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A trait-based framework for predicting when and where microbial adaptation to climate change will affect ecosystem functioning

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Abstract As the earth system changes in response to human activities, a critical objective is to predict how biogeochemical process rates (e.g. nitrification, decomposition) and ecosystem function (e.g. net ecosystem productivity) will change under future conditions. A particular challenge is that the microbial communities that drive many of these processes are capable of adapting to environmental change in ways that alter ecosystem functioning. Despite evidence that microbes can adapt to temperature, precipitation regimes, and redox fluctuations, microbial communities are typically not optimally adapted to their local environment. For example, temperature optima for growth and enzyme activity are often greater than in situ temperatures in their environment. Here we discuss fundamental constraints on microbial adaptation and suggest specific environments where microbial adaptation to climate change (or lack thereof) is most likely to alter ecosystem functioning. Our framework is based on two principal assumptions. First, there are fundamental ecological trade-offs in microbial community traits that occur across environmental gradients (in time and space). These trade-offs result in shifting of microbial function (e.g. ability to take up resources at low temperature) in response to adaptation of another trait (e.g. limiting maintenance respiration at high temperature). Second, the mechanism and level of microbial community adaptation to changing environmental parameters is a function of the potential rate of change in community composition relative to the rate of environmental change. Together, this framework provides a basis for developing testable predictions about how the rate and degree of microbial adaptation to climate change will alter biogeochemical processes in aquatic and terrestrial ecosystems across the planet.

Keywords Microbial adaptation · Climate change · Ecosystem function · Thermal adaptation · Microbial community structure · Trait-based ecology

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Introduction

Microbial communities are nimble entities, capable of rapidly adapting to changing environmental conditions through changes in community structure, which controls functional traits that emerge at the ecosystem scale. In response to experimental soil warming in a temperate forest, the temperature sensitivity of soil microbial respiration declined in warmed plots (Bradford et al. 2008), which contributed to a declining stimulation of respiration at the ecosystem scale over a period of several years (Melillo et al. 2002). A recent metanalysis showed that the temperature sensitivity of soil N mineralization rates were greater for soils originating from colder climatic zones (mean annual temperature, MAT <2°C) compared with warmer climate zones (MAT >6°C) (Dessureault-Rompre et al. 2010). In lake ecosystems, planktonic bacterial communities demonstrated highest nutrient use efficiency nearest in situ temperature (Hall et al. 2009), with bacterioplankton P:C negatively correlated with MAT and decreased available dissolved phosphorus (Hall et al. 2011). Marine microbial communities have shown evidence for functional adaptation to local environmental temperature with lower temperature optima at higher latitudes (Simon et al. 1999). Microbial communities have also been observed to adapt to fluctuations in redox status (DeAngelis et al. 2010), and to altered precipitation regimes (Szukics et al. 2010; Evans and Wallenstein 2011). These examples suggest that microbial adaptation is a common phenomena that occurs across diverse habitats with the potential to strongly affect ecosystem functioning under future climate regimes (Allison et al. 2010).

The word ‘adaptation’ has traditionally been applied at the organismal or population level, as a generic term to describe the process by which organisms increase their fitness in a particular environment (Rose and Lauder 1996). Although it is often used to describe a specific process such as a change in gene frequency at the population level, the term does not itself imply any specific mechanism (Hochachka and Somero 2002). Here, we propose that it can also be applied at the community level (as previously suggested by Bradford et al. 2008) to describe changes in the aggregate function of microbial communities in response to environmental change. Changes in function that can be observed at the community level result from changes in the relative contribution of microbial populations to the total aggregate function of the community. We define microbial community adaptation as the process by which the observed level of particular trait within a community becomes better suited to current environmental conditions.

Although it is clear that microbial communities are capable of adapting to their local climate, microbial adaptation is often not fully realized. For example, some studies have reported no evidence of thermal adaptation in warming experiments (Hartley et al. 2008; Rinnan et al. 2009; Vicca et al. 2009). In oceans, microbial communities from cold environments often have growth optima above the in situ temperature (Johnson et al. 2006). This suggests that there are fundamental constraints on microbial adaptation. These may be due to constraints on the rate of adaptation (i.e. a temporal decoupling or lag between shifts in environmental parameters and physiology of the extant microbial community), or there could be fundamental physiological trade-offs that preclude perfect adaptation in natural environments. We suggest that focusing on the rate of microbial adaptation relative to environmental change, physiological constraints to adaptation, and the interaction between these two aspects of adaptation should provide additional insight into how microbial adaptation will affect the rates of biogeochemical processes under future climates. Here, we propose a framework for predicting where, when, and how microbial adaptation is most likely to contribute significantly to ecosystem responses to climate change.

Functional trade-offs constrain microbial adaptation to climate change

Trade-offs, a negative correlation between two traits, are a well-documented biological phenomenon known to structure ecological communities (Aerts 1999; Kneitel and Chase 2004). One example is the well-documented trade-off between resource use efficiency and maximum growth rate for bacteria (Lipson et al. 2008; Pfeiffer et al. 2001). Hall et al. (2010) proposed that aquatic microorganisms adapt to temperature by adjusting their composition of fatty acids in their outer membrane This results in either the ability to take up resources at low temperatures or the ability to limit respiratory costs at high temperatures (Hall et al. 2008). Fundamental trade-offs such as these have constrained the evolution of microbial traits, and produced diverse microbial taxa with vastly different phenotypes, rather than a few super-taxa that are optimized for all traits (Fig. 1). Microbial taxa are considered to be specialists if they are particularly optimized for a particular trait, or generalists if they demonstrate an intermediate level of ability for a range of traits. For any particular trait, there is a distribution of ability among the global pool of microbial taxa. We propose that, in most environments, low abilities for many of these traits will result in low fitness. Thus, most species in the global pool are likely to be generalists (Fig. 1), resulting in a normal frequency distribution of values for most traits (Fig. 1). In any local environment, the community-level trait distribution is a function of the pool of species with access to that environment, which is then filtered by local environmental conditions (Fig. 2).

There has been considerable excitement in recent years about the potential of trait-based approaches to elucidate the interactions of ecological communities with their environment (Lavorel and Garnier 2002). This approach was first developed for plant communities, where traits can be measured for each population within a community. Similarly, a recent application of a trait-based approach to algal community ecology, based on differences in population level algal traits, has provided new insight into how algal communities are structured across environmental gradients (Litchman and Klausmeier 2008; Litchman et al. 2007). There has also been an attempt to describe broad biogeographical patterns of bacterial community structure based on population-level traits (Green et al. 2008). However, microbial communities in natural environments are highly diverse and poorly characterized at the population level from a functional perspective, making it very challenging to characterize traits of specific populations within mixed communities in the environment. It is tractable, on the other hand, to characterize the ecological traits of whole microbial communities. In effect, this approach treats the community as a meta-organism where the relationship between community-level traits and environmental parameters are evaluated directly.

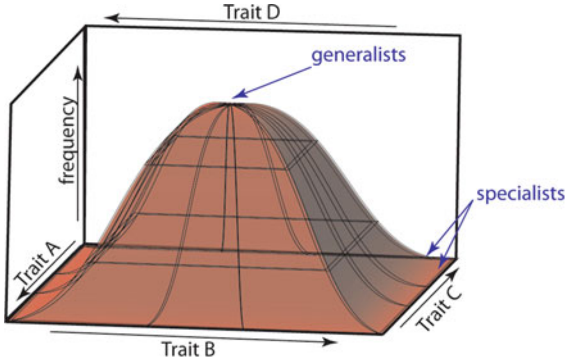

Fig. 1 The functional diversity of individual taxa is governed by fundamental trade-offs in phenotypic traits. Specialists are optimized for a single trait, at the expense of low values for one or more other traits. Generalists have intermediate values for multiple traits. In this figure opposing axes (Traits A and C, Traits B and D) represent traits that are governed by a trade-off. Better performance of on Trait is countered by decreased performance in another. This is a two-dimensional representation of what may be an n-dimensional phenomenon

One advantage to this approach is that community-level traits contribute directly to ecosystem and food web dynamics. For example, in aquatic ecosystems from headwater streams to estuaries, dissolved organic carbon and total dissolved nitrogen were inversely correlated (Taylor and Townsend 2010). They observed that when the ratio of DOC:NO_3^- in the environment drops below the C:N ratio of the total microbial biomass, a community-level trait, NO_3^- begins to accumulate rapidly. From a food web perspective, bacteria can be thought of as a grouped resource. While there is some evidence for selective feeding by protists independent of cell size (Gonzalez et al. 1990) many bactivores consume bacteria using a size selective cut-off (Pernthaler 2005). In this case, size-distribution affects propagation of microbial resources through the food web, and the community trait of cell size distribution—a composite of the populations in a given size class—drives secondary production. Resource (in this case bacterial biomass) stoichiometry as well as the contribution of other resources such as essential fatty acids can drive the fecundity of secondary consumers. Both microbial stoichiometry and fatty acid content can be affected by independent environmental parameters such as temperature (Hall et al. 2009, 2010). These are examples where community-level traits that are likely to be influenced by climate change and microbial adaptation are in direct interplay with ecosystem processes (i.e. nutrient regeneration or food web dynamics). Beyond these two examples, there are other measurable community-level microbial traits that directly interact with ecosystem processes including pH sensitivity (Rousk et al. 2009), phenotypic plasticity (Bergwall and Bengtsson 1999), stress tolerance (Philippot et al. 2008; Tobor-Kaplon et al. 2006), and many others.

We suggest that a trait-based view applied at the level of the microbial community is particularly useful

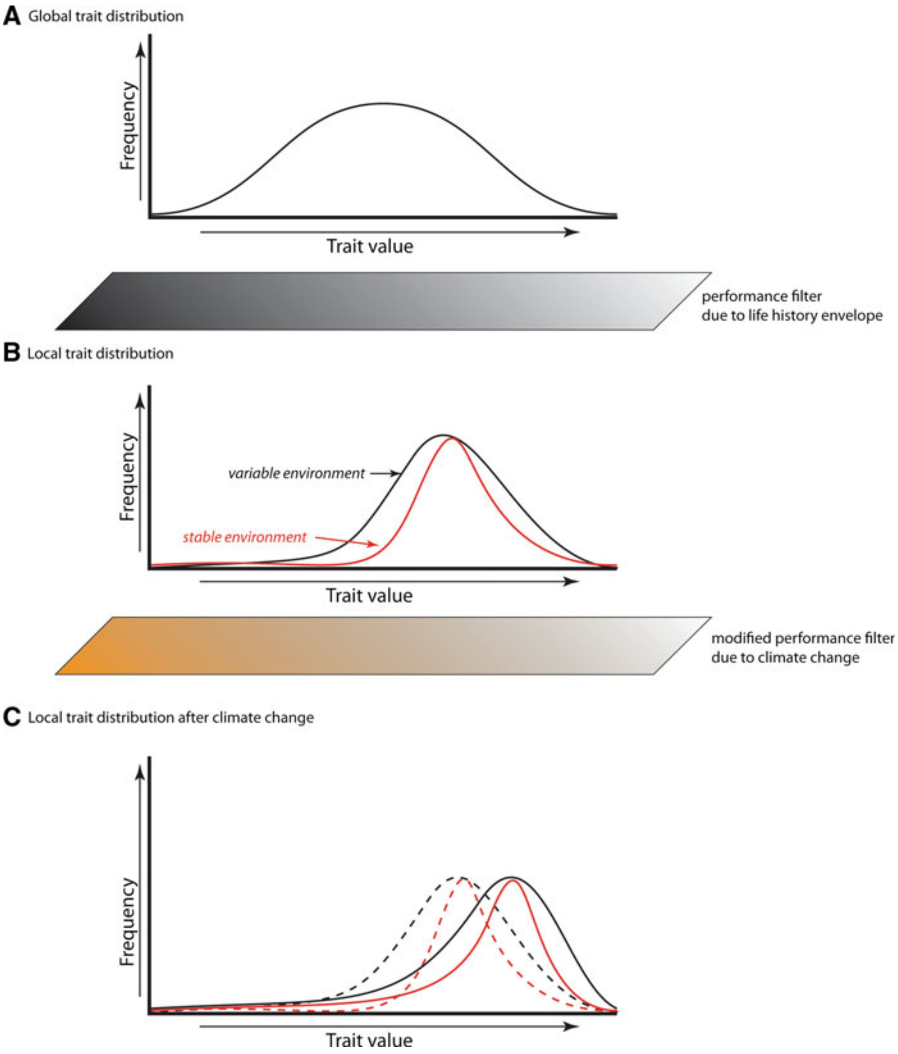

Fig. 2 **a** The frequency distribution of traits in the global species pool (all microbial taxa) is a function of fundamental trade-offs between traits. **b** In any local environment, the trait distribution of the extant community is a function the local life history envelope (species sorting integrated through time) and mass effects. Stable environments (*red line*) will favor amore narrow distribution of traits than variable environments (*black line*), and will favor specialists over generalists. **c** As the life history envelope changes due to climate change, shifts in trait distributions will be determined by the rate of environmental change relative to the rate of community population dynamics, and by the diversity of functional traits within the extant community. Given a fixed genetic diversity, communities dominated by specialists will be limited by mass effects, whereas communities dominated by generalists will be limited by resource availability (which determines phenotypic plasticity and growth rate of the constituent populations). In resource-limited environments (*dashed lines*), the rate and extent of adaptation will be constrained compared to resource-rich environments (*solid lines*) where larger shift in community structure and function should occur. Modified from Webb et al. (2010)

in understanding how microbial adaptation will affect biogeochemistry in the context of climate change. Specifically, from a biogeochemical perspective, we see two inherent advantages of a trait-based approach applied at the level of the microbial community. First, functional traits of microbial communities are in direct interplay with biogeochemical processes. For example, community-level nutrient use efficiency (rather than that of any single microbial taxa) maintains an important control on the amount of mineral nutrient available in a given ecosystem. The second advantage of a trait-based approach is the identification of trade-offs between two traits that constrain the possible response of microbial community function.

Placing limits on the possible landscape of microbial response to climate change by defining the mechanisms that underlie community adaptation should improve our ability to project how climate change will alter microbially-mediated biogeochemical cycles.

Community-level adaptation is determined by contribution of different taxa to total activity

Although microbes are capable of adapting to environmental change through genetic evolution (Bennett and Lenski 2007; Cooper et al. 2001) which may be accelerated by lateral gene transfer (Rensing et al. 2002; Trevors et al. 1987), and physiological plasticity (Schimel et al. 2007), we posit that shifts in community structure, and in the relative contribution of different taxa to total activity are the most relevant mechanisms driving adaptation to climate change at the ecosystem scale. In a survey of published studies, Allison and Martiny (2008) found that in the majority of global change experiments, community composition (as determined by ribosomal rRNA genes) changed in response to the treatments, suggesting that shifts in community structure is a ubiquitous response to environmental change. Given this, the ability of a microbial community to adapt to a given environment is a function of the rate at which microbial community composition changes due to the growth and turnover of individual cells, relative to the rate of change of the environmental parameters that limit physiological processes.

Shifts in the relative abundance of populations due to differential growth or mortality, known as species sorting, is primarily driven by local environmental conditions (e.g. resources, temperature) (Van der Gucht et al. 2007). Microbial community composition is also affected by the loading of allocthonous populations through immigration, or loss of populations through emigration (e.g. wash-out), which are collectively referred to as mass effects (Leibold et al. 2004). At a given moment, microbial community composition and structure (the presence and relative abundance of the constituent populations) is determined by the relative effect of species sorting versus mass effects. Similarly, the change in function of the extant microbial community is determined by the relative rate at which the members of the community are able to undergo physiological acclimation and the rate at which they are able to acquire novel genes through mutations or lateral gene transfer (Portner et al. 2006). Physiological acclimation can occur through numerous mechanisms including regulation of intracellular solutes (Csonka and Hanson 1991; Roessler and Muller 2001) and changes in lipid composition (Hall et al. 2010). These two mechanisms for shifts in the function of the extant community, coupled with novel functions gained and lost through shifts in community composition, define the potential microbial community function in response to environmental change (i.e. adaptation).The realized function of a microbial function is determined by the relative activity of different members of the community, since only a portion of the community is active under any particular condition (Lennon and Jones 2011).

There are many examples where community composition is strongly correlated with changing environmental gradients on relatively short seasonal time-scales. Recurring seasonal patterns in aquatic microbial communities have been shown to strongly correlate with temperature, in lake (Shade et al. 2007), stream (Crump and Hobbie 2005; Hullar et al. 2006) and marine (Fuhrman et al. 2006) ecosystems. Presumably, these shifts in microbial community structure are due to selection of the constituent populations that are more fit for a given environment. These changes in microbial community composition can, in turn, affect ecosystem functioning. For example, when different microbial communities degraded the same leaf litter, community composition alone accounted for 20% of the variation in respiration rates (Strickland et al. 2009). In another study, the metabolic byproducts of Aspen leaf litter decomposition depended on the microbial community degrading them (Wallenstein et al. 2010a). Thus, microbial community composition can affect both the rate of metabolic processes, but can also determine the catabolic and anabolic pathways by which resources are utilized and transformed. In the above examples, each of these effects has important implications for carbon cycling in a given environment.

By focusing on the rate of community change relative to the rate of environmental change we can identify how microbial communities inhabiting distinct ecosystems (e.g. aquatic vs. terrestrial) may be affected by both short-term (seasonal) and long-term (climate change) environmental change. Here we use temperature as an example of an environmental parameter that will change with climate change and discuss how the microbial response may differ between distinct habitats. As discussed in detail by Treseder et al. (2011), the rate of microbial adaptation to climate warming may determine the nature of ecosystem feedbacks to climate change.

Thermal adaptation of microbial communities

Temperature provides a clear example of an environmental parameter that structures microbial communities and will be affected by climate change. In the short-term, temperature controls the rates of metabolic processes (Davidson and Janssens 2006), and in the longer-term, temperature can directly affect microbial community composition and physiology (Adams et al. 2010; Stres et al. 2008; Zogg et al. 1997). In a comparison of soil microbial communities from three sites with a broad range in MAT, Balser and Wixon (2009) found that optimal temperatures for respiration broadly followed the patterns in MAT, meaning that each community performed most efficiently near its native temperature regime. Yet, the fundamental relationship between temperature and metabolic processes does not always scale to the ecosystem level. For example, several studies have found no relationship between MAT and soil organic matter turnover time across geographic climate gradients (Fissore et al. 2009; Giardina and Ryan 2000). In addition, the temperature dependence of microbial metabolism in aquatic ecosystems is generally considered to be ambiguous (Del Giorgio and Cole 2000; Rivkin et al. 1996). These discrepancies may be partially due to the dynamics of microbial adaptation (i.e. communities from different locales adapted to the local temperature regime with different temperature response curves) that are not captured in cross-system analyses.

How microbial communities respond to temperature may be strongly influenced by the temperature regime, both in time and space, to which they are adapted. At the broadest scale, the temperature regime of aquatic ecosystems differs from that of terrestrial ecosystems in a manner that should directly affect how microbial communities adapt to temperature. The temperature regime of an environment includes not only the average and range of temperatures experienced in a typical year, but also factors such as the range of diurnal fluctuations and interannual variability. Due to the high specific heat of water, aquatic ecosystems experience relatively slow shifts in ambient temperature. While soil temperatures in arid ecosystems may experience a 20–30°C shift over a diurnal cycle (Hansen et al. 1995), a similar temperature range is likely to be seen in lake ecosystems only over an annual cycle (with some notable exceptions). While large river ecosystems may experience a similar annual temperature range as lakes of similar latitudes, alpine and sub-alpine streams are likely to have an even lower and more constrained annual range. Such temporal stability of temperature suggests that aquatic microbial communities are more likely to be composed of temperature specialists than terrestrial microbial communities. This is important because microbial communities that have adapted to a limited range of temperature (e.g. temperature specialists) are more likely to be affected when the environment moves beyond that range than microbial communities that have adapted to a broad range of temperature (e.g. temperature generalists). While the specialized community has experienced loss of function, the generalized community retains the ability to deal with a large range either through a more diverse community or a community of generalists.

Given these differences in temperature regimes between soils and aquatic environments, it is likely that the soil microbial communities are composed of taxa that are temperature generalists (i.e. broad mesophiles) rather than specialist taxa (thermophiles and psychrophiles), because the rate of temperature change (~ 1–$2°\mathrm{C}\ \mathrm{h}^{-1}$) is significantly faster than the constituent populations can respond (generation time ~ 0.001–$0.1\ \mathrm{h}^{-1}$). However, these differences should also manifest themselves between habitats with even subtler differences in environmental regime. This effect was demonstrated in a reciprocal transplant experiment using shaded (under oak canopy) and unshaded (open grassland) soil communities (Waldrop and Firestone 2006). The open grassland experienced a broader range of environmental parameters including higher maximum temperature and lower soil moisture content. After the transplant the open grassland soils experienced little to no response in community composition or function while the shaded soils, with the more constrained environment, had pronounced shifts in both (Waldrop and Firestone 2006).

Similar patterns in how microbial communities from different habitats respond to climate change can be expected across latitudinal gradients as well. For example, microbial communities in the tropics and the poles currently experience a consistently narrow range of temperatures (Dai and Trenberth 2004; Hansen et al. 1995). If climate change simply shifts the thermal regime by increasing the minimum, maximum, and average annual temperature, we predict that thermal adaptation will be constrained by mass effects (e.g. the rate of immigration). In contrast, microbial communities from temperate environments with broader thermal regimes should be able to more rapidly adapt to climate warming through species sorting. As a consequence, warming is likely to have a greater effect on microbially-mediated biogeochemistry in the tropics and the poles than at mid-latitudes where shifts in the relative abundance of the extant communities should partially mitigate the stimulatory effect of warming on the rates of biogeochemical processes. Thermally stable climates near the equator, along coastlines, in mid-ocean gyres or at the poles, are more likely to favor temperature specialists than dynamic climates found at mid-latitudes and should be therefore more affected by climate change.

It is possible that selection for temperature specialists in thermally stable environments drives broad-scale patterns in microbial community composition and diversity. However, whether thermal tolerance is a trait that is phylogenetically conserved depends on the mechanism. For example, thermal adaptation in *E. coli* (Riehle et al. 2001) and viruses (Knies et al. 2006) appears to be driven by single mutations resulting in amino acid substitutions. These substitutions can alter the tertiary structure of folded proteins, which can alter their thermal stability (Wallenstein et al. 2010b). These changes in protein folding can result in increased fitness in response to a changing thermal environment (Pena et al. 2010). Thus, thermal tolerance can evolve rapidly within populations if driven by changes in protein structure, and is not likely to be highly conserved across the tree of life, nor necessarily associated with mutations to the ribosomal gene. Other mechanisms of thermal tolerance, such as changes in fatty acid composition (Hall et al. 2010) should be phylogenetically conserved at least at broad taxonomic levels. At the global scale, temperature does not appear to structure microbial community composition or microbial diversity in soils, based on rRNA genes (Chu et al. 2010; Lauber et al. 2009), which may indicate that other factors override temperature-based selection at this scale, or that the mechanisms of thermal adaptation are not reflected in rRNA-based assessments of community structure. On the other hand, temperature-driven patterns in aquatic microbial community composition (Crump and Hobbie 2005; Fuhrman et al. 2006; Hullar et al. 2006; Shade et al. 2007) suggest that the mechanisms driving thermal adaptation in these ecosystems are phylogenetically conserved.

As the climate changes, microbial communities have the potential to adapt to altered thermal regimes. The degree to which they adapt will be constrained by the diversity of traits within the taxa that compose the extant community, as described above, but also by resource availability. When communities composed of specialists are shifted beyond their adapted range, large shifts in physiology (e.g. respiration) can occur with direct effects on ecosystem processes (e.g. CO_2 efflux). Eventually these shifts should lead to a competitive disadvantage and shifts in community composition. However, in nutrient rich environments, populations remain in high cell abundance beyond their optimal range resulting in sustained physiological shifts (Hall et al. 2008). Hall et al. (2008) showed in a theoretical study that the competitive advantage of the warm adapted species is lost under higher resource supply, so that the cold adapted species were maintained beyond their thermal niche. This result was supported by a study of two freshwater bacterial isolates that demonstrated that acclimation to higher temperature was resource dependent (Hall et al. 2010). In a separate study, Arctic marine bacterioplankton did not demonstrate nutrient limitation near ambient temperature (Kritzberg et al. 2010); therefore the authors concluded that the increase carbon demand of the microbial community may be sustained over prolonged periods. Strong temperature dependence of microbial respiration has also been noted in boreal lake sediments (Gudasz et al. 2010) suggesting that these thermally stable environments should also be highly impacted by climate change, consistent with the mechanisms discussed above.

Microbial adaptation to altered precipitation regimes

The principles that govern microbial adaptation to shifting temperature regimes can be generalized to changes in other environmental parameters likely to be influenced by climate change and that are key drivers of microbially mediated biogeochemical cycling. For example, soil moisture, which is likely to be influenced by climate change, is an important master variable in microbially mediated biogeochemical processes (Firestone and Davidson 1989; Wilson and Griffin 1975). Soil moisture is a strong proximal control on the rates of microbial function: the rates of aerobic processes increase with increasing soil moisture (up to the point where oxygen becomes limiting). However, the historical soil moisture regime experienced by a microbial community can also act as a distal control on contemporary rates (Evans and Wallenstein 2011).For example, the slope of the relationship between soil moisture and process rates could differ between microbial communities due to community-level adaptation to different moisture levels, in the same manner that desert plant communities are adapted to function at lower soil moisture than are plant communities from mesic climates. At the community-level, the aggregate moisture tolerance of these communities is likely to be skewed towards higher activity under low moisture conditions, because they are assembled of taxa that tend to be specialists at functioning under low moisture conditions. The trade-off for this trait is that these communities should have lower maximal activity rates at higher moistures than communities adapted to higher moisture. We hypothesize that microbial communities inhabiting environments that experience a range of soil moisture levels within a typical year are composed of generalist taxa with broad moisture tolerance, and are thus able to maintain function under a broad range of soil moisture levels. The trade-off for the trait of broad moisture tolerance is a lower maximal activity rate than specialists at any particular moisture level. An alternative possibility is that these communities are assembled of specialist taxa that have narrow moisture tolerances, collectively allowing the community to maintain function across a broad range of soil moisture levels. However, we speculate that this is unlikely unless the frequency of moisture fluctuation is shorter than the generation time of the constituent populations, because these specialists would also need to be adapted to survive long periods of inactivity when conditions are outside of their soil moisture niche, which is a resource intensive life-history strategy.

Another ecological trait that affects fitness under changing precipitation regimes is the ability to maintain function in response to moisture pulses, which can be stressful to microbes due to rapid changes in redox status and osmotic and matric potential. There are multiple strategies that can be considered adaptations to soil moisture pulses (Schimel et al. 2007). First, microbes can be ‘resistant’ to moisture pulses, meaning they are able to maintain function without a physiological response. However, the trade-off for this strategy is that resources must be allocated to building structures such as the thick peptidoglycan cell walls found in gram-positive bacteria, which should negatively impact growth rates. An alternative strategy can be generalized as ‘resilience’ or the ability to quickly recover following moisture pulses. Taxa that have adapted this strategy are generally susceptible to cell death in response to rewetting stress, but they are capable of rapid population growth from surviving cells and may quickly recover(Lennon and Jones 2011). However, this strategy requires high resource availability to be competitive since high growth rates can be inversely correlated with low resource use efficiency (Pfeiffer et al. 2001), another trade-off that should influence community structure. Finally, microbes can have inducible mechanisms for coping with rewetting stress. These mechanisms, such as the production of osmolytes during drying followed by release during rewetting, require substantial resource investment, and may constrain microbial function when this mechanism is induced (Sleator and Hill 2002). The relative fitness of each strategy may depend on factors such as resource availability and predation rates—all of which vary at fine spatial scales (Young et al. 2008) and change through time.

At the community-level, the average aggregate tolerance to moisture pulses is a product of the increased fitness associated with each of these strategies relative to costs of the associated trade-off. A soil microbial community inhabiting tropical soils with a fluctuating moisture regime was found to be highly adapted to this precipitation regime in that it was able to maintain function (respiration, methanogenesis, N_2O production, and iron reduction) in response to experimental cycles in redox potential (DeAngelis et al. 2010). This community appears to be assembled primarily of taxa that are specialized in maintaining activity under fluctuating conditions. However, there is likely a trade-off to this trait because when soils from a fluctuating environment were incubated under static moisture conditions, community composition changed (Pett-Ridge and Firestone 2005), likely favoring taxa that are either moisture generalists or are specialists for a more constant moisture regime. In a grassland soil, Evans and Wallenstein (2011) found that microbial communities exposed to a decade of experimentally intensified precipitation regime were adapted to moisture pulses in that their activity rates were more constant in the face of laboratory moisture pulses compared to soils from the ambient precipitation regime. However, the microbial communities from the ambient precipitation regime at this site were able to adapt within 110 days, apparently through a shift in community composition (Evans and Wallenstein 2011). As microbial communities adapt to altered precipitation regimes, it is likely that taxa with a range of adaptive strategies will co-exist, and it is difficult to predict which adaptations will be favored. Because ecological trade-offs are ultimately biochemical in nature, identifying the mechanism behind the trait that is adapting will help identify the trade-off with other traits.

How do these adaptive mechanisms translate to ecosystem level effects? All of these adaptations to moisture require allocation of resources including the primary macronutrients: C, N, and phosphorus (P). Therefore, we might expect to observe patterns in microbial biomass across precipitation gradients. Here we note two studies that report results consistent with our physiological mechanisms for adaptation described above. First, the metabolic quotient (qCO_2; respiration/microbial biomass) of the soil microbiota decreased with increasing annual precipitation across a climatic gradient on the Mongolian Steppe (Liu et al. 2010). In other words, carbon use efficiency (CUE) declined with decreasing soil moisture, suggesting higher maintenance costs at lower soil moistures. In desert soils, microbial biomass C:N increased with increasing annual precipitation, consistent with an investment in C-rich solutes at low soil moisture (Gallardo and Schlesinger 1992). These shifts in C:N and CUE may be driven in part by shifts in community structure at broad phylogenetic levels. A recent culture based study suggested that the higher C:N of fungal biomass relative to bacteria resulted in increasing CUE as fungal:bacterial ratios increased (Keiblinger et al. 2010). These examples independently suggest that microbial adaptation to intensified precipitation regimes will be constrained in soils where labile C is limiting. Similarly, if adaptation to changing temperature is dependent on the ability to synthesize novel phospholipids de novo (Hall et al. 2009), this would imply that shifts in thermal regimes will alter microbially-mediated P cycling in aquatic environments. Marine studies have shown that under chronic P limitation, some cyanobacteria substitute sulfolipids for phospholipids (Van Mooy et al. 2006). Thus, increasingly dynamic temperature regimes may increase P use by the extant microbial community and alter P cycling at the ecosystem level. Each of these examples suggest that adaptation of microbial communities and the mechanism by which the communities adapt can have significant influence on the rates of biogeochemical processes.

Integrating microbial adaptation and biogeochemistry

The framework we have presented provides a basis for making predictions about where, when, and how microbial community adaptation will affect ecosystem responses to climate change. Specifically, we make the following predictions about the types of environments where microbial adaptation is most likely to mitigate the affects of climate change on ecosystem function:

(1) Environments with low intraannual climate variability are more likely to experience large biogeochemical shifts due to a lag in microbial adaptation relative to highly variable environments. In relatively constant environments, the rate of adaptation will be limited by mass effects (e.g. immigration), and members of the extant communities will be forced to function beyond their optimal environmental niche resulting in perturbations to existing biogeochemical cycles (e.g. increased CO_2 flux due to stimulated respiration). Environments that

experience a broader range of climate on an intraannual basis, should more rapidly adapt to changing climate by shifting the relative abundance of their constituent populations (e.g. shifting community structure).

(2) Resource availability should constrain the rate and extent of community adaptation and will therefore also affect the magnitude of the biogeochemical shift due to climate change. In low resource environments, acclimation of the extant community (i.e. phenotypic plasticity) will be limited due to the resource costs of physiological adjustments. In addition, shifts in community structure will be slow due to resource limitation of growth rate of the constituent populations. In high resource environments, low diversity communities will be able to achieve maximal phenotypic plasticity, while more diverse communities will respond rapidly through shifts in community structure (Fig. 3).

(3) The magnitude of the biogeochemical perturbation in response to climate change for a given environment will be determined by the rate of environmental change relative to the rate of community adaptation. Therefore, in order to better project the potential impact of climate change on biogeochemical processes, research questions should focus on the relationship between the rate of environmental change and the dominant mechanism for community adaptation in that environment. The greater the disparity between those two rates, the greater the potential for a large perturbation to the biogeochemical status quo due to climate change.

To make headway in improving projections of biogeochemical responses to climate change, we suggest a three-pronged approach. First, the measurement of community-level traits should become common practice, in contrast to the current emphasis on measuring potential rates under idealized conditions or net rates under fluctuating field conditions (Todd-Brown et al. 2011). For example, rather than measuring nitrification potential under optimized conditions, a more useful approach would be to measure nitrification kinetics across a range of soil moisture content and temperatures in lab assays. Second, researchers should measure the rate of change in community-level functional traits in response to changes in environmental conditions. This can be done by evaluating the time it takes a community to return to a basal process rate (e.g. respiration) after an environmental perturbation (e.g. increased temperature). Third, new biogeochemical models need to be developed that can incorporate empirical measurements of community-level functional traits (McGuire and Treseder 2010; Moorhead and Sinsabaugh 2006). By integrating an improved knowledge of microbial functional traits into existing models, we will improve our ability to predict when and how microbial adaptation will influence the rate of ecosystem processes under future climate regimes (Allison et al. 2010).

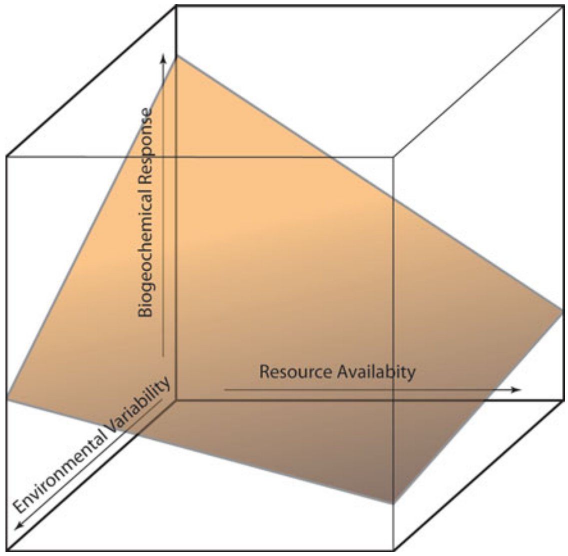

Fig. 3 Due to the microbial dynamics outlined in the text, predicted biogeochemical response to climate change varies with environmental stability (which drives microbial trait diversity) and resource availability. The largest biogeochemical response to climate change should be in stable (i.e. low temporal variability), oligotrophic environments (*grey region* of the plane), while the smallest response (due to rapid adaptation of the microbial community) should be in temporally variable, resource-rich environments (*dark orange region* of the plane)

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