for microbial composition–ecosystem functioning experiments

To investigate the composition–functioning relationship in macroorganisms, ecologists can manipulate community composition in the field. For instance, researchers sow and weed plant communities to alter composition while controlling for the abiotic environment. In contrast, microbial taxa cannot be manipulated one at a time in a field setting. Instead, whole-community manipulations are necessary to investigate how microbial composition is related to ecosystem functioning.

Whole-community manipulations of microbial communities can be categorized into three related, experimental approaches: environmental treatments, common gardens, and reciprocal transplants (Table 1). In this section, the approaches are discussed in order of their increasing ability to tease apart the effects of microbial composition vs. environmental parameters on ecosystem functioning. Studies that fall within each of the categories are reviewed, while highlighting how the particular approach and duration of the study affects its interpretation (Table 1).

### Environmental treatments

Perhaps the most common experiments in ecology manipulate environmental parameters among replicates of similar community composition. For example, environmental treatment experiments modify abiotic factors such as nutrients, precipitation, and temperature to identify species’ resource limitations (Tilman, 1984; Seastedt et al., 1991; Vitousek et al., 1993; Knapp et al., 2002). Compared with microbial composition, abiotic factors are relatively easy to manipulate in the field or the laboratory. Furthermore, pre-existing environmental gradients – i.e., natural ‘experiments’ – can be used to support more controlled experiments (Connell, 1978; Vinton & Burke, 1997).

| Table 1. A comparison of three experimental approaches that have been used in microbial ecology to examine the relationships between microbial composition, environmental parameters, and ecosystem functioning* |
|---|---|---|
| Experimental approach | Time scale of experiment | Long term |
| Environmental treatment | Tests for an effect of many environments on the functioning of one community | Tests for an effect of many environments on the composition of one community; can test for a correlation between composition and ecosystem functioning |
| Common garden | Test for an effect of composition (many communities) on functioning in one environment | Tests if composition converges in one environment; as long as composition still varies among communities, tests for an effect of composition on functioning |
| Reciprocal transplant | Tests for effects of both environment and composition (and their interactions) on the functioning of multiple communities in multiple environments | Tests all points listed above for long-term environmental treatment and common garden experiments |

*The timescale of the experiments influences their interpretation. A short-term experiment refers to an experiment that measures ecosystem functioning before community composition changes, whereas a long-term experiment is conducted over a period of time that encompasses such changes.
The duration of an environmental treatment experiment is fundamental to its interpretation (Table 1). The experiments begin with the same community composition in all treatments. In the short term, before community composition has time to change, this type of experiment tests how the environmental parameter affects ecosystem functioning (e.g. carbon mineralization or nitrification rates) (Fig. 1). Many studies demonstrate that environmental parameters affect ecosystem processes that are mediated by microbial activities. For instance, nitrogen availability can affect rates of gross nitrogen mineralization (West et al., 2006), nitrification (Horz et al., 2004), methane consumption (Steudler et al., 1989), and litter decomposition (Hunt et al., 1997).

In the long term, environmental treatment experiments test whether the manipulated environmental parameter affects community composition. 'Long term' is defined here as a time period that allows for shifts in community composition in response to environment (thus in general, a long-term experiment on trees requires more time than one on microorganisms) (see also Balser et al., 2002). Many environmental treatment studies demonstrate that microbial composition responds to various environmental parameters, including temperature (Zogg et al., 1997; Avrahami et al., 2003), nitrogen (Bruns et al., 1999; Avrahami et al., 2002; Horz et al., 2004), fire (Treseder et al., 2004), and organic substrates (Griffiths et al., 1999), as well as plant composition.

Many of these studies also investigate whether the response of community composition and ecosystem functioning to environmental treatments is correlated (inset in Fig. 1) (Rich et al., 2003; Treseder et al., 2004; Carney & Matson, 2005; Webster et al., 2005; Lipson et al., 2006). For instance, Pett-Ridge & Firestone (2005) exposed tropical soils to different treatments of anoxic/oxic cycles over 21 days. These treatments affected both community composition and the rates of denitrification, nitrification, and iron reduction. Similarly, Waldrop & Firestone (2004) found that temperature altered both microbial composition and enzyme activities after a 100 days.

Such a correlation suggests a causal link between microbial composition and ecosystem functioning; however, caution must be exercised in interpreting these correlations. While a correlated response between composition and ecosystem functioning is consistent with this hypothesis, one cannot reject the alternative: changes in ecosystem functioning may be independent of the changes in microbial composition and due to the environmental treatments themselves.

Schimel & Gulledge (1998) review examples of environmental treatment studies that try to move beyond correlative results. In these studies, researchers subject microbial communities from different habitats to parallel short-term, environmental treatments and compare the communities’ physiological responses. For instance, Gulledge et al. (1997) found that methane consumption rates by methanotroph communities in response to ammonium fertilization varied depending on whether the communities were associated with paper birch or white spruce taiga forests. This result suggests that differences in methanotroph composition are responsible for differences in the physiological responses. Still, even in these studies, composition effects cannot be completely separated from the abiotic differences in the different habitats.

Nonetheless, studies demonstrating a correlated response between microbial composition and ecosystem functioning greatly aid in generating new hypotheses and formulating future experiments. For example, Horz et al. (2004) examined the effects of multiple global change factors on both ammonia-oxidizing bacterial composition and nitrification rates. They found that nitrogen additions increased the relative abundance of a clade of ammonia oxidizers, and this compositional shift was correlated with greater nitrification rates. In a follow-up laboratory experiment, the authors demonstrated that soils with increased abundance of this clade expressed increased rates of nitrification.

In sum, environmental treatment experiments are useful for understanding which abiotic factors influence ecosystem processes, and in the longer term, influence microbial composition. However, by themselves, this type of experiment cannot establish a causal effect of microbial composition on ecosystem functioning. To do that, one must perform a common garden experiment.
which controls environmental conditions while varying biotic composition.

**Common gardens**

Ecologists have long utilized ‘common garden’ experiments to tease apart environmental vs. genetic effects on an organism’s phenotype. These experiments rear individuals in a uniform environment; the remaining phenotypic differences among the individuals should be due to genetic differences (Silvertown & Charlesworth, 2001). In the classic common garden study, Clausen *et al.* (1948) used this method to demonstrate genetic differences among populations of the plant *Achillea lanulosa*.

A common garden can also be applied to whole communities to test the hypothesis that microbial composition affects ecosystem functioning. A common garden of transplanted microbial communities (community genotypes) ideally standardizes all abiotic environmental parameters. Differences in ecosystem functioning (the community phenotype) can then be directly attributed to differences in microbial composition (Fig. 2).

In practice, however, transplanting microbial communities while standardizing all environmental parameters is a huge challenge. First, the treatment communities must be kept isolated from one another and the new surrounding community. Thus, most microbial common garden experiments are executed in the laboratory. At the same time, the new environmental conditions should be allowed to permeate through the communities, an especially difficult objective for communities intimately associated with their habitat matrix such as soils. To minimize residual effects of matrix characteristics, many studies provide similar laboratory environments and ‘nonlimiting’ conditions, rather than trying to modify all abiotic variables. These laboratory incubations, a common tool particularly in soil microbiology, are essentially attempting to create common garden conditions (Cavigelli & Robertson, 2000; Horz *et al.*, 2004).

Cavigelli & Robertson (2000) used this laboratory approach. Focusing on two soil community types (tilled and grassland), they compared denitrification dynamics under standardized, nonlimiting conditions in the laboratory (optimizing temperature and diffusion conditions and adding excess amounts of nitrate in optimal proportion with carbon sources). Assuming that the denitrifying communities experienced the same conditions, the different denitrification rates found among the soil types were attributed to differences in community composition.

Another way to achieve a common garden is to inoculate replicates of a sterile environment with different microbial communities, such as has been used to study soil food webs (e.g. Coleman *et al.*, 1977; Elliot *et al.*, 1979; Ingham *et al.*, 1985). The benefit of an inoculum study is the researcher’s ability to control the environmental conditions. Not only can one define the abiotic conditions, but residual effects from the communities’ native environments are immediately removed. The downside of such a study is that the resulting microbial community will be different from the original inoculum as rapid-growing, laboratory-adapted organisms will out compete others that were more abundant in their native environment.

In an inoculum study, Langenheder *et al.* (2006) introduced eight different aquatic communities into identical batch culture conditions in the laboratory. After 3 weeks, they found that composition of the final microbial communities still differed by inoculum type. In addition, except for biomass production, the functional parameters measured differed among the communities, providing evidence that in general, microbial composition influences ecosystem processes.

As in environmental treatment experiments, a key element to interpreting common garden experiments is the duration of the experiment (Table 2). In the short term, when the initial composition is known to vary between treatments, any differences in functioning among treatments can be attributed to the influence of microbial composition. In the long term, composition may change in response to the new environmental conditions (and this new composition may feed back to alter the environment). However, as long as composition still varies between the community treatments, one can conclude that functional differences are due to initial compositional differences. Furthermore, long-term common garden experiments provide an insight into whether different microbial communities are constrained in how their composition changes in response to the new garden environment. For instance, if ‘everything is everywhere’ (Baas-Becking, 1934) and all communities contain the same taxa that just vary in abundance, then under
similar environmental conditions, the composition of all communities should converge.

**Reciprocal transplants**

Reciprocal transplants combine environmental treatment and common garden experiments. The approach simultaneously tests the effects of both community composition and environment on ecosystem functioning by exposing organisms from multiple environments to each other's native environments. In larger organisms, this approach has been used extensively to examine whether an organism's distributional limits are determined by its genotype, the environment, or both (e.g. Altieri, 2006). In microbial ecology, the approach has recently been adopted for whole-community experiments (e.g. Rawls et al., 2006).

Figure 3 illustrates hypothetical results of a reciprocal transplant of two communities (A and B). If microbial composition, but not the environment, influences ecosystem functioning, then communities A and B would perform differently regardless of the environment (Fig. 3a). In contrast, if the environment, but not community composition, matters to functioning, then the communities would perform similarly to one another within an environment but differently across environments (Fig. 3b). Finally, reciprocal transplants can also detect the interactive effects of composition and the environment on functioning. In this case, the two communities function differently from one another, and how they differ depends on the environment they are experiencing (Fig. 3c). Such interactions also reveal whether the effects of composition are more important in certain environments than in others.

Cavigelli & Robertson (2000) conducted an experiment similar to a reciprocal transplant with the tilled and grassland soils described above. Considering the importance of pH on denitrification, they mimicked a reciprocal transplant by comparing denitrification rates in the laboratory at the pH associated with both soils (so each community experienced both a native and a foreign pH). They found that community composition and the pH environment interacted to affect denitrification rates. Specifically, the grassland community exhibited greater rates of denitrification at its native pH than the foreign pH, while the tilled community displayed similar denitrification rates at both pH levels.

In another laboratory study, Langenheder et al. (2005) also adapted the reciprocal transplant study using inocula from different aquatic communities. They introduced inocula from four lakes into four media environments that represented the native lake environments. After 11 days, they measured a variety of functional parameters. A complex interaction existed between inoculum type and media environment on ecosystem processes. Although the experiment was well implemented, for the purpose of teasing apart composition effects on functioning, the results were difficult to interpret; at the time of sampling, composition within inoculum treatments was as variable as across treatments.

As with the other two experimental approaches, the duration of reciprocal transplant experiments is key to interpreting their results (Table 1). As long as composition still varies more among than within community treatments, both short- and long-term reciprocal transplants can tease apart community vs. environment effects. However, community composition and the environment must be surveyed at the time of functional assays. Community composition can change in a matter of weeks when sterile media are freshly inoculated (Langenheder et al., 2005), while in soil, at least, it takes some time for the surrounding abiotic environment to penetrate a transplanted community (Balser & Firestone, 2005; Waldrop & Firestone, 2006).

Reciprocal transplants of microbial communities have also been carried out in the field (Bottomley et al., 2004, 2006; Balser & Firestone, 2005; Boyle et al., 2006; Waldrop & Firestone, 2006). For instance, Waldrop & Firestone (2006) transplanted soil cores between grassland and oak habitats in polycarbonate tubes capped with 1-mm mesh to examine microclimate effects on microorganisms and carbon cycling. After 2 years, they found that oak soil cores transplanted into the grassland environment changed in terms of microbial composition and some functional characteristics. In contrast, the grassland microbial communities transplanted...
into the oak environment did not respond to the new environment. Hence, the results revealed an interaction between community type and the environment, with the oak community being more sensitive to environmental change. Similarly, Balser & Firestone (2005) transplanted soil cores between a forest and grassland site. Although the transplanted cores did not fully equilibrate with the external environment, a multiple regression analysis linked the cores’ composition and measured processes (e.g. soil respiration, potential nitrification, and gross N mineralization).

The above studies also demonstrate the enormous challenges in performing field experiments with microbial communities. Indeed, the ideal transplant may be nearly impossible in complex matrix habitats such as soil for several reasons. First, the geophysical properties of the transplant’s matrix may not change when transplanted to a new environment. In addition, the matrix itself may impede permeation of gases, nutrients, and other biologically important resources. Even after 2 years since transplantation (partially enclosed to impede immigration), Balser & Firestone (2005) found that the water content and inorganic carbon and nitrogen of soil cores did not equilibrate with their new environment. Finally, even if the physical nature of the matrix is controlled for, it is difficult to prohibit migration of microorganisms into the transplants, while allowing certain abiotic conditions to permeate. A kind of microbial ‘cage’ could accomplish this. Gasol et al. (2002) constructed such a cage that can be used in aquatic environments using dialysis tubing. With a molecular weight cutoff (MWCO) of c. 8 kDa, the tubing prevents movement of microorganisms (including many viruses) across the membrane while allowing the movement of most solutes. Unfortunately, both drying and biofilm growth can compromise the integrity of the membrane. Consequently, its use is limited to water-saturated environments and must be replaced often for long-term experiments.

Despite these difficulties, reciprocal transplants are a powerful way to investigate the interactions and relative importance of environmental parameters and community composition. Although it may be impossible to achieve the ideal experimental design, the interpretation of the experiments can be strengthened the more one can control for the physical matrix, monitor community composition and abiotic parameters, and prohibit migration of microorganisms.

### Case study

An example from the authors’ own work of a reciprocal transplant using microbial cages demonstrates some of the insights provided by, and limitations of, this approach. The authors transplanted sediment cores between fresh and salt marsh sites along a river within the Scarborough coastal tidal marsh in Maine. Because the marsh environment is so wet, dialysis tubing can be used to construct the cages. The tubing is closed at the top and bottom with grooved PVC rings and o-rings, creating a cage that contains a sediment core (5 cm in diameter and c. 6 cm long). Staying within the same river basin allowed to control for the geophysical properties of the sediment substrate; total carbon, total nitrogen, and sediment texture were not significantly different between the sites. At the same time, the pore water chemistry of the sites differed markedly; for instance, sulfur ions, especially sulfate, dominate salt marsh sediments, while sulfur is negligible in fresh marsh sediments (Odum, 1988). The bacterial communities are also known to differ along salinity gradients in coastal marshes (e.g. Bernhard et al., 2005).

Sediment cores were taken from the riverbed at each site, placed in cages, and incubated at both sites in buckets filled

### Table 2. Two-way ANOVA of the reciprocal transplant case study (n = 10 replicates)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source of variation</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sulfatase</td>
<td>Composition</td>
<td>1</td>
<td>5004.50</td>
<td>5.67</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Environment</td>
<td>1</td>
<td>818.46</td>
<td>0.93</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>Environment X composition</td>
<td>1</td>
<td>397.26</td>
<td>0.45</td>
<td>0.51</td>
</tr>
<tr>
<td>Leucine amino peptidase</td>
<td>Composition</td>
<td>1</td>
<td>24408.11</td>
<td>0.46</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>Environment</td>
<td>1</td>
<td>5864.01</td>
<td>0.11</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>Environment X composition</td>
<td>1</td>
<td>314374.11</td>
<td>5.96</td>
<td>0.02</td>
</tr>
<tr>
<td>Phosphatase</td>
<td>Composition</td>
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<td>160.55</td>
<td>0.01</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>Environment</td>
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<td>60583.01</td>
<td>3.21</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Environment X composition</td>
<td>1</td>
<td>1044800.99</td>
<td>5.54</td>
<td>0.03</td>
</tr>
<tr>
<td>CO₂ production*</td>
<td>Composition</td>
<td>1</td>
<td>128.83</td>
<td>1.39</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>Environment</td>
<td>1</td>
<td>154.73</td>
<td>1.67</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Environment X composition</td>
<td>1</td>
<td>749.64</td>
<td>8.08</td>
<td>0.008</td>
</tr>
<tr>
<td>Net CH₄ production*</td>
<td>Composition</td>
<td>1</td>
<td>261.51</td>
<td>1.77</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Environment</td>
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<td>516.33</td>
<td>3.49</td>
<td>0.07</td>
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<tr>
<td></td>
<td>Environment X composition</td>
<td>1</td>
<td>95.42</td>
<td>0.65</td>
<td>0.43</td>
</tr>
</tbody>
</table>

*P*-values < 0.05 are in bold.

*Data did not fit a normal distribution and therefore were rank transformed.
with the site’s river water. Previously, it was determined that a 5-day incubation allowed the sediment’s salinity to equilibrate with the surrounding incubating water. Therefore, it was assumed that after 5 days the community replicates would experience their new surrounding environment, but would not change much in microbial composition. After 5 days, ecosystem processes in the sediment cores were assayed by measuring respiration rates and net methane production rates in the field (modified from Holland et al., 1999) and sediment enzyme activities (sulfatase, amino peptidase, and phosphatase) in the laboratory (Saiya-Cork et al., 2002).

Microbial composition influenced four of the five functional assays (Table 2). The fresh marsh community expressed greater sulfatase activity than the salt marsh community, regardless of the environment to which it was exposed (Fig. 4a), an example of a main effect of community composition (Fig. 3a). In three other assays, composition had a significant influence through an interaction with the environment (Fig. 3c). Both fresh and salt-marsh communities exhibited higher respiration rates in their native environment (Fig. 5a). A composition–environment interaction was also found for leucine aminopeptidase activity (Fig. 4b) and phosphatase activity (Fig. 4c). Finally, methane production was not significantly influenced by either microbial composition or the environment (Fig. 5b).

These results suggest that differences in microbial composition between fresh and saltmarshes are functionally significant for a suite of processes in coastal marsh sediments. Moreover, the dominance of interactive effects between composition and the environment suggests that the effect of microbial composition is strongly mediated by the environmental conditions.

Even with the use of cages, this study raises some of the same issues that apply to other microbial transplants. While substrate material and salinity equilibrated with the transplanted environment were controlled for, the possibility that other abiotic parameters associated with the native environment still influenced the sediment’s process rates cannot be eliminated. Another issue is the extent to which physical stress of transplantation influenced the results. Many microorganisms will experience a shock if moved abruptly to a new salinity. At the same time, the ability of microorganisms...
Conclusions: microbial composition and ecosystem responses to global change

The composition of microorganisms cannot be manipulated as readily as that of macroorganisms, especially in field experiments. However, well-designed whole-community experiments, such as those described above, often can begin to tease apart the effects of microbial composition from environmental parameters on ecosystem functioning. Indeed, a number of studies discussed above provide evidence that, at least in some cases, microbial composition influences ecosystem functioning.

These results are particularly relevant in light of the current rates of global change. Environmental treatment studies demonstrate that microbial composition is likely to respond to new environmental conditions (Avrahami et al., 2002, 2003; Horz et al., 2004; Treseder et al., 2004). However, most global change models assume that an ecosystem’s functional response to environmental changes is fixed and any changes in microbial composition are functionally irrelevant. For instance, a model may include a response curve relating temperature to an ecosystem process such as respiration, nitrogen fixation, or decomposition. Figure 6 (adapted from Schimel & Gulledge, 1998) illustrates this hypothetical ‘contemporary response’ curve. These functions are usually based on data from short-term environmental treatment studies where microbial composition has little time to shift. Based on this model, if temperature rises, then the functional response is predicted based on moving from point A to point B. In the long term, however, changes in microbial composition may alter the response curve itself (the ‘future response’ curve in Fig. 6). In this case, predictions based on the contemporary response curve would be misleading, as the temperature increase would actually increase functioning to point C.

Hence, the ability of current global change models to predict future ecosystem responses depends in part on whether microbial communities display different contemporary vs. future functional response curves. Some of the experimental approaches described here offer a means to investigate this question. In particular, one could compare the functional response of a community in a short-term vs. long-term environmental treatment experiment. The short-term experiment would document the immediate functional response of a community under a variety of environmental conditions. The long-term experiment would allow community composition shift in response to the same variety of environmental conditions; then, the same functional parameters could be assayed. A large difference in results between the two experiments would demonstrate the importance of explicitly considering microbial composition when making global change predictions.

In sum, microbial composition, like that of larger organisms, can affect ecosystem functioning. Now microbial ecologists are challenged with pinpointing when and where these compositional differences are particularly important. The framework of experimental approaches offered here highlights a variety of methods commonly used in classical ecology, each with its own benefits and drawbacks when applied to microorganisms. While improvements on these approaches will be useful, there is ample room and need for entirely new and different approaches (e.g. Radajewski et al., 2000). After all, the potential returns of understanding the functional significance of microbial composition are great. This research may not only enhance one’s basic understanding of microbial diversity but also clarify how ecosystems may respond to global change.

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