

REVIEW

Emerging relationships among microbes, soil carbon storage and climate change

Microbes, memory and moisture: Predicting microbial moisture responses and their impact on carbon cycling

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Abstract

1. Soil moisture is a major driver of microbial activity and thus, of the release of carbon (C) into the Earth's atmosphere. Yet, there is no consensus on the relationship between soil moisture and microbial respiration, and as a result, moisture response functions are a poorly constrained aspect of C models. In addition, models assume that the response of microbial respiration to moisture is the same for all ecosystems, regardless of climate history, an assumption that many empirical studies have challenged. These gaps in understanding of the microbial respiration response to moisture contribute to uncertainty in model predictions.
2. We review our understanding of what drives microbial moisture response, highlighting evidence that historical precipitation can influence both responses to moisture and sensitivity to drought. We present two hypotheses, the 'climate history hypothesis', where we predict that baseline moisture response functions change as a function of precipitation history, and the 'drought legacy hypothesis', in which we suggest that the intensity and frequency of historical drought have shaped microbial communities in ways that will control moisture responses to contemporary drought. Underlying mechanisms include biological selection and filtering of the microbial community by rainfall regimes, which result in microbial traits and trade-offs that shape function.
3. We present an integrated modelling and empirical approach for understanding microbial moisture responses and improving models. Standardized measures of moisture response (respiration rate across a range of moistures) and accompanying microbial properties are needed across sites. These data can be incorporated into trait-based models to produce generalized moisture response functions, which can then be validated and incorporated into conventional and microbially explicit ecosystem models of soil C cycling. Future studies should strive to analyse realistic moisture conditions and consider the role of environmental factors and soil structure in microbial response.
4. Microbes are the engines that drive C storage and are sensitive to changes in rainfall. A greater understanding of the factors that govern this sensitivity could

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be a key part of improving predictions of soil C dynamics, climate change and C-climate feedbacks.

KEYWORDS

carbon, drought, legacy, microbial communities, modelling, rainfall, respiration, soil

1 | INTRODUCTION

In recent years, knowledge about the role of microbes in soil carbon (C) cycling has advanced (Cotrufo et al., 2013; Davidson et al., 2012; Liang et al., 2017; Manzoni et al., 2014; Moorhead et al., 2012; Wieder et al., 2013). Microbial communities are now explicitly represented in some ecosystem models as a biomass C pool and/or enzyme pool with temperature-sensitive growth efficiencies (Wieder, Grandy, et al., 2015; Zhou et al., 2021). While the inclusion of these pools can improve our ability to predict C cycling, our quantitative and conceptual understanding of microbes in C cycling is still limited; for instance, even the most advanced models explain only 50% of the spatial variation in current soil C pools (Wieder et al., 2013, 2018).

Soil heterotrophic respiration is a major global C flux and important for C models. Substantial efforts have gone into understanding the sensitivity of soil respiration to temperature, but moisture is also a primary constraint on microbial activity (Brzostek et al., 2012; Hursh et al., 2017; Moyano et al., 2013). Yet, there is no consensus on the shape of the microbial moisture response. Soil moisture is also expected to change in the future; much of the global land area will experience reductions in soil moisture through reduced rainfall, more variable rainfall, increased temperatures or all these changes. The result will be more frequent and severe drought worldwide, interspersed with more intense rainfall (IPCC, 2021).

Models represent the effect of climate on heterotrophic respiration using environmental response functions. While it is generally known that microbial processes depend on water and decrease as moisture decreases (Manzoni et al., 2012), soil moisture response functions for respiration in current models exhibit a wide range of forms (Figure 1). (These functions are empirically derived from measurements of respiration across a range of moistures, and we refer to the resulting curves as 'moisture response curves'). Such variation in moisture response function may exist because there is no consensus on the shape of the curve. For instance, substrate diffusion theoretically limits respiration at low moistures, and oxygen limitation causes low respiration at high moistures, which would give rise to hump-shaped curves. But such hump-shaped relationships are less commonly observed experimentally than linear or saturating functions (Franzluebbers, 1999; Franzluebbers et al., 2002; Liu et al., 2009; Manzoni et al., 2012; Thomsen et al., 1999). In addition to lack of consensus on the shape of this curve, most models use one single curve for all sites. The underlying assumption is that the physiology of microbial communities is the same, regardless of biome or climate history, which is not supported by recent studies showing that history affects microbial community function.

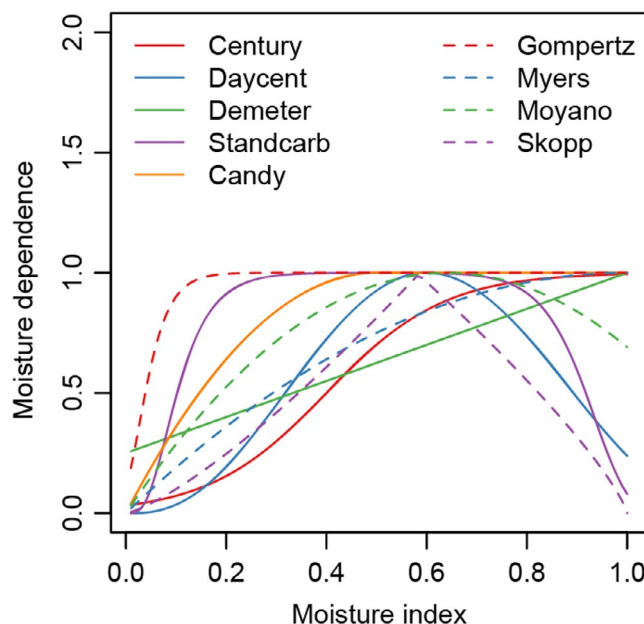


FIGURE 1 Current ecosystem models use different functions to portray respiration response to moisture because there is no data-driven consensus on the shape of this curve. Shown here are moisture response functions from nine ecosystem models. Modified from Sierra et al. (2015)

Deciphering accurate moisture response functions is important because they have major consequences for global C predictions. Such consequences are further compounded by climate-C feedbacks (Falloon et al., 2011; Sierra et al., 2015). A recent analysis found that variation in moisture response functions had a bigger effect than model type (microbial versus conventional) on projections for soil heterotrophic respiration (Zhou et al., 2021). The magnitude of errors in C pool size that emerges from imprecise response curves can rival the effect of different long-term soil management practices (Paul et al., 2015). And at global scales, differences in soil moisture functions can make 100-year predictions of soil C change vary from positive to negative (Falloon et al., 2011).

Empirically derived, mechanistic and generalizable moisture response functions must be developed (Manzoni et al., 2012) and integrated into models (Bradford et al., 2016; Yan et al., 2018). To address this need, we (1) review historical precipitation as a potential driver of moisture response functions, (2) introduce two novel hypotheses, the 'climate history hypothesis' and 'drought legacy hypothesis' for understanding variation in moisture response functions, and (3) present an approach for investigating moisture response and integrating it with

ecosystem models. While some models do account for how moisture responses are altered by soil properties (e.g. texture, C, N), biological factors are not currently considered. Yet, differences in microbial communities emerge under different rainfall regimes and alter moisture responses (Evans & Wallenstein, 2012; Hawkes et al., 2017), which could result in predictable variation in the moisture response functions driving C cycling with changing climates.

2 | HISTORICAL PRECIPITATION AS A DRIVER OF MICROBIAL FUNCTION AND MOISTURE RESPONSE

By assigning a single moisture response function to all soils, ecosystem models assume that soil microbes across the globe have the same environmental dependencies, independent of climate history. This assumption may be made for mathematical convenience or be based on the argument that microbes are widely dispersed, physiologically plastic, fast-growing and functionally redundant, thus 'rising to the occasion' for a given environment, while other factors determine process rates. Yet, many studies show that precipitation history affects microbial function through biotic selection. Functions that are controlled by phylogenetically narrow groups of micro-organisms may be more sensitive to shifts in microbial community composition than heterotrophic respiration (Schimel, 1995; Schimel et al., 2005); however, C cycling traits may be linked to drought tolerance and sensitivity, which can be influenced by traits that are phylogenetically narrow (Evans & Wallenstein, 2014). For example, drought tolerance traits include biofilm formation and the synthesis of small molecules (osmolytes) that balance osmotic pressure (Schimel et al., 2007). Differences in drought tolerance among both fungal and bacterial taxa, observed *in situ* (Chase et al., 2021; Evans & Wallenstein, 2014; Malik, Swenson, et al., 2020; Placella et al., 2012) and in culture (Lennon et al., 2012; Figure 2), affect microbial survival, community size, and C use efficiency, and impact respiration response.

Through selection on traits related to moisture response, microbes specialize on historical moisture regimes in ways that can affect function (Chase et al., 2021; Evans & Wallenstein, 2014). As certain microbes change in abundance in a community, the entire community functional response to moisture can vary. Indeed, many studies have now documented patterns consistent with local adaptation (also called 'home field advantage', which here includes both ecological and evolutionary processes) in microbial communities, for many environmental pressures. For instance, some microbial communities specialize on certain plant substrates (Austin et al., 2014; Ayres et al., 2009; Strickland et al., 2009). Other accounts suggest temperature shapes microbial community traits and function (Rousk et al., 2012).

Similar specialization has been observed in a few studies in response to rainfall. Hawkes et al. (2017) measured the moisture response of respiration in soils collected from a precipitation

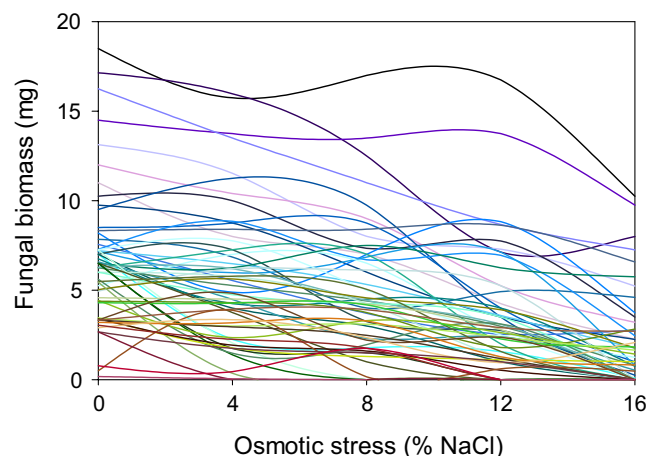


FIGURE 2 Variation in physiological tolerances to osmotic stress (% NaCl) across 65 fungi in culture. Data from (Giauque et al., 2019) and Hawkes (unpublished data)

gradient in Texas, USA (mean annual precipitation (MAP) = 40–90 cm). Respiration generally increased with increasing soil moisture in the laboratory, as is the case with the vast majority of non-saturated soils (Manzoni et al., 2012; Figure 3). But a key finding was that differences in precipitation history across the sites resulted in different moisture response curves (Figure 3a). Soils from wetter sites respired twice as much as soils from drier sites under the highest moisture conditions (Hawkes et al., 2017). While one explanation of this could be that wetter sites have higher soil C or different mineralogy driving higher respiration, the data did not support this. Differences in C content were negligible across sites, and soils were all rocky clay Mollisols on a continuous plateau. In addition, when the authors experimentally increased C availability by adding litter, wetter sites continued to respire more at higher moistures (Figure 3b). While indirect factors like soil properties certainly could still play a role, it could also be that differences in moisture response curves developed because rainfall selects for soil microbial communities that differ in composition, physiology or other traits, like C use efficiency (Leizeaga et al., 2020).

These data support climate history as a major factor influencing moisture response via microbial community selection (which we expand on below, see climate history hypothesis). While other studies support this idea (Averill et al., 2016; Evans & Wallenstein, 2012; Fierer et al., 2003; Hawkes & Keitt, 2015; Hawkes et al., 2017; Song et al., 2021)—some also find the microbial moisture response to be independent of past climate. One meta-analysis found there was no difference in the respiration response for communities extracted from dry versus wet environments (Manzoni et al., 2012). In addition, de Nijs et al. (2018) found that soil microbes exposed to 18 years of drought were not more resistant to drought but did respond more quickly to rewetting. In addition, as mentioned above, differences across sites observed in previous studies could have emerged not from biotic selection but from other factors that are shaped by long-term climate history. Large-scale empirical measurements are

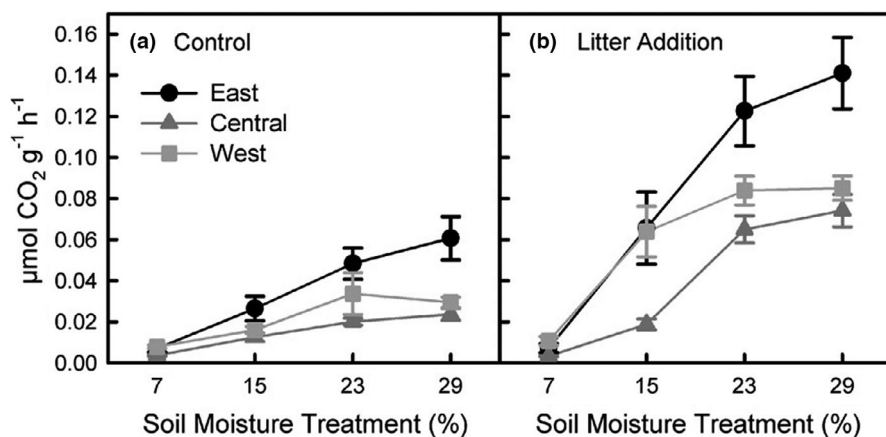


FIGURE 3 Reprinted from Hawkes et al. (2017) with permission. Soils from drier (West), moderate (Central) and wetter (East) regions in Texas, USA, show variation in soil respiration response to moisture (a), which is accentuated by litter addition (b). $n = 4$ sites per region. Moisture treatments in A and B represent the range observed in the field. This study did not include saturation so functions were linear rather than hump-shaped

needed to determine the extent to which historical precipitation directly or indirectly shapes microbial response. It may be that different aspects of precipitation patterns (e.g. mean versus extremes) are important at different sites, or other factors like substrate quality or quantity overwhelm the impact on respiration rate, compared with climate-determined microbial community size or composition (Schimel, 1995).

Altered rainfall conditions, including extreme drought, will occur in the future (IPCC, 2014). It is unclear how microbial communities will respond to increasing drought frequency and intensity, but such events may be novel enough to alter moisture response functions long term. Some studies have examined moisture responses during and following extreme drought induced by precipitation manipulations. The sensitivity of microbial communities and moisture response curves seems to vary across studies and sites. Some microbial communities are compositionally and functionally resistant to a change in rainfall (Averill et al., 2016; Bond-Lamberty et al., 2016; DeAngelis et al., 2015; Hawkes et al., 2017; Ochoa-Hueso et al., 2018; Waring & Hawkes, 2018), whereas others show some change in composition, with or without a change in function (Evans & Wallenstein, 2014; Evans et al., 2014; Fuchslueger et al., 2019; Roy Chowdhury et al., 2019). There is some evidence that this varied sensitivity to drought can be predicted from historical rainfall (Evans & Wallenstein, 2012, 2014; Fierer & Schimel, 2002), particularly the variability of rainfall, which may increase communities' ability withstand extreme events. Across the precipitation gradient in Texas introduced above, Hawkes et al. (2020) found that moisture curves and microbial communities were surprisingly insensitive to rainfall manipulation, potentially because the highly variable climate at all sites in the semi-arid region selected for an abundance of generalist taxa. We formalize this second role of climate history in predicting response to novel precipitation events below (see drought legacy hypothesis).

Determining why moisture responses shift under drought in some soils but not others is key for improving the accuracy of forward projections. While there are many explanations for this variation, one possibility is that microbial communities differ in sensitivity to changes in rainfall, which itself could be shaped by historical conditions (directly or indirectly). Specifically, we suggest historical

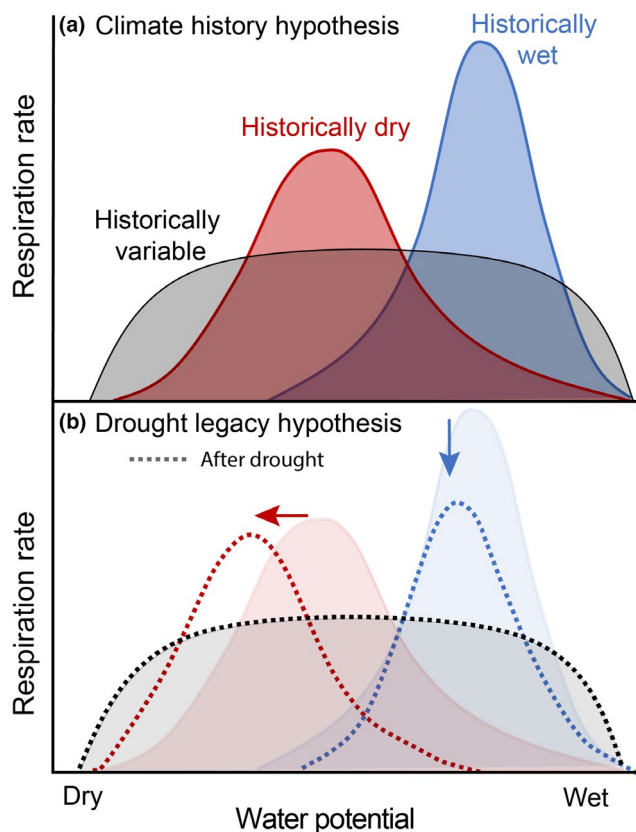


FIGURE 4 Hypothesized changes in moisture response functions across sites, as a function of historical precipitation patterns (climate history hypothesis, (a) and in response to novel drought (drought legacy hypothesis, (b). Shifts in the moisture response curves in B depend on the resident microbial community shaped by precipitation: at historically dry sites, the curve optimum and dry threshold (see Figure 5) are expected to shift left presumably because selection increases drought tolerant traits (red arrow), whereas at historically wet sites maximum respiration declines as mesic-adapted taxa reach physiological limits (blue arrow). Curves could take on many functional forms, and hypotheses are not mutually exclusive

variation in rainfall may be an important determinant of moisture response through impacts on microbial physiology and survival. This expectation is derived from trait-based frameworks (Wallenstein &

Hall, 2012) as well as theoretical (Hawkes & Keitt, 2015) and empirical studies on moisture response.

3 | NEW HYPOTHESES FOR PREDICTING VARIATION IN MOISTURE RESPONSE FUNCTIONS

3.1 | Climate history and drought legacy hypotheses

Together, this body of work shows that, contrary to model assumptions, moisture response functions differ across sites, and may or may not change following severe drought. The next step is developing general theory to predict how and why moisture response functions differ so that this variation can be incorporated into models. We propose two hypotheses for developing this theory, grounded in the idea that soil moisture regimes regulate moisture response functions through impacts on microbial community size, traits and functioning. Such impacts can arise directly through biotic selection or in combination with soil forming factors and mineralogy.

First, we hypothesize that long-term precipitation history determines geographical variation in moisture response functions ('climate history hypothesis', Figure 4a). Specifically, the mean and variance in rainfall will impact moisture response function parameters (e.g. dry threshold, moisture optima and breadth). Over long time-scales, precipitation history could shape parameters directly through microbial selection, or through other factors that alter microbial habitat, like soil physical and chemical properties or vegetation chemistry (Jenny, 1941). Separating these direct and indirect pathways should be a goal of future studies. Alternatives to this hypothesis are that moisture response functions are the same across all sites, with respiration dependent only on contemporary soil moisture and soil properties, or that curves vary across sites as a function of other factors. Note that in Figure 4 we have depicted our expectations as simple differences in magnitude, breadth or optima, of a hump-shaped function, but more complex differences are possible given potential interactions among micro-organisms and microbial processes, as well as between biotic and abiotic drivers.

In addition to climate-driven geographical variation in moisture response functions, we also hypothesize that moisture response functions change after severe drought in ways that depend on prior drought ('drought legacy hypothesis', Figure 4b). Prior drought shapes the traits and drought tolerance of resident microbial communities, affecting the magnitude and direction of shifts in moisture response functions following contemporary drought. If drought-tolerant taxa are already present, like in xeric sites that have higher rainfall variance with periodic extreme drought, curves may shift left as dry-adapted microbial taxa increase in response to drought selection (Figure 4b, red arrow). Conversely, mesic-adapted communities may reach physiological limits more quickly and collapse, moving curves down (Figure 4b, blue arrow), unless rescued by rapid adaptation or immigration. These mechanisms may occur together and

also interact with other changes (e.g. substrate quality and quantity) that trigger drought legacies.

3.2 | Microbial mechanisms underlying moisture response functions

At the heart of our hypotheses are changes in aggregate microbial physiology through biological processes such as selection, environmental filtering, and biological traits and trade-offs. Indeed, our understanding of these biological processes (even if limited, at times) is what makes these hypotheses powerful: potentially, curves could be predictable from climatic variables, because they influence biology, and in turn function, in a predictable way. As such, increased understanding of underlying mechanisms, and examining mechanisms over large scales, will be key to testing the generality of both the climate history and drought legacy hypotheses we describe, to improve predictive power, and to understand the impacts on long-term C storage. We review the many frameworks for understanding this complex relationship, focusing on mechanisms that may underlie our moisture response hypotheses.

How microbial communities respond to perturbations, and implications for function, have been reviewed elsewhere (Bardgett & Caruso, 2020; De Vries & Shade, 2013; Hawkes & Keitt, 2015; Shade et al., 2012). For instance, Bardgett and Caruso (2020) highlight functional diversity, functional redundancy, asynchrony of species response and drought tolerance traits as key to increasing resilience. Related specifically to rainfall history, Evans and Wallenstein (2014) showed that 10 years of more variable rainfall resulted in more taxa with life histories tolerant to drying-rewetting, likely making the community more resilient to moisture disturbance. A taxonomic profiling approach with the same dataset revealed that exposure to more variable rainfall led to communities with higher resistance to drying and rewetting in the laboratory (Evans & Wallenstein, 2012). Characterizing life-history strategies over time showed that this resistance was due to changes in the number of drought-tolerant and drought-sensitive taxa.

Mechanistic insight can be gained by characterizing the traits that underlie these moisture-based life histories, as well as the associated trade-offs constraining trait distributions (Malik, Martiny, et al., 2020). For instance, Malik, Martiny, et al. (2020) defined trait-based microbial strategies that putatively govern physiological responses to stress, as they are shaped by trade-offs in resource allocation. Wang and Allison (2021) implemented these strategies in the DEMENT model to show quantitatively how trade-offs with drought tolerance traits can lead to legacies in the microbial community capacity for decomposition (see below). This approach is powerful because it captures the intrinsic microbial properties that confer resilience and lead to legacies that affect microbial respiration.

Classification of microbial life histories along a generalist-specialist continuum is a simple yet powerful approach for understanding ecological response (Loreau, 2001), and may be especially useful if this distribution can be predicted by mean and variance of

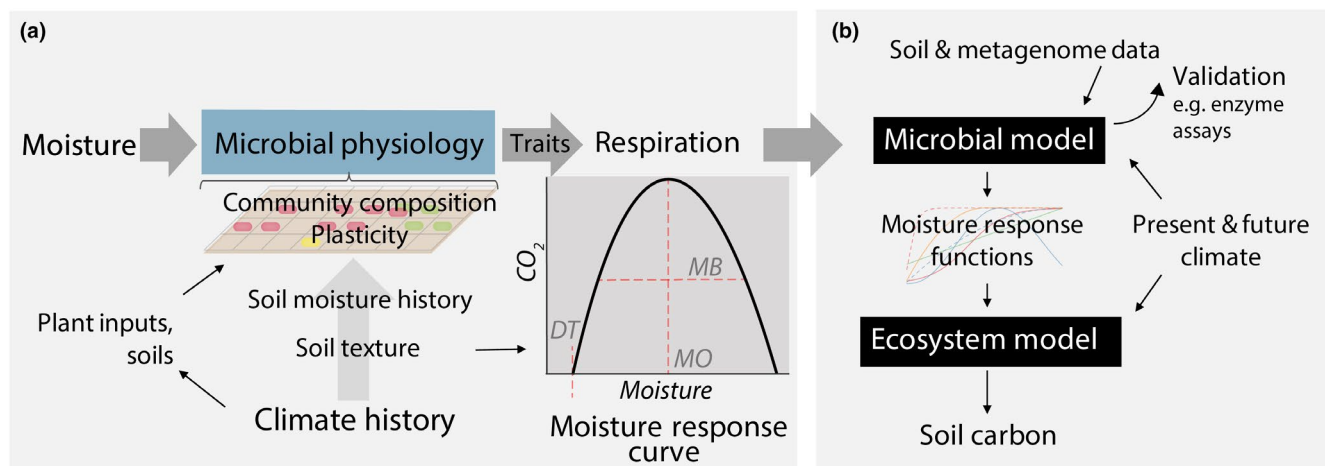


FIGURE 5 Conceptual framework for understanding and improving moisture responses. (a) Microbial respiration in response to a gradient of moistures, or the moisture response curve, is determined by the physiological traits of a microbial community that are filtered by climate history and other environmental variables (see Figure 4). Relevant parameters for moisture response curves may vary with which functional form it assumes, but assuming a hump-shaped function, we identify the dry threshold (DT), moisture breadth (MB) and moisture optimum (MO). (b) Empirically derived moisture response functions and microbial traits are used to parameterize trait-based microbial models, and the resulting moisture-response functions can be used in ecosystem models to predict C cycling when driven by present and future climate scenarios

historical precipitation (Figure 5a). This approach could be combined with trait-based approaches described above, to understand the distribution of generalists versus specialists, and the functional implications of the relative distribution of these strategies. The relative abundances of generalists versus dry- or wet-adapted strategists could affect the optimum, threshold and breadth of the community's moisture response function. In addition, relative to specialists, generalists are likely to have more stable function after perturbations based on simulations (Hawkes & Keitt, 2015). In Texas, the lack of change in moisture response after severe drought was explained by the dominance of generalist taxa, which may be abundant because they tolerate the high coefficient of variation (CV) of this region's rainfall (mean CV = 86% for monthly rainfall based on the 100-year record) (Waring & Hawkes, 2018). In fact, 99% of bacterial and 98% of fungal taxa were classified as generalists in a 4.5-year extreme rainfall manipulation at one site, where no change in moisture response function was found (Hawkes et al., 2020). Several approaches for classifying taxa along a generalist-specialist continuum could be used, including using a 'generalist index' (Mariadassou et al., 2015) or RNA:DNA ratio across a range of moisture levels. In this way, 'generalist' communities could have more generalist species with broad physiological niches, or have greater functional redundancy, or both.

3.3 | Environmental factors shaping microbial response at the macro- and micro-scale

Aside from moisture availability, other factors may correlate with rainfall and influence microbial mechanisms underlying moisture response functions. For example, soil properties and plant communities depend on historical climate and will play an important role in shaping microbial response. Especially over long time-scales, these

confounding factors will need to be accounted for in tests of the climate history hypothesis. The sensitivity of these factors to drought, which may itself vary across ecosystems as a function of climate history, should also be considered when evaluating the drought legacy hypothesis. Drought sometimes alters plant communities, and shifts in litter substrate quality and quantity affect microbial drought tolerance (Malik, Swenson, et al., 2020). Nitrogen availability (Evans & Burke, 2013), solutes or extracellular enzymes (Schaeffer et al., 2017) and rhizodeposits (Williams & de Vries, 2020) also shift under drought. In one study, immediate microbial responses to moisture (or microbial 'moisture niche'), which identified wet- versus dry-adapted taxa, was not a good predictor of long-term microbial abundances under drought (Evans et al., 2014), presumably because plant productivity or substrate chemistry more strongly shaped microbial communities over decadal time-scales.

A final consideration is the scale at which environmental conditions impact microbial physiology and function. We have thus far focused on rainfall as a predictor of microbial function, but rainfall mean or variance, or even bulk soil moisture, may not translate well to the micro-scale conditions that govern microbial physiology (Schimel, 2018; Smercina et al., 2021). For instance, microbes may remain in isolated water films even as bulk soils dry, and the rate by which water films dry relative to bulk soils depends on soil physical and chemical properties. As moisture decreases, increased habitat heterogeneity may also cause resource limitation, or changes in predation (Erktan et al., 2020; Schimel, 2018). These multiple selection pressures occurring simultaneously (e.g. predation, osmotic stress, resource limitation) may or may not act on the same microbial traits. For example, response traits for starvation and desiccation can be similar (Potts, 1994). In this case, microscale information might not increase our ability to understand moisture response functions, but in other scenarios, additional measurements may be needed.

4 | EMPIRICAL AND MODELLING FRAMEWORK FOR ADVANCING FUTURE KNOWLEDGE

4.1 | Overall approach and curve parameters

We present a novel approach for examining our hypotheses and their underlying microbial mechanisms with the ultimate goal of increasing our understanding of the microbial role in mediating the response of respiration to moisture (Figure 5a), and improving moisture response functions in models (Figure 5b). Moisture affects respiration through the physiology of individual cells aggregated at the community level and is shaped by soils and climate history. In this way, communities that experience different climate histories may show moisture response functions with different shapes. We propose these measurements—both curve parameters and underlying microbial processes—can be used to improve ecosystem models. Measurements can first be used to parameterize trait-based microbial models (e.g. DEMENT, Allison, 2012), producing moisture response functions that consider multiple interacting factors. The validated set of response curves can then be used in ecosystem models to test implications for C storage.

The true shape of moisture response functions is currently unknown (see Figure 1). We assume hump shape for the sake of discussion (Figure 4). Regardless of the functional form, studies should identify key parameters that can be linked to underlying physiology as it is shaped by climate history. Here, using a hump-shaped curve, we identify three: *DT*, *MO* and *MB* (Figure 5a). The dry threshold (*DT*) is the water potential at which respiration ceases, and where the curve crosses the x-axis. The moisture optimum (*MO*) is the water potential at which respiration is highest. Finally, the breadth (*MB*) describes the width of the curve at half of the optimum, akin to niche breadth (Wallenstein & Hall, 2012). Note that while the wettest end of the curve is rarely tested, it could be relevant to saturated or flooded soils (e.g. wetlands) and may require a fourth parameter for wet threshold. Nonlinear model fitting could be employed if there is no consensus on functional form and may be essential for understanding C cycling under drought.

4.2 | Estimating consequences for soil C storage through model integration

Because of differences in the underlying microbial mechanisms, we expect differences in moisture response functions to alter long-term C storage. Although selection by climate history may be a primary driver of moisture response functions via climate effects on microbial traits, it is also possible that factors such as soil texture, C content and plant inputs could override this driver in some soils. Models will be essential for balancing these factors, scaling microbial mechanisms to whole-community moisture response functions, and then scaling whole community respiration responses to global C cycling (Figure 4b). Highly parameterized microbial (trait-based) models

can facilitate this scaling process when combined with ecosystem models. Such a hierarchical modelling approach (further described in Allison, 2017) could update the response functions in ecosystem models by capturing key mechanistic information and empirical support from smaller scales without adding excessive complexity.

Trait-based models can represent the mechanisms by which soil moisture affects microbial respiration (Wieder, Allison, et al., 2015), which is the aggregate of many respiratory processes occurring on micro-scales that are difficult to measure. The trait-based model DEMENT represents community dynamics and microbial physiology (Allison, 2012; Allison & Goulden, 2017), including respiratory mechanisms associated with resource acquisition and drought tolerance. The model also incorporates physiological trade-offs that affect C cycling under drought but are difficult to account for empirically. Together, traits and trade-offs determine microbial growth rates, emergent C use efficiency and respiration responses to soil moisture (Hagerty et al., 2018). The model imposes environmental filtering as microbial communities assemble under a given historical climate (as in our conceptual framework, see Figure 4a).

DEMENT simulates how moisture history is likely to shape microbial traits, microbial functioning and C cycling (Wang & Allison, 2021). Under drought (Year 6), microbial communities allocate greater resources towards stress tolerance, reducing the community's biomass-specific investment in enzyme production (Figure 6a, left side). Drought-exposed communities had higher drought tolerance (Figure 6b), but lower capacity to decompose organic material; severe drought reduced microbial biomass and litter decomposition by more than 50% (Figure 6c). When conditions were returned to ambient, DEMENT simulations revealed a drought legacy of reduced decomposition driven by these trait shifts and consistent with the drought legacy hypothesis. After moisture was restored to ambient levels for 3 years (Year 9), decomposition rates remained 48% lower for communities with a simulated history of severe drought (Figure 6c, right column).

The next step in scaling up these model predictions and mathematically formalizing our hypotheses is site-specific parameterization and validation. For example, resource acquisition and drought tolerance traits could be extracted from genomic datasets and used to generate DEMENT parameters (Berlemont et al., 2014). Model outputs at the community level, such as enzyme activity and respiration rates, can be validated with empirical measurements across moisture gradients, and used to generate equations for changes in moisture response functions. Furthermore, DEMENT simulations could distinguish the relative importance of site-specific soil, vegetation and metagenomic (trait) parameters in predicting respiration, allowing us to address whether precipitation history alters function through effects on edaphic variables or biotic selection. DEMENT can also represent other microbial C pathways and trade-offs that occur with changes in moisture.

Trait-based models like DEMENT represent local-scale microbial community dynamics, but other models are needed to project moisture responses at the ecosystem to global scale. Validated moisture response functions generated from a trait-based model could be

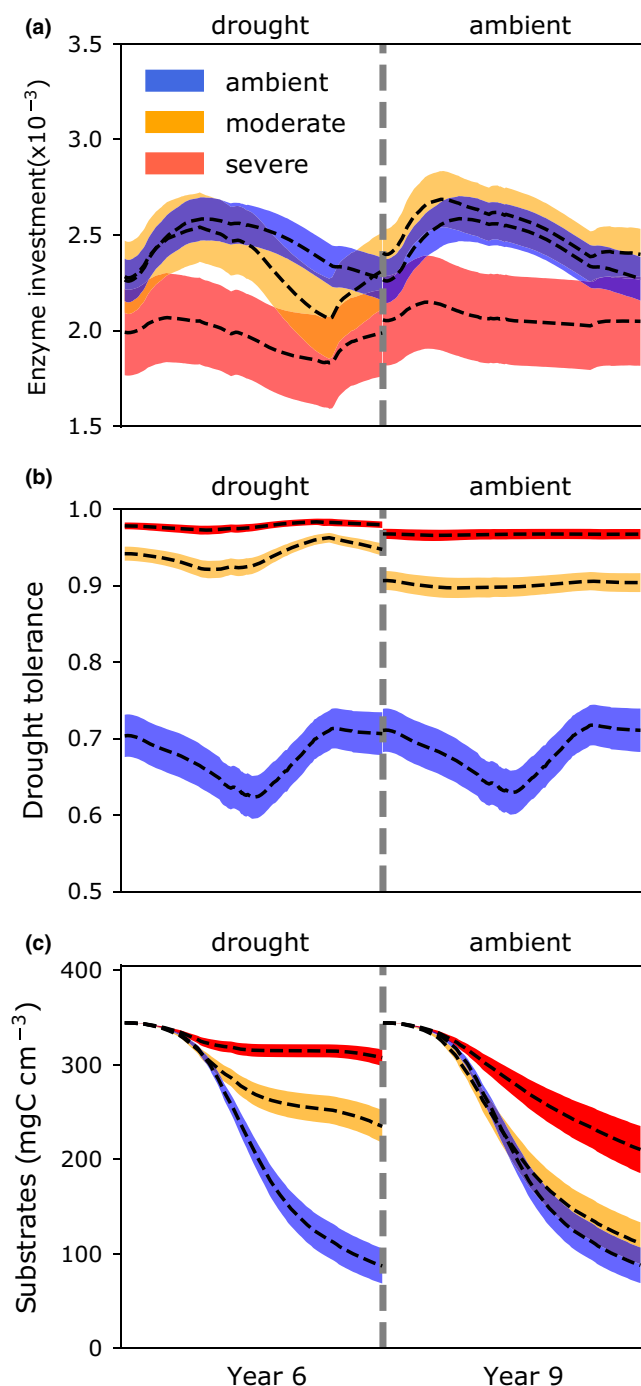


FIGURE 6 DEMENT simulations reveal possible effects of drought and drought history on microbial community traits and function. Exposure to 6 years of moderate or severe drought (Year 6), and a subsequent 3 years of ambient conditions (Year 9) altered community-level enzyme investment (a), drought tolerance (b) and rates of litter substrate degradation (c). Modified from Wang and Allison (2021) with permission. Dashed lines and colored bands are means and 95% confidence intervals ($n = 40$), respectively

used in traditional and microbially explicit ecosystem models to simulate long-term C storage under different climate scenarios. For example, models such as DayCent (Del Grosso et al., 2001) and MIMICS (Wieder, Grandy, et al., 2015), which currently assume constant or

no moisture dependence, could be parameterized with the moisture response functions and adaptive mechanisms predicted by a trait-based model. It is unclear whether microbially explicit models can better represent moisture-mediated dynamics; one recent study found that the shape of the moisture response function itself had a bigger impact on C cycling under moisture variability than whether or not the model included microbially explicit mechanisms (Zhou et al., 2021). Both types of ecosystem models should thus be tested to simulate the consequences of this mechanistic information for larger-scale and longer-term C storage.

4.3 | Experimental considerations and recommendations

Additional empirical studies are needed that measure microbial moisture responses and probe the mechanisms underlying variation in these responses across sites. Ideally, more studies should span multiple sites, standardize methods or coordinate efforts to achieve generality. Global coordinated research networks could play an important role in this effort (Yahdjian et al., 2021), such as DroughtNet's International Drought Experiment (<https://droughtnet.colostate.edu>), which assesses ecosystem response to a standard rainfall reduction across many sites globally. We also suggest that researchers regularly measure moisture response curves (incubations of soils at a range of moisture levels) to inform development and consensus among moisture response function. In some sites, field measurements may be possible with controlled drying and wetting, given the number of sensors that may be installed at well-studied locations. In general, however, field measurements of soil moisture response curves are not practical. For laboratory incubations to be relevant for the field, experimental designs should recognize that physical structure is a major determinant of moisture dynamics and moisture response (Moyano et al., 2012). Field soil structure could be preserved by incubating intact cores. Additional studies should test how soil structure affects the respiration response to moisture, either by measuring structure explicitly (e.g. micro-scale tomography; Kravchenko et al., 2019) or by quantifying how sieving affects moisture response (Herbst et al., 2016). While studies on sieved soil may help separate microbial and soil physical factors, understanding micro-scale dynamics in situ will be essential for scaling moisture responses across soil types.

Metrics of water availability used in empirical studies should be relevant to microbial physiology. Gravimetric water content is easy to measure, but soil water potential is likely a better metric of water availability. Although water content and water potential are related (i.e. through soil water retention curves), the relationship is nonlinear and subject to uncertainties due to poor model fits and differences among sieved and undisturbed soils (Herbst et al., 2016). Work in this area is needed to better link moisture responses to microbial microhabitats, stress and trait selection. Such studies could utilize recent advances in micro-scale imaging, sensors and biosensors (Del Valle et al., 2021). With no current

consensus on moisture response functions, studies might simply measure a range of water potentials spread evenly across field conditions. Later studies may consider targeting certain areas of the curve that need greater resolution or to help identify non-linearity. Finally, as others have emphasized (Malik, Martiny, et al., 2020; Wallenstein & Hall, 2012), microbial traits are crucial for linking microbial mechanisms with moisture response functions. Traits are also relevant for C cycling processes beyond respiration (Cotrufo et al., 2013; Liang et al., 2017). Therefore, more studies are needed that address moisture effects on traits such as C use efficiency, necromass chemistry and osmolyte production. These trait measurements are most powerful when integrated into a trait-based model to account for microbial processes that are difficult to measure.

Although our current synthesis focuses on respiration responses to stable moisture levels and long-term respiration trends, understanding the mechanisms that underlie the Birch effect (Birch, 1958) is also essential for improving models. The Birch effect is the higher-than-expected respiration pulse that occurs after long dry periods and may constitute a large proportion of annual respiration (Kim et al., 2012). This response may be controlled by factors other than those influencing moisture responses under more stable conditions, so studies should carefully consider the timing of moisture manipulations and review the many empirical and modelling studies on this topic (Evans et al., 2016; Göransson et al., 2013; Patel et al., 2021; Waring & Powers, 2016). Rewetting pulses are mediated by some combination of nonlinear biotic and abiotic processes, and as such, sometimes a microbially explicit approach can improve predictive ability (Schimel & Weintraub, 2003; Waring & Powers, 2016).

5 | CONCLUSION

Accurate predictions of global C cycling rely on accurate moisture response functions, yet there is an astonishing lack of consensus in the shape of these functions. Empirical measurements of moisture response curves are needed, at a broad range of sites, and with careful consideration of soil properties. These functions could eventually be predictable from data on historical precipitation and microbial traits. To facilitate this predictive advance, new studies of microbial dynamics are needed that are generalizable, scalable and linked to ecosystem function. Standardization of the approaches that link process rates with microbial mechanisms, climate and soil properties could be especially powerful for improving our understanding of C cycling as precipitation patterns change. Large-scale ecological networks (e.g. NEON, LTER) could play an important role in enabling a collective effort to systematically analyze moisture responses across sites. Development of a mechanistic, theory-driven framework for interpreting moisture response functions is an important first step towards predicting changes in soil C and C-climate feedbacks across ecosystems and in a drier and more variable future.

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CONFLICT OF INTEREST

The authors have none to declare.

AUTHORS' CONTRIBUTIONS

All authors contributed to the concepts in the paper. S.E.E. led the writing of the manuscript. All authors contributed to the drafts via writing, critical review and revision, and gave final approval for submission.

DATA AVAILABILITY STATEMENT

All data included in this Perspective are previously published, and appropriately cited. No new data were generated.

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