
Climate Change, Microbes and Soil Carbon Cycling

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Timothy H. Keitt, Colin Addis, Daniel Mitchell, Andria Salas and Christine V. Hawkes

Abstract

Microbial responses to climate change will partly control the balance of soil carbon storage and loss under future temperature and precipitation conditions. We propose four classes of response mechanisms that can allow for a more general understanding of microbial climate responses. We further explore how a subset of these mechanisms results in microbial responses to climate change using simulation modelling. Specifically, we incorporate soil moisture sensitivity into two current enzyme-driven models of soil carbon cycling and find that moisture has large effects on predictions for soil carbon and microbial pools. Empirical efforts to distinguish among response mechanisms will facilitate our ability to further develop models with improved accuracy.

Introduction

There is twice as much carbon in soils as in the atmosphere (Jenkinson *et al.*, 1991), making below-ground responses to climate change an important aspect of ecosystem responses and feedbacks to climate. Nevertheless, below-ground responses to climate change remain a large source of uncertainty (Solomon *et al.*, 2007), such that earth system models poorly predict current soil carbon pools (Todd-Brown *et al.*, 2013). This is probably due, in part, to historical assumptions of purely abiotic controls of soil carbon cycling and the lack of a strong mechanistic framework for how soil microbes respond to environmental change and the resulting impacts on the fate of soil carbon (Chapin III *et al.*, 2009; Ogle *et al.*, 2010).

Soil respiration is the main pathway for the transfer of carbon from terrestrial to atmospheric pools

(Schlesinger and Andrews, 2000). Soil microbes may also make a larger contribution to the building of soil organic carbon than previously thought (Kindler *et al.*, 2006; Liang and Balsler, 2008, 2011; Potthoff *et al.*, 2008). For example, mycorrhizal fungi can be the dominant pathway through which carbon from plants enters the soil pool, with hyphal turnover representing ~60% of soil organic matter inputs and the remaining ~40% due to fine root turnover and leaf litter (Godbold *et al.*, 2006). Furthermore, the type of mycorrhizal fungus can determine soil carbon: Averill *et al.* (2014) found that ecosystems dominated by plants colonized by ectomycorrhizal fungi stored 70% more soil carbon per unit nitrogen than ecosystems dominated by plants associated with arbuscular mycorrhizal fungi. Thus, the effects of climate change on the activity and physiology of the soil microbes will partly determine what proportion of annual soil carbon input is respired versus stored in the long-term reservoir of soil organic carbon (Chapin III *et al.*, 2002).

Shifts in microbial community composition, abundance and function have been observed in climate change experiments manipulating temperature, precipitation, carbon dioxide and their interactions (e.g. Castro *et al.*, 2010; Cheng *et al.*, 2012; Harper *et al.*, 2005; Hawkes *et al.*, 2011; Horz *et al.*, 2004, 2005; Lindberg *et al.*, 2002; Liu *et al.*, 2009; Staddon *et al.*, 2003; Zogg *et al.*, 1997). Although results appear to be site specific, some broader patterns can be gleaned from meta-analyses. Based on 32 experimental temperature manipulations, warming increased soil respiration by 20% and net nitrogen mineralization by 46% (Rustad *et al.*, 2001). Blankinship *et al.* (2011) analysed 75 experimental climate studies and found

that bacteria decreased in response to warming, fungi increased in response to altered precipitation, and total microbial biomass increased with elevated carbon dioxide (Blankinship *et al.*, 2011); however, these groups were represented by as few as two studies, so more work is needed to confirm the generality of their responses.

The mechanisms regulating process rates in below-ground ecosystems are complex, lending these systems a high potential for varied and seemingly idiosyncratic empirical behaviour (May, 1976). To usefully integrate empirical data into even more complicated regional and global modelling, below-ground observations must be systematized by comparison with simplified mathematical representations. There exists a long history of terrestrial ecosystem modelling, including below-ground process modelling, but only recently have these addressed variation in microbial functioning (e.g. Allison, 2012; Allison *et al.*, 2010; Orwin *et al.*, 2011; Wang *et al.*, 2014; Waring *et al.*, 2013; Wieder *et al.*, 2013). Furthermore, the role of water in regulating process rates has received comparatively little attention relative to mass-balance and nutrient-driven approaches.

In this chapter, we focus on how soil microbes respond to changes in soil moisture, which is a primary controller of soil microbial activity, but remains poorly understood relative to other factors such as temperature. We first provide an overview of what is known about microbial responses to changes in moisture availability, review microbial mechanisms that are likely to be important for improving our understanding of microbial responses, and discuss the current state of microbial and ecosystem models. In addition, as a demonstration of the potential relevance of moisture to microbial function, we integrate moisture functions into two microbial process models.

Microbial responses to altered soil moisture

The magnitude and shape of microbial functional responses to soil moisture will directly affect ecosystem responses, as well as how we model microbial process responses to climate change. Water is a primary controller of soil microbial activity (Liu *et al.*, 2009), limiting both soil respiration and enzyme activities. However, microbial responses to

moisture can be highly variable. Water availability can act as a resource that limits microbial processes (either directly or by limiting nutrient acquisition), such that microbial responses to water might be linear or at least monotonic. Yet because both too little and too much water can act as stressors for soil microbes (Davidson *et al.*, 2012; Schimel *et al.*, 2007; Stark and Firestone, 1995), we might also find non-linear, threshold and/or non-monotonic responses of microbial communities to water availability (e.g. Curiel-Yuste *et al.*, 2007).

Broad consistency in microbial functional responses to moisture should allow for microbe-driven soil carbon processes to acclimatize given a change in precipitation regime, and lead to straightforward predictions based on water availability. Manzoni *et al.* (2011) found that the lower moisture limit for microbial activity was consistent across 15 studies, probably representing universal constraints on solute diffusion and dehydration tolerance. However, individual microbial taxa have unique physiological response curves to moisture, including both specialist and generalist strategies (Lennon *et al.*, 2012). Therefore, we may be able to generalize the lower endpoint of microbial moisture responses, but we also expect variability in responses to increasing moisture and its upper limits. The challenge is then to understand the distribution of variability in microbial moisture responses and whether/how it influences aggregate function.

Microbial moisture responses that are specific to biomes, ecosystems, habitats, microbial functional groups, or taxa could lead to historical contingencies that modify how functions such as respiration respond to a change in precipitation regime. In this scenario, predictive models might require modifications based on local factors. For example, soil microbial responses may fundamentally differ between arid and mesic regions, because arid soils are expected to be dominated by fungi, have higher potential decomposition (particularly of recalcitrant material), and have greater decoupling of plant and microbial activities (Collins *et al.*, 2008). Similarly, regions with a longer history of drought may have a reduced capacity to respond to water based on both climate change experiments and lab tests of soils exposed to different periods of drought (Evans and Wallenstein, 2012; Göransson *et al.*, 2013; Meisner *et al.*, 2013a). More complex

scenarios may impede our ability to make accurate predictions for soil functional responses to climate change.

An additional key to considering microbial moisture responses is the dynamic distribution of rainfall. Rainfall punctuated by dry periods results in pulses of biological activity that can decouple plant and microbial processes (Collins *et al.*, 2008). Pulsed rainfall distributions may become more important in the future given that predictions often include larger events and fewer days of rain (IPCC, 2007; Jentsch *et al.*, 2007; Jiang and Yang, 2012; Leung and Gustafson, 2005). Pulsed rain events can drive transitions between alternative stable states representing high and low microbial functioning, and the duration of the pulse events may differentially affect fast and slow components of the microbial community. Transient rain events may contribute disproportionately to soil carbon cycling, particularly when microbial responses are both rapid and large, or when short-duration rain pulses allow older soil carbon pools to be accessed (Carbone *et al.*, 2011; Collins *et al.*, 2008; Sala and Lauenroth, 1982). In addition, microbial responses upon rewetting may outweigh apparent reductions in process rates during dry periods, particularly if extracellular enzymes are retained in dry soils (Schimel *et al.*, 2007). Most studies of microbial pulse responses have been in single sites, however, and do not provide us with a sufficiently broad understanding of these processes.

Microbial response mechanisms

An understanding of the mechanisms underlying microbial responses is critical to generalize soil microbial contributions to soil carbon cycling and other ecosystem functions under future climate scenarios. When an environment is altered by a press disturbance such as climate change, we can observe changes in functions such as soil respiration, enzyme activity, and litter decomposition, but often we lack the information necessary to discover through what mechanisms those changes occurred. Whole-soil, aggregate functional responses result from the individual activities of a diverse community of soil microbes, meaning that different mechanisms can be operating simultaneously to create the observed function.

Here, we consider four classes of response

mechanisms that are likely to be at play: physiology, community composition, feedbacks, and evolution. Traits linking individual physiology and performance to environmental conditions will lead to species sorting and compositional change over gradients (Leibold *et al.*, 2004). Community states may also be influenced by dispersal limitation combined with landscape connectivity patterns (Ehrlén and Eriksson, 2000). In addition, positive feedbacks that reinforce alternative stable states may override sorting and immigration locally, and introduce strong history dependence in community responses (Keitt *et al.*, 2001; Scheffer *et al.*, 2001). Finally, trait variation owing to evolutionary change is yet another mechanism modulating community response to environmental change and is perhaps the least understood in terms of interactions with sorting, migration and positive feedbacks (Johnson and Stinchcombe, 2007). We discuss each of these in more detail below.

Microbial physiology

Microbes are often considered to have broad physiological capabilities and thus physiological acclimatization to environmental change may be common. Aggregate functional responses could be due to the physiological breadth of individual taxa in the community, but alternatively might represent the diversity of physiologies among taxa. Functional plasticity has been observed in microbial community responses to short-term changes in temperature and moisture (Bradford *et al.*, 2010; Griffiths *et al.*, 2003; Heinemeyer *et al.*, 2006), although this is not always the case (Malcolm *et al.*, 2009). Dormancy is another form of plasticity that is widespread in soil microbes and can allow for avoidance of temporary periods of environmental stress such as drought (Lennon and Jones, 2011). Resuscitation of dormant taxa can result in rapid and predictable functional resilience once conditions improve (Placella *et al.*, 2012). However, the success of dormancy strategies in the face of climate change will depend on both the persistence of dormant propagules and the nature of the new environment; for example, long-lived spores will be needed to withstand long-term drought.

Even if plasticity is common, however, we might expect that microbial responses to altered climate might be constrained by local climatic history, with larger, more variable, or less predictable responses

when outside the range of historical selection pressures. Reciprocal transplants of intact soil cores between plant communities support this idea: Waldrop (2006) found little change in microbial community composition and aggregate function for soil cores transplanted from grasslands to beneath oak canopies (where environmental conditions were entirely within the range normally found in grasslands), but observed rapid changes when oak canopy cores were transplanted into grasslands (where conditions were outside the normal range). Understanding the limits of microbial physiological plasticity will provide the boundary conditions for potential microbial functional responses to altered climate.

Microbial community composition

Differences in microbial performance in altered environments can lead to shifts in community composition either via changes in the relative abundance of taxa already present or dispersal from the regional species pool. As the environment shifts, some microbial taxa will benefit more than others, resulting in changes in dominance and function (e.g. Pett-Ridge and Firestone, 2005). Dispersal will also provide new immigrant taxa, and species sorting should result in the presence of organisms best suited to the local environment (Leibold *et al.*, 2004). Species sorting has been observed in bacterial communities (Hovatter *et al.*, 2011; Van der Gucht *et al.*, 2007), but not in protists (Finlay, 2002). The degree of sorting versus mass effects can depend on dispersal, which is often assumed to be unlimited in microbes; however, recent studies support microbial dispersal limitation (Kivlin *et al.*, 2011; Martiny *et al.*, 2011; Öpik *et al.*, 2009) and even a high degree of endemism (Cho and Tiedje, 2000; Talbot *et al.*, 2014). If there are local differences in microbial species pools, empirical responses of microbes in experimental climate manipulations may be limited by available taxa. Many climate change experiments impose drought on small plots embedded in an ambient high rainfall region, which may lack a regional species pool containing drought-adapted individuals if dispersal is limited.

Positive feedbacks

When ecosystem states reinforce their own persistence, multiple stable states arise (Beisner *et al.*,

2003). As an example, in arid rangelands, plants can reinforce their own water availability via shading and their influence on soils. The result is dramatic pattern formation that gives way abruptly to collapse under severe water limitation (Rietkerk and van de Koppel, 2008). Similar positive feedbacks could play a role in below-ground microbial responses to climate change. Positive reinforcement of an existing microbial community may create resistance to climate change initially followed by a rapid shift or collapse as the degree of change grows. Invasion dynamics that could introduce change-adaptive varieties into local communities can be shutdown by positive feedbacks, sometimes referred to as Allee effects, because small founder populations cannot survive at low density (Keitt *et al.*, 2001). Life history traits of microbes are generally not consistent with Allee effects; however an Allee effect might be observed in the case of microbial consortia requiring sufficient densities to enable cooperative functioning. Similarly, positive feedback may produce frequency dependent competitive asymmetries whereby larger established populations cannot be replaced by potentially more fit varieties invading at low densities. The net effect is a large potential for historical ecosystem and community structures to persist under change, increasing temporary resistance, but ultimately limiting resilience when an abrupt state shift occurs. Historical legacies in microbial function have been observed for drought (Evans and Wallenstein, 2012; Göransson *et al.*, 2013; Meisner *et al.*, 2013b), but do not always occur (Rousk *et al.*, 2013). If positive feedbacks dominate in soil microbial communities, then historical legacies of past climate may play a strong role in how these communities change in the future and the resiliency of ecosystem functions.

Evolution

Periodic selective sweeps in microbial populations (Koch, 1974; Levin, 1981; Notley-McRobb and Ferenci, 2000) suggest the potential for rapid adaptive responses to climate change. In the lab, *Escherichia coli* adapted to altered temperature within 2000 generations (Bennett *et al.*, 1992) and cultured soil bacteria appeared to be locally adapted to edaphic conditions at the scale of a few metres (Belotte *et al.*, 2003). Identifying adaptation outside the lab, however, is constrained by our inability to measure fitness in complex, highly diverse communities. We

are often limited to deducing adaptation through aggregate function, which results from the sum of traits in the microbial community. Comparisons of local and non-local litter decomposition provide evidence for functional specialization of microbial communities to the environment: microbial communities are generally most efficient at degrading litter from plant species growing immediately above them, termed the 'home-field advantage' (e.g. Ayres *et al.*, 2009; Keiser *et al.*, 2014; Strickland *et al.*, 2009). The breadth of decomposition may also be constrained by resource history if some functional strategies are eliminated (Keiser *et al.*, 2011). Although rapid adaptation represents a viable strategy for microbes facing climate change, existing specialization may prevent selective sweeps (Dykhuisen and Dean, 2004), which could limit responses to environmental change.

Current microbial and ecosystem models

Microbial contributions to both soil CO₂ fluxes and carbon pools in a changing climate are likely to be substantial and more explicit representation of their role could improve the accuracy of ecosystem carbon models. Nevertheless, the vast majority of ecosystem carbon cycling models do not include explicit microbial mechanisms (Chapin III *et al.*, 2009; Ostle *et al.*, 2009; Treseder *et al.*, 2011) or, when microbes are included, all microbial taxa are treated as functional equivalents (Lawrence *et al.*, 2009). This simplification arises from our historical assumption that high microbial diversity and apparently broad distributions equate to ecological redundancy (Allison and Martiny, 2008; Torsvik *et al.*, 2002). It is clear, however, that there is high beta-diversity in both fungi (Kivlin *et al.*, 2011; Öpik *et al.*, 2006, 2009, 2010) and bacteria (Fierer *et al.*, 2009; Lauber *et al.*, 2009). Such differences in microbial community composition can directly influence ecosystem process rates (e.g. Fukami *et al.*, 2010; Gulledege *et al.*, 1997; Hawkes *et al.*, 2011; Strickland *et al.*, 2009).

Even simplified representations of microbial community functional groups can improve models. In an enzyme-drive biogeochemical model, for example, moving from one microbial pool (Schimel and Weintraub, 2003) to two pools of fungi and bacteria (Waring *et al.*, 2013) significantly improves

our ability to capture real patterns of carbon and nitrogen cycling by including differences in physiology between these groups. Other examples of microbial functional groups include active versus dormant states (Blagodatsky and Richter, 1998; Hunt, 1977), generalists versus specialists (Moorhead and Sinsabaugh, 2006), decomposers of fresh litter versus soil organic matter (Fontaine and Barot, 2005), decomposers versus builders of soil organic matter (Perveen *et al.*, 2014), and ectomycorrhizal versus saprotrophic fungi (Orwin *et al.*, 2011).

Current state-of-the-art soil carbon models have adopted explicit representation of extracellular enzyme activities as a key factor influencing decomposition (Allison *et al.*, 2010; Wang *et al.*, 2013). The major innovation of these efforts is dynamically modelling enzyme pools and their influence on microbial carbon uptake through regulation of the rate of soil carbon conversion to dissolved organic carbon. For example, Wieder *et al.* (2013) recently modified the Community Land Model (Lawrence *et al.*, 2011; Oleson *et al.*, 2010) by adding microbial biomass pools and decomposition via enzyme-driven, temperature-dependent Michaelis–Menten kinetics, including above-ground, surface, and subsurface soil horizons. In doing so, they were able to explain 50% of the variation in global soil carbon pools, approximately a 20% improvement compared with traditional carbon models (Wieder *et al.*, 2013). Other existing models differ primarily in the degree of detail and realism in representing different carbon states (e.g. Allison, 2012; Allison *et al.*, 2010; Wang *et al.*, 2013).

While these models explicitly include effects of temperature on process rates, they typically do not consider effects of soil moisture. The lack of soil moisture effects limits model applicability to forecasting, as it is known that soil moisture is a significant factor influencing both microbial and soil carbon dynamics (e.g. Bontti *et al.*, 2009; Carbone *et al.*, 2011; Curiel-Yuste *et al.*, 2007; Inglima *et al.*, 2009; Lellei-Kovács *et al.*, 2011). An exception is the dual Arrhenius Michaelis–Menten (DAMM) model of Davidson *et al.* (2012). The DAMM model includes both temperature and soil moisture effects to predict soil respiration. The current version of DAMM is not a dynamic state model, but it does define key rate functions that can be included in a dynamic process model.

There are other direct and indirect effects on soil microbes that might affect microbial responses to climate change and thus potentially improve model predictions. Chapin *et al.* (2009) point out that partitioning of carbon into roots, mycorrhizas, and exudates, as well as their effects on respiration and soil organic carbon, remain unknown for any ecosystem, despite these carbon pools having very different residence times and potential climate change responses. Mycorrhizas may increase soil organic carbon by hyphal aggregation of soil particles (Rillig and Mummey, 2006; Wilson *et al.*, 2009) or reduce carbon pools via hyphal respiration under some climate change scenarios (Hawkes *et al.*, 2008). Priming effects may occur in response to an increase in labile carbon exudates resulting in depletion of soil organic carbon pools, although the magnitude is soil-specific (Blagodatskaya and Kuzyakov, 2008; Paterson and Sim, 2013). Finally, trophic interactions are likely to be important, despite similar responses of soil fauna to different climate change factors in experimental settings (Blankinship *et al.*, 2011). Although we do not address these further here, these effects likely warrant further consideration.

Integrating moisture into microbial carbon cycling models

As a first step towards integrating soil moisture into decomposition models, we have fused the DAMM model of Davidson *et al.* (2012) with two enzyme-based, temperature-dependent soil carbon cycling models to produce models where rates depend on both soil moisture and soil temperature (Fig. 7.1). Specifically, we focus on the models developed by Allison *et al.* (2010) and Wang *et al.* (2013), hereafter referred to as the AWB and MEND models, respectively. While we believe that soil moisture could have complex effects throughout the models, we integrate the models initially by substituting available dissolved organic carbon, as computed in the DAMM model, for the particulate dissolved organic carbon pool used in the AWB and MEND models. Additionally, we incorporate oxygen limitation by adding an additional oxygen-driven Michaelis–Menten term to the microbial biomass growth equation. The MEND model differs slightly in how temperature enters into the model, but is otherwise similar to the AWB model, except for

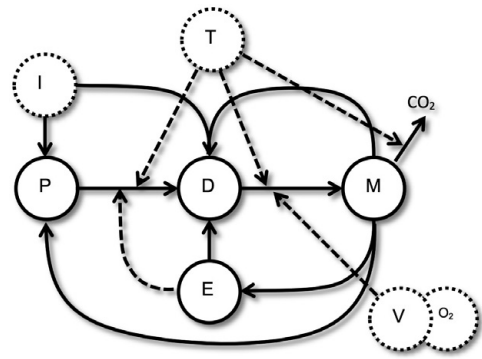


Figure 7.1 Carbon pools and fluxes in the AWB-DAMM model. Symbols are I=carbon input, P=particulate carbon, D=dissolved carbon, M=microbial biomass, E=enzymes, V=volumetric soil moisture, O₂=oxygen and T=temperature. Dashed lines indicate effects on rates. Dashed circles represent boundary conditions. The MEND-DAMM model is analogous but with the phosphorus pool divided into three separate pools and the E-pool divided into two separate pools.

splitting particulate organic carbon pool into three different pools and the inclusion of adsorption-desorption dynamics.

The integration of the models generates an initial set of four model–hypotheses to be compared and confronted with data: AWB (unmodified), MEND (unmodified), AWB–DAMM, and MEND–DAMM. Our initial merger of these models does not explicitly include oxygen uptake dynamics. We expect, however, that we can ignore the oxygen limitation term from the DAMM model as it will have a relatively small impact in arid ecosystems that are the focus of this initial effort. However, we also acknowledge that oxygen limitation may be large during extreme wetting events. In ecosystems where empirical validation suggests the inclusion of explicit oxygen dynamics, this should be introduced as a state variable.

Enzyme-driven models with sensitivity to temperature and soil moisture

Carbon exists in many forms in soils (Robertson *et al.*, 1999). Newer models of soil carbon dynamics more finely divide pools, explicitly model biological feedbacks, and use more realistic uptake kinetics. A key factor regulating rates of carbon flux in soils

is enzymatic catalysis involved in the breakdown of particulate organic carbon into biologically available dissolved organic carbon (Schimel and Weintraub, 2003). Soil microbes produce extracellular enzymes that react with particulate carbon to produce soluble carbon, which can then be consumed. The extracellular enzymes are themselves a pool of dissolved organic carbon and contribute to the overall soil carbon budget.

Allison *et al.* (2010) developed an extracellular enzyme-driven model of soil carbon (AWB). The model is not a full ecosystem model but captures in a simplified way the essential details of the enzyme-driven particulate-to-dissolved carbon pathway. The model includes four carbon pools: particulate organic carbon (P), dissolved organic carbon (D), microbial biomass (M) and extracellular enzymes

(E). The AWB model is given by the following system of equations (Equations 7.1 to 7.4) (symbols defined in Table 7.1):

$$\frac{dP}{dt} = I_p + (1 - \alpha)\delta M - v_1 \left(\frac{P}{K_1 + P} \right) E \quad (7.1)$$

$$\frac{dD}{dt} = I_D + \left(\alpha\delta - v_2 \frac{D}{K_2 + D} \right) M + \left(v_1 \frac{P}{K_1 + P} + r_1 \right) E \quad (7.2)$$

$$\frac{dM}{dt} = \left(\varepsilon v_2 \frac{D}{K_2 + D} - \delta - r_2 \right) M \quad (7.3)$$

$$\frac{dE}{dt} = r_2 M - r_1 E \quad (7.4)$$

The AWB model is sensitive to temperature, which

Table 7.1 Symbols used in the AWB–DAMM model

Variable	Description	Units	Default value
P	Particulate organic carbon	mg/cm ³	111.876
D	Dissolved organic carbon	mg/cm ³	0.00144928
M	Microbial biomass	mg/cm ³	2.19159
E	Extracellular enzymes	mg/cm ³	0.0109579
I_p	Input rate of particulate carbon	mg/cm ³ /h	0.0005
I_D	Input rate of dissolved carbon	mg/cm ³ /h	0.0005
α	Soluble fraction of dead microbial matter	Dimensionless	0.5
δ	Microbe death rate	h ⁻¹	0.0002
v_1	Maximum rate of conversion from particulate to dissolved carbon	h ⁻¹	Function of temperature
n_2	Maximum dissolved carbon uptake by microbes	h ⁻¹	Function of temperature
\dot{v}_1	Conversion rate scaling constant	h ⁻¹	10 ⁸
\dot{v}_2	Uptake rate scaling constant	h ⁻¹	10 ⁸
K_1	Half-saturation of particulate carbon conversion	mg/cm ³	Function of temperature
K_1^I, K_1^S	Least-squares K_1 intercept and slope	mg/cm ³ , mg/cm ³ /T	500, 5
K_2	Half-saturation of dissolved carbon uptake by microbes	mg/cm ³	Function of temperature
K_2^I, K_2^S	Least-squares K_2 intercept and slope	mg/cm ³ , mg/cm ³ /T	0.1, 0.01
ε	Microbial carbon use efficiency	Dimensionless	Function of temperature
$\varepsilon^I, \varepsilon^S$	Least-squares CUE intercept and slope	Dimensionless, T ⁻¹	0.63, -0.016
r_1	Rate of enzyme loss	h ⁻¹	0.001
r_2	Enzyme production rate	h ⁻¹	0.000005
η	Dissolved organic carbon diffusion factor	Dimensionless	72.3
t	Scaling factor for O ₂ limitation	Dimensionless	2.0
V	Volumetric soil moisture	Dimensionless	0.24
O_2	Oxygen concentration	l O ₂ /l air	Function of soil moisture
K_3	Oxygen half-saturation	l O ₂ /l air	0.121

affects both the maximum rates n_1 and n_2 , the half-saturation coefficients K_1 and K_2 , and carbon-use efficiency e . The maximum rates are governed by the Arrhenius function: $v_{1,2} = \dot{v}_{1,2} e^{-5653/(T+273)}$, where T is temperature in celsius. The numerator in the exponent is derived from the activation energy and ideal gas constant. This function captures the well-known increase in reaction rates with increasing temperature. Temperature effects on the half-saturation coefficients and carbon-use efficiency are linear regression functions constructed from empirical data: $K_1 = K_1^I + K_1^S T$, $K_2 = K_2^I + K_2^S T$ and $\varepsilon = \varepsilon^I - \varepsilon^S T$.

While the AWB model is responsive to temperature, it does not integrate soil moisture effects. Changes in soil moisture have multiple potential influences on soil carbon dynamics. First, soil moisture content is the carrier for dissolved organic carbon diffusing through the soil pore space. Hence, the rate of microbial uptake of dissolved organic carbon is dependent on available soil moisture. A second effect is the decreasing rate of gas exchange as soil pore space becomes saturated with water. Reduced gas exchange can limit aerobic respiration of acquired carbon reducing not only microbial biomass, but also production of extracellular enzymes, an energetically costly activity. The net effect is to shutdown the entire carbon feedback loop at either end of the moisture spectrum: lack of liquid transport when dry and lack of oxygen when saturated.

The effect of soil moisture on dissolved organic carbon available for microbial uptake and on gas exchange is captured in the DAMM model (Davidson *et al.*, 2012). Although not a fully dynamical model, the DAMM model framework identifies functions to model available carbon and incorporates soil oxygen content into microbial carbon kinetics. Integration of these functions into a combined AWB–DAMM model results in the following updated equations (Equations 7.5 and 7.6) for dissolved organic carbon and microbial biomass:

$$\frac{dD}{dt} = I_D + \left(\alpha \delta - v_2 \frac{\eta DV^3}{K_2 + \eta DV^3} \frac{\tau O_2}{K_3 + O_2} \right) M + \left(v_1 \frac{P}{K_1 + P} + r_1 \right) E \quad (7.5)$$

$$\frac{dM}{dt} = \left(\varepsilon v_2 \frac{\eta DV^3}{K_2 + \eta DV^3} \frac{\tau O_2}{K_3 + O_2} - \delta - r_2 \right) M. \quad (7.6)$$

The term ηDV^3 models the diffusion of dissolved organic carbon to the cell surface where it is available for uptake. The parameter η is related to the diffusivity of dissolved organic carbon. In our merged model, η is scaled such that the dissolved organic carbon available for uptake is the same as in the unmodified AWB model when volumetric soil moisture is 24%, the time average of soil moistures from our study sites. The cubic dependence of available carbon on soil moisture generates a strong limitation to microbial growth at lower soil moisture content, a mechanism absent from the AWB model. Oxygen concentration is modelled purely as a function of diffusion into the soil pore space; microbial consumption is neglected. We retain the default values of soil bulk density, particle density, gas diffusion and O_2 fraction in air given in Davidson *et al.* (2012). With these values, the oxygen concentration is calculated as $O_2 = 0.35(0.68 - V)^{4/3}$. Similarly to the scaled factor h , the parameter t scales the influence of O_2 such that there is no net effect on dissolved carbon concentration D when volumetric soil moisture is 24%. In the absence of this scaling, it would have been necessary to re-parameterize the AWB model. With these modifications, we have a model sensitive to both soil temperature and moisture content.

We also explore adding soil moisture sensitivity to the more elaborate enzyme-driven microbial MEND (microbial–enzyme-mediated decomposition) model proposed by Wang *et al.* (2013). The MEND model (Wang *et al.*, 2013) divides the three soil carbon pools (enzymes, particulate and dissolved) of the AWB model into six separate components: (1) particulate and (2) dissolved carbon pools as in AWB, (3) an adsorbed-phase dissolved carbon pool, (4) a mineral-associated carbon pool, and two enzyme pools, (5) one acting on particulate carbon and the other (6) acting on mineral associated carbon. The MEND model gives an unprecedented level of detail in below ground carbon dynamics relative to older models that divide below-ground pools into labile, recalcitrant and immobile pools without consideration of enzyme dynamics. Wang *et al.* (2013) demonstrate strong differences in carbon kinetics compared to these traditional models. We refer the reader to Wang *et al.* (2013) for additional details of the model formulation and parameterization.

We utilized the same approach applied to the AWB–DAMM model to merge the MEND model with the DAMM model. As in the AWB model (Equation 7.7), the MEND model uses Michaelis–Menten kinetics to model the rate of microbial uptake as a function of dissolved organic carbon concentration. Our modification of the MEND model uses the dual Michaelis–Menten formulation of the DAMM model by making the substitution

$$\frac{D}{KD+D} \Rightarrow \frac{\eta DV^3}{K_2 + \eta DV^3} \frac{\tau O_2}{K_3 + O_2} \quad (7.7)$$

where, again, η and τ are scaled parameters that assure a neutral influence on dissolved carbon concentration at the mean soil moisture. The half-saturation coefficient K_D is specific to MEND (see Wang *et al.*, 2013).

Model simulations with and without soil moisture sensitivity in wet and dry sites

The models described above primarily allow us to consider physiological response mechanisms, as well as the potential for alternative stable states (positive feedbacks). We contrast outputs of the model combinations (AWB, AWB–DAMM, MEND, and MEND–DAMM) driven by soil moisture and soil temperature time series for two locations on the Edwards Plateau, TX, USA. A steep precipitation gradient is found across the Edwards Plateau, with mean annual rainfall ranging from 90 cm in the east to 40 cm in the west, decreasing by ~10 cm every 40–50 km westward. Across this gradient, the plant communities are savannah grasslands (McMahan *et al.*, 1984) and soils are limestone-derived clay Mollisols (Werchan *et al.*, 1974). In order to analyse the potential differences in model outcomes based on soil moisture, we have chosen one drier and one wetter site from the west and east ends of the gradient as the basis for the simulation. Mean annual precipitation at these sites is approximately 500 mm and 1000 mm, respectively.

Our soil moisture and temperature time series are extracted from the National Centres for Environmental Prediction's (NCEP) reanalysis dataset (Kalnay *et al.*, 1996). Reanalysis provides a uniform procedure for fusing all available climate data into a consistent historical record. A climate model is used to integrate data inputs and to produce gridded

outputs. A stepwise update procedure is utilized to force the climate model simulation to conform to the historical climate data. As the model computes soil climate, it provides a way to obtain soil moisture and temperature time series for specific locations. Although not the same as direct measurements, the modelled reanalysis outputs nonetheless represent realistic scenarios constrained to conform to historical climate patterns.

The soil climate time series represented three years of moisture and temperature data sampled hourly beginning 1 January 2008. Moisture and temperature values are for the first 10 cm of soil below the surface. Both sites were centred at 30.44° north latitude. The dry site was centred on 85.62° west longitude. The moist site was centred on 77.49° west longitude. To make the climate time series continuous for integration, we used cubic spline interpolation. We used the *deSolve* package (Soetaert *et al.*, 2010) in R (R Development Core Team, 2011) to numerically integrate the models. Initial conditions were those given in Allison *et al.* (2010) and Wang *et al.* (2013). For each model we ran ten simulations over the climate time series, each time initializing the model with the time-average of the state variables from the previous run. This allowed the models to converge to their long-term behaviour. Output of the 10th run is shown in Fig. 7.2 and summarized in Fig. 7.3.

As expected, the moist site showed greater soil moisture (Figs. 7.2A and B and 7.3A and B). Temperatures were similar between the two sites with the dry site showing greater variability. The covariance of moisture and temperature is entirely different between the two sites with the dry site showing warm-season increases in soil moisture, likely driven by summer rains, whereas the moist site exhibits the greatest soil moisture during the winter months. In addition to changes in mean values, the dry site shows greater variation, both daily and seasonally. Crucially, the dry site commonly reaches near-zero soil moisture potentially imposing a large reduction in process rates during these extreme drying events.

All of the models (Fig. 7.2C–J) showed seasonal variation in microbial biomass driven by temperature effects. Microbial biomass peaked in late spring or early summer. Similarly, dissolved organic carbon fluctuated seasonally in the AWB and MEND models (Fig. 7.2C, D, G and H).

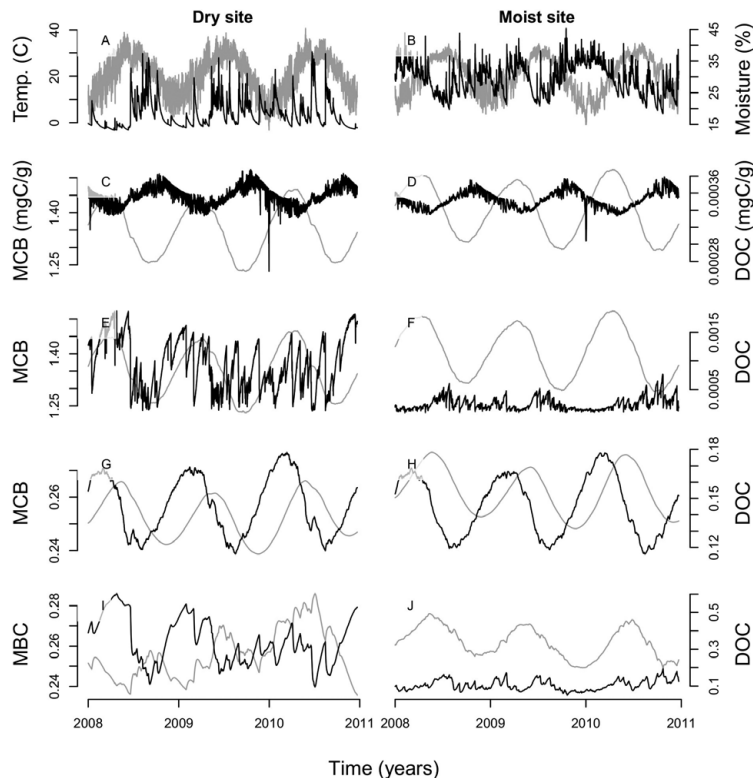


Figure 7.2 Comparison of models driven by reanalysis soil temperatures and moistures for a xeric site and mesic site. (A and B) Soil moistures and temperatures for the wet and dry sites. Modelled microbial biomass (MIC) and dissolved organic carbon (DOC) for (C and D) AWB model, (E and F) the AWB-DAMM model, (G and H) the MEND model, and (I-J) the MEND-DAMM model. The time series start on 1 January and spans a three-year period.

Fluctuations in dissolved organic carbon were fully (AWB) or partially (MEND) out-of-phase with peaks in microbial biomass reflecting the uptake of dissolved organic carbon by microbes. Interestingly, dissolved organic carbon in the MEND model peaks before microbial biomass. This effect is likely the result of accelerating soil enzyme activity during the spring months and eventual drawdown of dissolved organic carbon by microbial uptake later in the season.

The most striking result is the dynamics of dissolved organic carbon in the AWB-DAMM and MEND-DAMM models (Figs. 7.2E, F, I and J and 7.3D and F). When soil moisture sensitivity is built into the model, we see strong fluctuations in dissolved carbon, largely shadowing variation in soil moisture. Interestingly, we observe a large increase in the average concentration of dissolved organic carbon in the dry site relative to the moist site for the moisture-sensitive models (Figs. 7.2E and I and

7.3D and F). There is also a marked increase in the variance of dissolved organic carbon through time, although these fluctuations have relatively minor influence on microbial biomass, which turns over more slowly and is therefore more buffered. The exception is the MEND-DAMM model in the dry site (Fig. 7.2I) where the dynamics of both microbial biomass and dissolved organic carbon appear to be strongly driven by soil moisture. Although some seasonal temperature-driven trends are apparent, finer-scale fluctuations corresponding to rapid changes in soil moisture appear to dominate. Unlike the other simulations, the MEND-DAMM output for the dry site shows strong negative covariance: increases in dissolved organic carbon are mirrored by decreases in microbial biomass indicated by a strong and rapid influence of soil moisture on microbial carbon uptake.

We also compared total respiration between the models with and without the DAMM modifications.

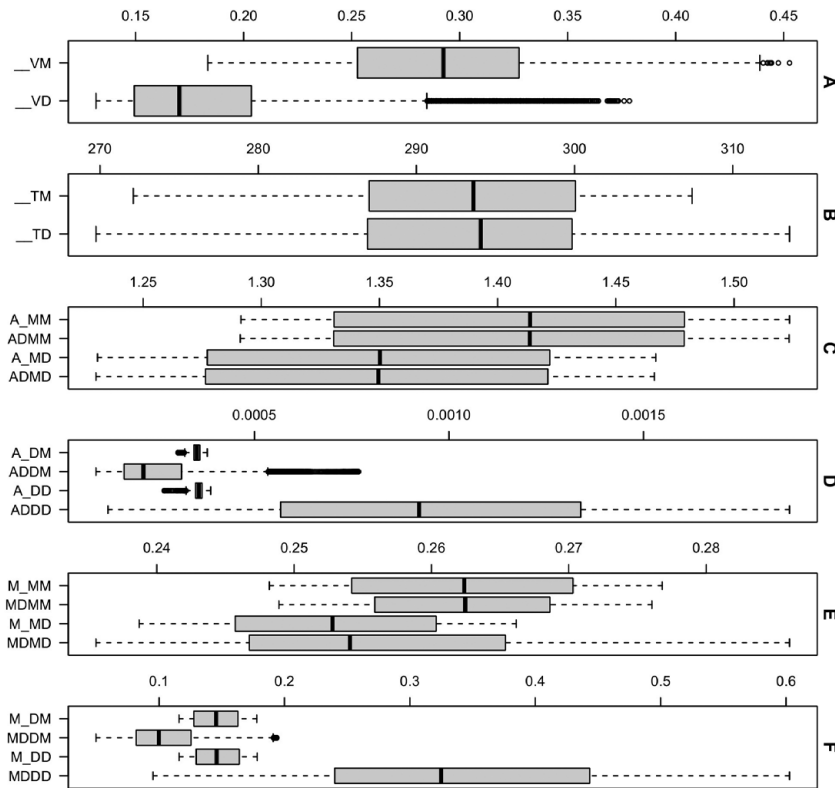


Figure 7.3 Box plot of model outputs. (A) Volumetric soil moisture. (B) Soil temperature. (C) Microbial biomass for AWB and AWB–DAMM. (D) dissolved organic carbon for AWB and AWB–DAMM. (E) microbial biomass for MEND and MEND–DAMM. (F) dissolved organic carbon for MEND and MEND–DAMM. The four letter codes on the x-axis correspond to model (two characters: A_ = AWB, AD_ = AWB–DAMM, M_ = MEND, MD_ = MEND–DAMM, __ = climate), variable (one character: V = soil moisture, T = temperature, M = microbial carbon, D = dissolved carbon) and site (one character: M = moist, D = dry).

Interestingly, respiration rates primarily tracked temperature and did not differ strongly between the models. Again the MEND–DAMM model run on the dry site showed the strongest differences in respiration rates compared to the model without the DAMM modifications. However, the differences were small and overwhelmed by the seasonal temperature-tracking dynamics.

Simulation results and microbial mechanisms

Based on our merged models, soil moisture has a strong influence on predictions for microbial enzyme-mediated ecosystem processes, including large differences in carbon pools and pool size variability between wetter and drier regions. This was particularly evident in the dynamics of dissolved organic carbon. Moisture is known to be a key factor

in arid land biogeochemical cycling with pulsed rainfall patterns (Collins *et al.*, 2008) and adding moisture as a rewetting factor to biogeochemical models for arid ecosystems can significantly improve model performance (Li *et al.*, 2010). However, soil moisture is likely to constrain microbial processes more broadly as drought increases with climate change and, as noted by Moyano *et al.* (2013), current models are limited approximations and substantial work is needed to improve their predictive capacity.

Of the four proposed response mechanisms of physiology, community composition, feedbacks, and evolution, these results are primarily related to physiology. Through integration of the DAMM model with the AWB and MEND models, we have shown how dynamic moisture and temperature drivers can influence physiological process rates in a transient manner. However, the physiological

plasticity built into these models may not be realistic in situations where environmental history constrains responses. For example, a history of drought can alter microbial community structure (Evans and Wallenstein, 2012), change microbial carbon use efficiency (Göransson *et al.*, 2013), decouple microbial growth from respiration (Meisner *et al.*, 2013a), and create feedbacks to plant communities (Meisner *et al.*, 2013b).

The dynamic nature of soils indicated in the driving climate time series of the models presented here also has bearing on the other mechanisms. A variable environment is a mechanism that can allow for coexistence of species in communities (community composition mechanism) that would otherwise exclude each other through resource competition (Chesson, 2000). This variation is at least in part an attribute of the physiological rates incorporated into our models. Moisture and other climate variation may therefore maintain more diverse communities, and as a result more resilient communities with multiple players than can compensate for losses of past dominants when conditions change.

We did not find strong evidence of multiple stable states (positive feedback mechanism) for the ranges of climate we investigated. Nevertheless, sudden changes in dynamics could occur at extremes of soil temperature and moisture. We notice, for example, a sharp drop in dissolved organic carbon in the second cold season (around day 650) corresponding to an extreme low temperature event that influenced both the wet and dry sites. Whether this corresponds to a shift between stable states or a more simple transient effect cannot be ascertained without additional analysis. However, this observation suggests the models are capable of rapid shifts in response to extremes in climate.

Whether variability in soil climate impacts evolution is not directly addressed in the modified enzyme-driven models examined here. Similar to the community composition mechanism, a variable environment could maintain genetic polymorphisms with populations, and this genotypic variation could maintain functional phenotypic variation lending greater resilience under climate change. Evolutionary tradeoffs must certainly abound in soil microbial systems (Gudelj *et al.*, 2010). A key tradeoff is the fast–slow spectrum characterized by maximizing rate of reproduction at the expense of survivorship versus long lifespan

with lower fecundity. The observed strong variation in dissolved organic carbon – the energy resource fuelling microbial population growth – under a variable soil moisture regime has bearing on the fast-slow tradeoff. Rapid changes in resources should favour the fast end of the tradeoff spectrum. However a live-fast life history provides little population buffer to prolonged or directional changes in environment and thus limit resilience to certain types of disturbance. Conversely the shorter generation times on the fast end of the spectrum could enable more rapid adaptive evolution and rescue populations impacted by major environmental changes (Gonzalez and Bell, 2013).

Conclusions and future needs

Here we demonstrate that adding moisture sensitivity to enzyme-driven models of carbon cycling changes their outcomes when parameterized for a wet and a dry ecosystem located on the same soil type. However, these outcomes have not been validated against field data and the particular moisture function that we incorporated may not produce the best fit. As ecosystem models become more and more sophisticated, we expect discovery of the tipping point at which additional realism ceases to improve the accuracy of model predictions. For example, Talbot *et al.* (2014) recently found high endemism in the fungal communities of North American pine forests, but this did not translate into local variation in enzymes, suggesting a high degree of functional redundancy. Distinguishing among physiological, compositional, and other microbial mechanisms will help us to generalize expectations across ecosystems. Linking of modelling activities to data collection in the field and experimental plots will promote greater understanding of critical processes and build that understanding into a new generation of advanced soil carbon models.

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