Integrating microbial ecology into ecosystem models: challenges and priorities

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Abstract Microbial communities can potentially mediate feedbacks between global change and ecosystem function, owing to their sensitivity to environmental change and their control over critical biogeochemical processes. Numerous ecosystem models have been developed to predict global change effects, but most do not consider microbial mechanisms in detail. In this idea paper, we examine the extent to which incorporation of microbial ecology into ecosystem models improves predictions of carbon (C) dynamics under warming, changes in precipitation regime, and anthropogenic nitrogen (N) enrichment. We focus on three cases in which this approach might be especially valuable: temporal dynamics in microbial responses to environmental change, variation in ecological function within microbial communities, and N effects on microbial activity. Four microbially-based models have addressed these scenarios. In each case, predictions of the microbial-based models differ—sometimes

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substantially—from comparable conventional models. However, validation and parameterization of model performance is challenging. We recommend that the development of microbial-based models must occur in conjunction with the development of theoretical frameworks that predict the temporal responses of microbial communities, the phylogenetic distribution of microbial functions, and the response of microbes to N enrichment.

Introduction

Ecosystem processes are governed to a large extent by microorganisms and their metabolic activities (Schlesinger 1997). For example, microbes perform critical roles in the global carbon (C) cycle, by decomposing organic material and releasing greenhouse gases such as CO_2 and CH_4 into the atmosphere (Conrad 1996). In addition, microbes often respond to alterations in environmental conditions, including many aspects of global change. Anthropogenic N enrichment, global warming, and alterations in water availability have received particular attention in terms of their effects on microbes (e.g., Evans and Wallenstein 2011; Wallenstein and Hall 2011; Yavitt et al. 2011). In field experiments, microbial biomass and/or community composition can be altered by warming (Allison and Martiny 2008 and references therein; Allison and Treseder 2008; Bradford et al. 2008; Castro et al. 2010; Frey et al. 2008; Joergensen et al. 1990; Rillig et al. 2002), N fertilization (reviewed in Allison and Martiny 2008; Lecerf and Chauvet 2008; Treseder 2008), and sometimes in manipulations of precipitation regimes (Castro et al. 2010; Evans and Wallenstein 2011; Hawkes et al. 2011; Schimel et al. 1999; Williams 2007). If these shifts alter rates of decomposition or the production of greenhouse gases, then microbes can potentially mitigate or accentuate climate change (e.g., Strengbom et al. 2002; Todd-Brown et al. 2011; Wagner and Liebner 2009), which is a critical scientific, political, and economic issue (IPCC 2007).

In this idea paper, we ask whether we can improve our predictions of C dynamics in response to global change by explicitly including microbiological details in biogeochemical models, and if so, are the improvements over conventional models (i.e., those with more limited microbial detail) substantial enough to merit the effort? We address C cycling in three cases: temporal dynamics of microbes, variation in ecological function within microbial communities, and N loading in ecosystems. For each case, we first briefly survey pertinent empirical evidence. Next, we present a description of the relevant models and their explicit microbial mechanisms. We performed an exhaustive search for published models that (1) explicitly couple microbes to the processes that they control, (2) predict changes in C dynamics, and (3) are compared with more conventional models. To the best of our knowledge, only the four "case study" models discussed below meet these criteria. We then evaluate the degree to which these models improve predictions of C cycling compared to conventional models. Finally, we provide ideas for prioritizing future work in this area.

Incorporating temporal responses of microbes into ecosystem models

The speed and duration with which microbes respond to global change can influence the extent to which ecosystems form positive or negative feedbacks on global climate (Table 1; Allison and Martiny 2008). Rapid and sustained responses could generate strong feedback loops. For example, if global warming led to sustained (i.e., strong short- and long-term) increases in soil CO_2 efflux, then the greenhouse effect could be greatly amplified (Trumbore 1997). In comparison, if microbes are resistant (i.e., weak short- and long-term), resilient (i.e., strong short-term but weak long-term), or delayed (i.e., weak short-term but strong long-term) in their responses to environmental change, then their contributions to ecosystem feedbacks may be more constrained. For instance, microbial community composition, biomass, and respiration often do not change markedly in response to alterations in water availability in natural systems (e.g., Cruz-Martinez et al. 2009; Evans and Wallenstein 2011; Lutgen et al. 2003; Singh et al. 1989; Vourlitis et al. 2009).

Table 1 Examples of temporal responses of microbes to global change, with potential feedbacks on climate

Short-term response	Long-term response	Type of response	Feedback potential	Potential contributing mechanisms	Example of positive feedback (i.e., acceleration of global warming)	Example of negative feedback (i.e., mitigation of global warming)
Strong	Strong	Sustained	Significant	Physiological responses, phenotypic plasticity, population growth and turnover, adaptation, community composition shifts	C fixation by phytoplankton declines under warming (Behrenfeld et al. 2006)	C sequestration by mycorrhizal fungi increases under elevated CO_2 for up to 20 years (Rillig et al. 2000)
Strong	Weak	Resilient	Temporary	Adaptation, community composition shifts, cumulative physiological effects, physiological acclimation, population recovery	Warming-induced increases in soil respiration last <10 years (Rustad et al. 2001)	Severe fires reduce microbial respiration for several years (e.g., Waldrop and Harden 2008)
Weak	Strong	Delayed	Low where global change is transitory	Adaptation, change in community composition, cumulative physiological damage, physiological acclimation	N_2O production increases with duration of N fertilization (Hall and Matson 1999)	N fertilization-induced declines in decomposer biomass increase with exposure time (e.g., Treseder 2008)
Weak	Weak	Resistant	Minimal	Dormancy, slow population turnover, generalist taxa, physiological adjustments	Stable microbial biomass or respiration under drying/wetting (e.g., Evans and Wallenstein 2011; Lutgen et al. 2003; Singh et al. 1989; Vourlitis et al. 2009)	

Changes in microbial activity can occur via a number of non-exclusive mechanisms, including physiological responses (e.g., Davidson and Janssens 2006; Schimel and Weintraub 2003), phenotypic plasticity (e.g., Schimel et al. 2007), population growth and turnover (e.g., Schimel et al. 1994), evolutionary adaptation (e.g., Portner et al. 2006), or shifts in community composition (e.g., Balser et al. 2002), each with potentially different rates of response. For instance, thermodynamic principles suggest that microbial enzyme activity and respiration should increase rapidly in response to rising temperatures, resulting in increased emissions of CO_2 to the atmosphere and a positive feedback on global warming (Davidson and Janssens 2006). Nevertheless, in field studies the warming effect often tends to diminish over time (Rustad et al. 2001), for reasons that are a matter of debate. Perhaps efficiencies of microbial growth or enzyme activities decline, enzymes are down-regulated, or slower-respiring taxa become dominant in the community (Bradford et al. 2008; Lopez-Urrutia and Moran 2007; Steinweg et al. 2008). The positive feedback could be dampened as a result, and the time lag between initial response and development of acclimation would influence the long-term strength of the feedback.

Case study for temporal responses: modeling microbial acclimation to global warming

Many conventional models of soil C dynamics predict that rates of microbial respiration will increase exponentially as temperatures rise, leading to a long-term decline in soil C sequestration (Eliasson et al. 2005; Kirschbaum 2004; Parton et al. 1988). However, in field-based studies, warming-induced increases in soil respiration rates can be short-lived, returning to pre-warming levels within a decade or so (Jarvis and Linder 2000; Luo et al. 2001; Melillo et al. 2002; Oechel et al. 2000; Rustad et al. 2001). One potential mechanism for this acclimation could be the depletion of labile C pools as organic matter turnover increases (Eliasson et al. 2005; Kirschbaum 2004). An alternate possibility is that the capacity of the microbial community to maintain these elevated respiration rates decreases over time, owing to acclimation. Acclimation can occur via

plasticity in physiological traits, shifts in community composition, or evolutionary trade-offs associated with adaptation to the new temperature regime. However, empirical evidence for this mechanism is mixed in field- (Bradford et al. 2008) and laboratory-based (Hartley et al. 2008) manipulations.

In a recent study, Allison et al. (2010) constructed a soil model that incorporated two mechanisms of microbial acclimation to predict soil C dynamics under 5°C warming. For the first mechanism, they allowed C use efficiency (i.e., microbial biomass produced per unit C assimilated) to decline with increased temperature. This response has been observed empirically (Steinweg et al. 2008), but not in every case (Lopez-Urrutia and Moran 2007). For the second mechanism, they forced a 50% reduction in maximal activity (V_{max}) of respiratory enzymes along with a 50% increase in their half-saturation constant (K_m) under higher temperatures. Together, these two mechanisms produced temporal patterns of soil respiration and microbial biomass that were qualitatively consistent with field data, although formal validation exercises were not performed. This model formulation elicited a subtle increase in soil C storage over thirty years of warming. In contrast, a comparable conventional model (without the two mechanisms) predicted a substantial decrease in soil C storage over the same time frame (Allison et al. 2010). Although further study is required to determine if these particular mechanisms are actually operating in the field, this case study illustrates that incorporation of temporal responses of microbes could reverse the direction of predicted soil C storage under global warming.

Case study for temporal responses: modeling microbial responses to moisture pulses

Another facet of climate change is the alteration of precipitation regimes. Over the next century, precipitation is expected to occur more sporadically, resulting in longer dry periods punctuated by pulses of moisture (Bell et al. 2004; Christensen et al. 2007). Although conventional models of soil dynamics often include moisture-response functions, they generally simulate quasi-steady-state conditions, which may not necessarily be appropriate for pulsed events (Melillo et al. 1995; Schimel et al. 1997; Smith et al.

1997). In a laboratory incubation, Miller et al. (2005) added water to chaparral soil every two or four weeks, allowing the soil to dry between additions. Additional treatments experienced constant moisture. Miller et al. (2005) found that the amount of C released via microbial respiration was higher in the pulsed than in the constant moisture treatments. Similar results have been observed in laboratory-based experiments on C-amended soils (Sorensen 1974) and annual grassland soils (Xiang et al. 2008). Together, these studies imply that sporadic rainfall may induce greater soil C loss than might be predicted by models of longer-term dynamics.

Lawrence et al. (2009) constructed soil models with and without explicit microbial mechanisms, and compared their accuracy in predicting the temporal pattern of soil respiration in the Miller et al. (2005) study. The models range in complexity and are either conventionally-structured (with first-order controls over turnover of active, slow, and passive soil C pools) or include more detailed microbial mechanisms (by splitting the active C pool into microbial, extracellular enzyme, or bio-available C pools). In the most complex microbial model, extracellular enzymes are produced in proportion to microbial biomass, and their activity generates bio-available C that accumulates if not immediately taken up by microbial biomass. This model assumes that uptake of bio-available C is sensitive to soil moisture, but enzyme activity is not. As a result, the pool of bio-available C expands during dry periods and then is processed quickly following a moisture pulse. Compared to the other models, this enzyme model predicts most accurately the pattern of soil respiration observed by Miller et al. (2005) in the 2 week rewetting treatment. However, this model performs more poorly than the others in regard to the constant moisture treatments, where respiration rates are either over- or underestimated, depending on the moisture level. Although the enzyme model functions well specifically for the pulsed system of Miller et al. (2005), it may not capture microbial mechanisms that operate under wide-ranging precipitation regimes. Other mechanisms such as breakdown of aggregates or lysis of microbial cells could be important (Fierer and Schimel 2002), but more empirical data are required to directly assess these possibilities and to parameterize and validate potential models (Lawrence et al. 2009).

Incorporating functional groups of microbes in ecosystem models

The idea that microbial community composition could influence ecosystem functioning has received much recent attention (Balser et al. 2002, 2006; Cavigelli and Robertson 2000; Fierer et al. 2007; Green et al. 2008; Levine et al. 2011; Schimel and Gulledge 1998). Microbial communities can shift under warming, N fertilization, and precipitation manipulations in natural ecosystems (Allison and Martiny 2008 and references therein; Castro et al. 2010; Evans and Wallenstein 2011; Hawkes et al. 2011; Schimel et al. 1999; Williams 2007), but consequences of these shifts for C dynamics are difficult to predict (Allison and Martiny 2008; Kent and Triplett 2002; Rousk et al. 2009). If microbial species vary in their ecological functions (e.g., decomposition of particular organic compounds) within ecosystems, then alterations in microbial community composition could accentuate or ameliorate ecosystem feedbacks. Alternately, if functions are highly redundant among taxa, then shifts in communities could be negligible.

Generally, functions that are more broadly distributed among taxa are likely to be more redundant within a given community. At least some species of bacteria and fungi overlap in their contributions to ecosystem processes (Strickland and Rousk 2010; Yin et al. 2000). For instance, multiple taxa can degrade cellulose or take up NH_4^+. Alternately, the random arrangement of chemical groups within humic compounds in the soil could provide innumerable targets for specialized decomposers, resulting in diverse opportunities for niche specialization. Some processes such as glycolysis and denitrification are conducted among a wide phylogenetic distribution of taxa (Philippot 2002), while others like glomalin production are more narrowly distributed (Wright and Upadhyaya 1996). Indeed, McGuire et al. (2010) found that use of tannin-protein complexes by Alaskan fungi is more phylogenetically clustered than is the use of glutamate, a common amino acid. Altogether, more narrowly-distributed functions may be more sensitive to microbial community composition, and these might benefit most from explicit consideration of separate functional groups in ecosystem models (McGuire and Treseder 2010; Schimel 1995; Schimel et al. 2004).

In microcosm studies of microbial diversity, rates of nutrient transformation often increase linearly as the first several microbial taxa are added (Bell et al. 2005; Degens 1998; Fernandez et al. 2000; Griffiths et al. 2000; Naeem et al. 2000; Naeem and Li 1998; Setala and McLean 2004; van der Heijden et al. 1998; Violi et al. 2007; Wertz et al. 2007; Wohl et al. 2004). These positive diversity-function relationships are expected if the microbial taxa perform different ecological functions (Heemsbergen et al. 2004) such as transforming different types of compounds. In a laboratory experiment, Strickland et al. (2009) inoculated plant litter with communities of microbes derived from grassland, pine, and rhododendron-dominated habitats. They found that community type explained between 22 and 86% of the variation in decomposition rates across samples, providing evidence for the functional dissimilarity of microbial communities. Even so, contrasting microcosm studies have documented significant redundancy in function among microbial groups (Kemmitt et al. 2008; Rousk et al. 2008), so this issue remains an important matter of debate.

Case study: modeling decomposition by distinct functional groups of microbes

If functional groups of microbes vary in their responses to environmental conditions, then rates of decomposition of organic material could be altered as those conditions change. Under these circumstances, models that distinguish among functional groups might better predict decomposition rates than those that gather microbes into a "black box". The guild-based decomposition model (GDM) takes this approach (Moorhead and Sinsabaugh 2006). The GDM uses three microbial guilds that target different organic matter components while varying in their responses to N availability. "Opportunists" colonize litter during the first stages of decay and consume labile, soluble C. They have a high N demand driven by high growth rates, and they are displaced by slower-growing guilds after the soluble-C substrate pool is depleted. "Decomposers" displace opportunists from litter and decompose cellulose (and, to a lesser extent, lignin) by producing cellulases. They have a lower N demand than opportunists and are more efficient at N uptake and retention. "Miners"

specialize on lignified cellulose, lignins and other condensed aromatic polymers by producing ligninases. They have the slowest relative growth rate and thus the smallest N demand. The GDM calculates litter decay rate as a function of the combined activity of the three guilds. Thus, N effects on decomposition occur as a function of the N demands of different microbial guilds in relation to pools of external N.

In general, the GDM predicts well the rates of total mass loss (soluble C + holocellulose-C + lignin-C) in 64 empirical decomposition studies, with mean r^2 values of 0.80–0.99 between simulations and empirical results (Herman et al. 2008). However, in terms of individual components of litter, GDM overestimates loss rates of soluble C and underestimates loss rates of holocellulose-C. Moorhead and Sinsabaugh (2006) compared the behavior of two versions of their GDM: one with three distinct guilds, and one with a single pool of decomposers ("black box"). They found that in the more complex version, the amount of relatively stable C remaining after litter decomposition was lower overall and was less sensitive to N relative to the black box version. In fact, in the black box version, the amount of stable C remaining tends to increase with N enrichment. In contrast, the complex version predicts a slight decline. Unfortunately, few decomposition studies have provided chemistry and mass loss data of sufficient resolution to rigorously validate GDM under multiple levels of N availability, and almost none have determined the identity and abundance of the relevant microbial guilds in situ.

Incorporating microbial responses to N in biogeochemical models

Nitrogen fertilization, cultivation of N-fixing crops, and fossil fuel burning by humans have approximately doubled the rate at which reactive (i.e., bioavailable) N is deposited on ecosystems globally (Galloway and Cowling 2002; Holland et al. 2005; Vitousek et al. 1997). In addition, global warming could stimulate N mineralization in soils—Rustad et al. (2001) noted a 46% increase, on average, in net N mineralization rates across 12 field-based warming experiments. Owing to the complexity of nitrogen dynamics, however, it is currently difficult to predict the potential feedbacks of N enrichment on climate (Holland et al. 2004).

At this point, it is not clear whether N enrichment will increase or decrease global soil C storage and the release of CO_2 or CH_4 into the atmosphere. In forests, N additions increase soil C content while reducing microbial biomass, heterotrophic respiration, and soil CO_2 efflux when averaged across 34–50 field-based experiments (Janssens et al. 2010). Nevertheless, as with many meta-analyses, N responses vary widely among studies, ranging between 57% decreases to 63% increases in heterotrophic respiration (Janssens et al. 2010). In other biomes, field-based N fertilization has elicited a range of responses in soil C stocks, including increases of 43% in an agricultural system (McAndrew and Malhi 1992) and declines of 17% in a temperate grassland (Rice et al. 1994). Wide variability in N effects among ecosystems has proven a challenge in forming large-scale predictions regarding ecosystem feedbacks on climate (Hobbie 2008).

A portion of this variability among ecosystems might be attributable to differences in the composition of soil organic matter among ecosystems, since N additions can speed the turnover rates of certain C fractions while slowing others (Fog 1988). In a meta-analysis of over 500 field- and laboratory-based decomposition studies, Knorr et al. (2005) observed that N additions stimulated mass loss rates of high quality (i.e., low lignin/high nutrient) plant litter by 2% while inhibiting loss rates of low quality litter by 5%. For soil organic matter, Neff et al. (2002) similarly found that N enrichment in the field increased the turnover rate of light (i.e., decadal residence times) compounds, and decreased turnover rates of heavy (i.e., multidecadal to century residence times) compounds in an alpine ecosystem. Comparable field-based results have been observed in a mixed conifer forest (Nowinski et al. 2009). It remains to be seen, though, whether these responses in soil organic matter (as opposed to litter) occur across a broad range of ecosystems.

The specific microbial mechanisms underlying opposing N responses for labile versus recalcitrant organic material are not well-understood. In a number of ecosystems, field-based N fertilization enhances the activity of extracellular enzymes that target labile compounds or reduces those that target recalcitrant compounds (Allison et al. 2008; Keeler et al. 2009; Waldrop et al. 2004). Microbes may be regulating the production of these enzymes by altering resource allocation following N fertilization. For example, an

investment of N toward the construction of labile C-targeting enzymes could increase supply rates of energy or C to support microbial growth. In this case, we would expect an increase in microbial biomass concurrent with an increase in activity of labile C-targeting enzymes (Schimel and Weintraub 2003). At the same time, microbes may down-regulate the production of extracellular enzymes that target recalcitrant C such as lignin and other polyphenols. Since these compounds are often cross-linked with nitrogenous compounds, microbes may invest in their breakdown to obtain N when N is scarce; when N is abundant, investment in these enzymes could decrease (Fog 1988). In this case, microbial biomass should remain constant (if N were not previously limiting to growth) or increase (if N limitation were alleviated). Alternately, evolutionary constraints may elicit negative effects on lignin-decomposing microbes (e.g., white rot fungi or actinobacteria) under high N conditions. This functional group might be relatively susceptible to toxic compounds that are produced via condensations between soil organic matter and nitrogenous compounds (Fog 1988; Haider and Martin 1967; Hodge 1953; Soderstrom et al. 1983). On average, microbial biomass decreases moderately (about 15%) in response to N enrichment in 29 field studies, and toxicity effects are one potential mechanism (Treseder 2008). However, a general decline in microbial abundance is not necessarily consistent with the increase in labile C use observed in some studies. Either the augmentation in labile C turnover was not common to the studies included in the Treseder (2008) meta-analysis, or the use of labile C does not scale linearly with the biomass of the microbial community as a whole.

Case study: modeling N feedbacks on global carbon cycling

Global C models occasionally incorporate N dynamics, but typically in a limited manner. Gerber et al. (2010) have developed one of the more comprehensive models of C–N interactions to date. They integrated a number of mechanisms that allowed soil microbes to respond to N, with consequences for C and N dynamics. Specifically, they assume that decomposers are N-limited, so that mineralization of litter C and N respond positively to inorganic N

availability. To ensure that N limitation of microbes is sustained, they incorporate a mechanism restricting microbial activity to the litter surface. In addition, C and N fluxes into the recalcitrant pool are allowed to increase as N availability rises, based on empirical findings from natural ecosystems (e.g., Neff et al. 2002; Nowinski et al. 2009). Gerber et al. (2010) did not determine if the inclusion of these microbial mechanisms improves the accuracy of the model. A sensitivity analysis indicated that compared to a conventional model formulation with no C–N feedbacks, addition of the microbial mechanisms results in a decrease in the predicted total terrestrial C pool. However, the decrease is subtle—about 6% for a temperate site and 3% for a tropical site. Further validation and experimental data are required to determine whether the microbial mechanisms are operating as assumed, and whether their inclusion in the model improves its accuracy.

Evaluation of model performance

The four case-study models indicate that the addition of microbial mechanisms could alter predictions of C dynamics in ecosystems in some cases (Table 2). Nevertheless, it has not been demonstrated that these additions can improve model performance across a broad range of conditions. Of the four case studies, only Lawrence et al. (2009) benchmarked model performance against empirical data in comparison with a conventional model. The accuracy of the remaining three case-study models was not explicitly evaluated in comparison to conventional models, so it is difficult to determine if the inclusion of microbial mechanisms improved predictions.

Many conventional soil models can fit empirical data reasonably well without a great deal of microbial detail (e.g., t values within $\pm\ t_{crit\ 2.5\%}$ for soil organic C, Smith et al. 1997; r^2 values: 0.72–0.93 for litter mass loss, Zhang et al. 2008). The integration of microbial details into ecosystem models often requires parameterization of new variables that can be difficult to assess (e.g., in situ V_{max} values for extracellular enzymes; Todd-Brown et al. 2011), or the invocation of mechanisms that are relatively unexamined in situ (e.g., moisture sensitivity of enzyme activity versus microbial C uptake, Lawrence et al. 2009). To substantiate the additional effort and

Table 2 Summary of evaluations of case study models

Model	Sensitivity: predictions substantially different from conventional model?	Validation: how accurate is the model?	Benchmark: does incorporation of microbial mechanisms improve the model predictions?
Microbial enzyme model, Allison et al. (2010)	Yes	Qualitatively similar to empirical results	Not determined
EC2, Lawrence et al. (2009)	Yes	Depends on environmental conditions	Yes, under certain circumstances
GDM, Moorhead and Sinsabaugh (2006)	No	Average r^2 values of 0.80–0.99.	Not determined
Version of LM3V, Gerber et al. (2010)	No	Predictions within ±1 standard error	Not determined

complexity of the new model formulations, we recommend performing benchmarking tests in comparison with conventional models (sensu Todd-Brown et al. 2011). Randerson et al. (2009) proposed a framework for benchmarking that includes tests of model performance against multiple sets of observations across a range of ecosystems and temporal scales. In terms of the case-study models, the relevant observations might include heterotrophic CO_2 respiration, extracellular enzyme activity, microbial biomass, relative abundance of microbial functional groups, litter decomposition rate, or soil C stocks. For the first four variables, especially, it is challenging to obtain long-term, high temporal resolution measurements from diverse ecosystems. It is not surprising that benchmarking exercises were limited in most of the case-study models.

Conclusion

Temporal dynamics in microbial responses, variation in ecological function within microbial communities, and effects of N enrichment on microbial activity are three cases in which the addition of microbial mechanisms to biogeochemical models could improve predictions of ecosystem responses to global change. Specifically, microbial responses to global change can be short-lived, as is suggested by warming experiments; or resilient, as has been documented for changes in water availability. These temporal dynamics could mediate positive or negative feedbacks on climate in ways that might not otherwise be predicted by conventional models. Furthermore, empirical studies

have demonstrated that microbial functions are not fully redundant among taxa, and that shifts in community composition can alter biogeochemical functions. "Black box" models may not sufficiently predict soil dynamics following changes in microbial communities. Finally, microbial responses to N enrichment are complex, highly variable, and involve mechanisms that are not well-understood, so it is important to formulate large-scale models that incorporate broadly-applicable N effects on microbial activity. Four case-study models have addressed these scenarios. In each case, additions of microbial mechanisms have altered (but not necessarily improved) model predictions, and the changes were substantial for two of the models.

Future directions

Many opportunities exist for foundational research integrating microbial ecology into ecosystem models, especially within the three highlighted cases (temporal responses, functional groups, and N feedbacks). Theoretical frameworks that provide general guidelines for modelers would be particularly useful for each of these cases. In terms of temporal dynamics, we recommend focusing on the relative rates of global change (i.e., gradual versus abrupt) compared to rates of microbial responses (i.e., sustained, resilient, delayed, or resistant), as discussed by Wallenstein and Hall (2011). In terms of modeling functional groups of microbes and their influence on ecosystems, we might consider the hypothesis that ecosystem processes that are narrowly-distributed within phylogenies should be most sensitive to changes in microbial community

composition (Levine et al. 2011; Schimel 1995; Schimel et al. 2004). If this hypothesis is valid, how might we develop a theoretical framework to predict how various functions (i.e., decomposition of recalcitrant versus labile compounds) are phylogenetically distributed? In addition, explicit incorporation of functional groups into ecosystem models may most likely improve model predictions where microbial species interactions or dispersal limitation of microbial species influence microbial community composition (McGuire and Treseder 2010). In terms of N feedbacks on the C cycle, we need to understand why ecosystems vary widely in responses to N enrichment. Where and when should decomposition rates increase or decrease?

We recommend a few priorities in the structure and evaluation of microbially-detailed models. As Todd-Brown et al. (2011) detail, second-order models that explicitly incorporate microbial biomass may improve predictions of CO_2 efflux and soil C sequestration. Benchmarking with multiple datasets and output parameters is also critical to establish the advantages of microbially-based models in comparison to conventional models. Ideally, modeling efforts would occur in collaboration with empirical campaigns, since model scenarios could inform data acquisition and vice versa.

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