Microbial Community-Level Responses to Warming and Altered Precipitation Patterns Determine Terrestrial Carbon-Climate Feedbacks

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Matthew D. Wallenstein

Contents

Abstract

Climate change will affect the biogeochemical processes driven by the complex microbial communities that inhabit soils. Microbial responses to climate change can result in both negative and positive feedbacks through soil decomposition and the release of CO_2 and CH_4 to the atmosphere. While the relationships between temperature and moisture with the rates of microbial processes are well known, it is possible that these relationships could change if microbial communities adapt to climate change. For example, the stimulation of soil respiration by experimental warming often declines after several years and has been attributed to thermal acclimation of microbial communities. Similarly, microbes could adapt to changes in precipitation regimes. Here, I review evidence for and against microbial adaptation, in relation to a framework for predicting when and where adaptation is most likely to affect climate-carbon feedbacks. While microbial community-level physiology can determine the rates of biogeochemical processes, there is much to learn before we can integrate these responses into a predictive framework.

M.D. Wallenstein
Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA

Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO, USA
e-mail: matthew.wallenstein@colostate.edu

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Introduction

As our climate changes in the coming decades, how will the microorganisms that drive biogeochemical cycling on Earth respond? Microbial responses to climate change can result in important climate-carbon feedbacks because microbial decomposition returns the carbon (C) that is fixed by plants through photosynthesis to the atmosphere as CO_2 or CH_4 (Fig. 41.1). One might assume that the responses of microbial activities to changes in the abiotic environment are easy to predict. After all, the effects of temperature and moisture on microbial processes such as litter decomposition or nitrification have been well described for decades. Based on these well-known relationships, most models assume that climate warming will stimulate soil decomposition, and that increased frequency and duration of droughts due to the intensification of the hydrological cycle will decrease microbial activity. Thus, the terrestrial climate-carbon feedback will depend on the balance of net primary productivity and decomposition (Fig. 41.1).

One might also assume that unlike plants or animals that may face challenges in migrating to suitable habitats as their local climate changes, the fast life cycle and widespread distribution of microorganisms mean that climate change adaptation is not important for microbes. However, recent evidence suggests that these long-held assumptions may not always apply, and that microbial responses to climate change can have direct effects on the rates of biogeochemical processes and cascading effects on all other organisms that depend on microbial activities for their own well-being.

Soils are rich habitats that support an incredible diversity of bacteria, fungi, and archaea that perform an equally diverse range of functions. Collectively, soil microbes play a key role in nutrient cycling, decomposition, degradation of pollutants, and in providing clean water. Recently developed molecular techniques have allowed scientists not only to discover the extent of this diversity but also to characterize the biogeography of microbes. For example, the distribution of bacterial phyla appears to be most strongly affected by soil pH and the availability of carbon (C) in soils (Fierer et al. 2007). Unlike macroorganisms, the diversity of microorganisms does not follow a latitudinal gradient, indicating that microbial taxa have adapted to the full range of climate on Earth. Are microorganisms uniquely adapted for the habitats they reside in? Do microbial communities adapt to changing conditions? The answers to these questions – still up for debate – have critical implications for the way in which microbes will respond to changes in their environment.

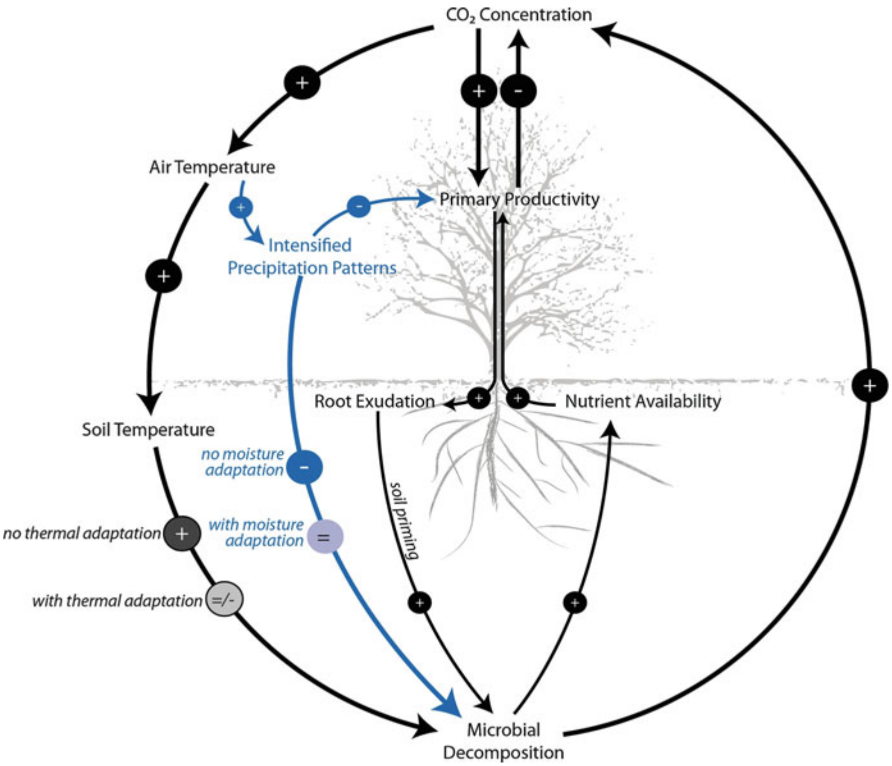

Fig. 41.1 Mechanisms for positive (+) and negative (−) feedbacks between climate change and microbial carbon cycling. Climate warming is expected to result in a positive feedback due to increased microbial decomposition and respiration, unless thermal adaptation occurs. Intensified precipitation patterns resulting in increased droughts may decrease soil carbon fluxes unless microbes adapt to new precipitation regimes

Microbial Responses to Climate Change: The Role of Community-Level Adaptation

In most locations, soil temperature and moisture vary widely across seasons or even within a single day. Microbial metabolism generally increases with temperature and increases with soil moisture to the point where oxygen diffusion becomes limiting. These changes in microclimate can result in seasonal turnover of microbial communities, as taxa that are better adapted to different climate conditions proliferate when conditions are favorable. In response to experimental climate change, the composition of bacterial communities (determined with molecular techniques) changed in the majority of studies (Allison and Martiny 2008). Even without a change in overall community composition, the taxa that are metabolically active can change rapidly with changes in microclimatic conditions (McMahon et al. 2011). In fact, the majority of microbial cells in soils are dormant at any particular time, laying in wait for substrates or favorable conditions (Lennon and Jones 2011). Thus, one might speculate that microbial communities are unusually well adapted to maintain function in the face of climate change. However, as the composition of these complex communities change, they may not function in the same way.

One trait that differs between microbial taxa is their response to temperature. For example, bacteria from cold environments tend to have lower temperature optima than their counterparts from warmer climates. The same pattern has been observed at the community level. For example, the temperature sensitivity of soil N mineralization rates was greater for soils originating from colder climatic zones (mean annual temperature (MAT) $<2\ ^{\circ}\mathrm{C}$) compared with warmer climate zones (mean annual temperature $>6\ ^{\circ}\mathrm{C}$) (Dessureault-Rompre et al. 2010). Similarly, the temperature sensitivity of substrate utilization was correlated to the MAT of native habitat for soil communities (Balser and Wixon 2009). These changes in community-level temperature sensitivity can apparently occur rapidly. 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.

The ability of microbial communities to adapt to climate change has important implications for predictions of future biogeochemical process rates. This was demonstrated by Allison et al. (2010) who showed that acclimation of microbes to warming (through decreases in the temperature sensitivity of enzyme activities) can decrease soil C losses (Fig. 41.1). Furthermore, each specific process will have a different response to warming. For example, in the absence of physicochemical protection, the decomposition of chemically complex soil organic matter (SOM) constituents will increase more in response to warming than labile constituents (Conant et al. 2011). Several studies have reported that extracellular enzymes that degrade N-rich compounds such as proteins and chitin are less temperature sensitive than enzymes that degrade C-rich compounds such as cellulose and hemicellulose (Wallenstein et al. 2009), which could lead to increasing N-limitation with warming. In turn, this would constrain net primary productivity, which would otherwise counteract the positive carbon-climate feedback related to the stimulation of SOM decomposition from warming (Fig. 41.1).

As with warming, microbial communities may be adapted to precipitation regimes, in the same manner that plant and animal communities show clear adaptation to their local climates. 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. 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). Thus, we cannot necessarily extrapolate the moisture sensitivity of microbial processes from extant communities under the current climate to future conditions.

While it is clear that microbial adaptation to climate change could be important, it is also clear that microbial communities are rarely optimally adapted to maintain function in their local environment. For example, temperature optima for growth and enzyme activity are often greater than in situ temperatures in their environment. What controls the rate at which microbial communities adapt to changing climates? Wallenstein and Hall (2011) developed a conceptual framework for predicting where microbial adaptation is most likely to occur. Adaptation is constrained by ecological trade-offs. For example, an increase in maximal growth rate is typically associated with a decrease in resource-use efficiency. Thus, thermal adaptation is more likely to occur in soils with high nutrient availability. In relatively invariable climates such as the tropics, microbial communities are likely composed of thermal specialists that will be unable to adapt to climate change and may be affected by the rate at which exogenous taxa from warmer climates are dispersed to those soils. In contrast, soils from temperate climates that experience wide temperature ranges are likely composed of thermal generalists that can more easily acclimate to climate change. This framework suggests that the most dramatic effects of climate warming on microbial processes are likely to occur in thermally stable environments where warming will extend temperatures beyond the historical thermal envelope. Similarly, sites that experience high seasonality or interannual variability in precipitation regimes will be less affected than sites with constant soil moisture like wetlands threatened with drought or deserts facing increasing precipitation events.

Conclusions

Human activities are already altering the Earth's climate in complex ways. As the mean global temperature continues to increase, primarily due to increased concentrations of greenhouse gasses, the nature of climate change varies across locales. One effect of warming is increased evaporation, which can result in soil drying in the short term but at regional scales results in intensified precipitation regimes. In the short term, warming will stimulate microbial metabolism, but as highlighted above, microbial responses over the longer term may mitigate this response. In addition, more rapid soil drying could counteract warming effects, and the stress induced by intensified precipitation regimes can cause microbes to reallocate resources away from growth toward maintenance. The simple case where long-term microbial responses to climate change are consistent with short-term assays measuring temperature or moisture effects on biogeochemical rates is likely to be rare. Rather, current evidence suggests that microbial physiology needs to be considered as an integral component of climate change responses, especially since microbial responses to climate change will feedback to affect the concentration of greenhouse gasses in our atmosphere. To achieve this, there is much to learn about the constraints on microbial adaptation, the linkages between microbial community composition and function, and interactions between above-ground and below-ground processes.

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