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Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes

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Abstract

Throughout Earth's history, drought has been a common crisis in terrestrial ecosystems; in human societies, it can cause famine, one of the Four Horsemen of the apocalypse. As the global hydrological cycle intensifies with global warming, deeper droughts and rewetting will alter, and possibly transform, ecosystems. Soil communities, however, seem more tolerant than plants or animals are to water stress—the main effects, in fact, on soil processes appear to be limited diffusion and the limited supply of resources to soil organisms. Thus, the rains that end a drought not only release soil microbes from stress but also create a resource pulse that fuels soil microbial activity. It remains unclear whether the effects of drought on soil processes result from drying or rewetting. It is also unclear whether the flush of activity on rewetting is driven by microbial growth or by the physical/chemical processes that mobilize organic matter. In this review, I discuss how soil water, and the lack of it, regulates microbial life and biogeochemical processes. I first focus on organismal-level responses and then consider how these influence whole-soil organic matter dynamics. A final focus is on how to incorporate these effects into Earth System models that can effectively capture dry–wet cycling.

Water is the critical resource for life, yet drought is pervasive in terrestrial ecosystems. Most ecosystems experience at least occasional drought, and droughts appear to be intensifying with climate warming (Sherwood & Fu 2014). Arid zones are expanding (Seager et al. 2018). Drought stresses all organisms, potentially killing them or driving evolution of drought-adapted life history strategies. In plants, these include deep roots, annual growth, and the production of small, waxy leaves (Kooyers 2015). Thus, water availability (or the lack of it) structures plant communities, but it also regulates soil communities and their function. The magnitude and extent of dry periods vary, from short, mild dry-downs to the decades-long drought of the Atacama desert; droughts lasting weeks to months are common in many regions. Drought affects soil processes in several ways, notably by directly stressing soil organisms—soil microorganisms rapidly equilibrate to the osmotic conditions (water potential) of their immediate environment—and to remain hydrated when the soil around them dries, they must accumulate solutes to retain water within their cells. But drought also affects soil processes indirectly, by altering the supply of substrates to microbes via dissolution, diffusion, and transport.

But, of course, droughts end. The first rains release microbes from stress, redissolve materials, and drive mass flow of resources through the soil. In fact, it remains unclear whether the greater effects of drought on soil processes result from physiological stress from drying or from rewetting. So, which is the real disturbance: drought or rewetting?

Drying and wetting are always coupled, and so drought might better be considered an integrated two-part disturbance: a disturbance that combines physiological, physical, and chemical perturbations to the soil system. As Earth's climate changes, capturing the effects of varying dry–wet cycles in Earth System models will be important to effectively describe and predict biogeochemical processes—but to do that, we need to know the key processes to incorporate.

In this review, I discuss how dry conditions affect microbial life and biogeochemical processes in soil, exploring how the different effects manifest. I start with the ways in which water (or the lack of it) influences the soil environment and then evaluate these influences on microbial systems, starting at the organismal level and then following the cascading effects up to the whole soil. I also discuss how researchers have incorporated these effects into simulation models to describe soil processes over yet larger scales and longer periods.

1. DRY SOILS AS A HABITAT FOR SOIL MICROBES

Water affects microbial dynamics in three fundamental ways: as resource, as solvent, and as transport medium (Tecon & Or 2017). Each is important in regulating microbial function. Working in concert, they produce complex patterns of microbial and biogeochemical responses (Moyano et al. 2013) (**Figure 1**).

1.1. Water as Resource: Water Potential

The availability of water as a resource is a function of its energy state—its water potential. The more energy available, the more easily accessible the resource. Water potential (notated by the symbol Ψ and expressed in units of pressure, pascals) (Papendick & Campbell 1981) is therefore fundamental in understanding soil moisture relations. Soil water potential is controlled primarily by the physical soil matrix and by solutes. Water interacts with solids through capillarity and adhesion to particle surfaces—these drive matric potential (Ψm); soils with more reactive surface area hold water more tightly. Dissolved materials stabilize water molecules, regulating the water's solute (osmotic) potential (Ψs). Ψs and Ψm are always negative in soil because they are measured against a reference of pure water (defined as having Ψs and Ψm of 0). The other components

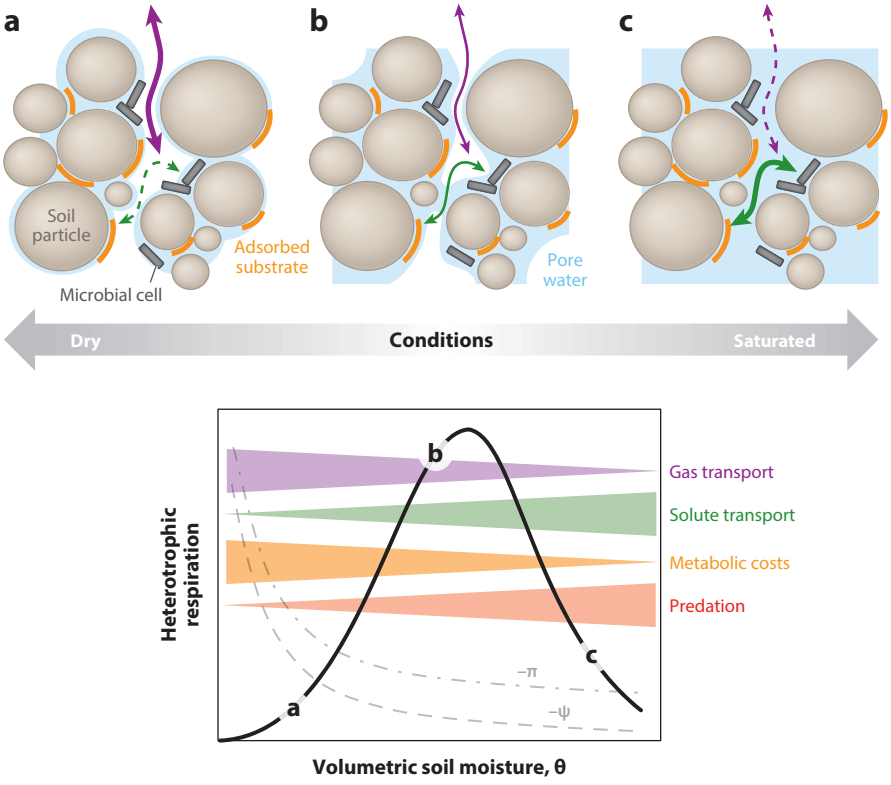

Figure 1

Moisture effects on soil microbial activity under conditions ranging from (*a*) dry to (*c*) saturated. Black rectangles represent microbial cells, and orange lines represent substrates adsorbed onto soil particles (*tan spheres*). (*Bottom panel*) The relationship between soil respiration (*black line*) and moisture results from interacting effects, including diffusion and physiological, biochemical, and ecological processes. ψ indicates the soil water potential, and π is the cell osmotic potential that would allow maintaining a stable turgor pressure as ψ declines. ψ and π are have negative values; to plot them on a positive axis, they are plotted as their negative values. Figure adapted from Moyano et al. (2013) with permission.

of water potential are macroscale: Water has gravitational potential (Ψg) that drives it to flow downhill (to lower Ψg); it can use that energy to erode hillsides and scour stream channels. The final component of water potential is pressure (Ψp)—water under pressure can fly out of a hose or spin a turbine.

These components sum to the overall total water potential (Ψw):

$$\Psi w = \Psi s + \Psi m + \Psi g + \Psi p.$$

Water always flows down a Ψw gradient. Thus, water flows downhill because of the Ψg gradient; in osmosis, water on the freshwater side of a membrane moves across because the solute potential on the salty side is lower. The Ψw gradient drives water from soil through plants to the atmosphere. Even when we might consider the air dripping wet, the actual Ψw is remarkably low—at a humidity of 98%, Ψw is below −2 MPa. At 47% humidity, Ψw is −100 MPa (Papendick & Campbell 1981). The difference between that and any likely soil Ψw (i.e., 0 to −10 MPa) drives water movement from the soil through a plant to the atmosphere.

For soil microbes, water potential is a fundamental control over survival and function. Microbes are small and in intimate contact with their environment; because nothing exists between them and the soil except their cell membrane and wall, they necessarily equilibrate with the water potential in the soil around them. As soil dries out and its Ψw drops (becomes more negative), microbial cells are challenged; to avoid losing water to their environment and dehydrating, they must accumulate solutes to lower their internal solute potential to match the water potential of the surrounding soil. To avoid this, they may form impermeable cell walls (such as occurs in *Bacillus* spp. spores), but then they cannot readily take up other resources.

As cellular water potential drops, it may cause a loss of cell turgor (Harris 1981), which is analogous to wilting in plants. The loss of turgor can interfere with microbial physiological functions, reducing metabolic rates. Eventually, a reduction in cell water potential can cause cellular functions to fail, killing the organism.

One of the key characteristics of the relationship between water content versus matric potential (Ψm) is the extreme nonlinearity (Papendick & Campbell 1981). When soils are wet, water content can change substantially without significantly reducing water potential. However, when soils are dry, even a slight change in soil water content can cause a large change in matric potential. These curves vary with the texture (particle size distribution) or organic matter content of the soil. In soils that are finer or that have more organic matter, the curves shift: At any water content, a finer-textured soil will have a lower (more negative) matric potential, and at any given water potential, a finer-textured soil will contain more water than a coarse-textured soil.

1.2. Water as Solvent

The second way in which water controls microbial activity in soils is as a solvent. With few exceptions, the substrates that microbes use as energy sources are water soluble; the exceptions are gases such as methane and nitrous oxide and a few volatile organics such as acetic acid, terpenes, and isoprenes (Cleveland & Yavitt 1997). Often, researchers distinguish between insoluble soil organic carbon (SOC) and dissolved organic carbon (DOC); however, this is an oversimplification. As soil dries, and the volume of liquid water decreases, some solutes become concentrated, whereas others likely precipitate out. Substrates that are sparingly soluble may show complex behaviors. For example, Qualls (2000) extracted forest floor samples with water daily (the extraction lasted the entire 24 h) for 21 days; it was not until at least 10 extraction cycles that additional DOC was no longer recovered. Whether material was insoluble or sorbed onto soil particles is unclear, but the presence of large pools of water-soluble materials that are not immediately in solution is an important characteristic of soils.

1.3. Water as a Transport Medium

Water in soil not only is a vital resource and solvent but also is the fundamental transport pathway for solutes and microorganisms. Microorganisms can take up only small molecules, and so they rely on extracellular enzymes to break down polymers and diffusion to access small molecules (Wallenstein & Weintraub 2008). Because most substrates are water soluble, connected water-filled pores are vital to allow transport of resources to microbes (Bailey et al. 2017, Tecon & Or 2017). As soils dry and water films on soil particles become thinner, paths for diffusion become longer and more tortuous (**Figure 1*b*** versus **Figure 1*c***) and may break altogether (**Figure 1*a*** versus **Figure 1*b*,*c***). In fact, a breakdown in hydrological connection has been argued as a primary rationale for the effects of soil drying on soil community dynamics (Carson et al. 2010) and biogeochemistry (Lawrence et al. 2009, Manzoni & Katul 2014, Manzoni et al. 2016, Or et al.

2007). As soils dry, macropores drain first; thus, the diffusivity of soil declines dramatically as moisture content drops (Tecon & Or 2017) (**Figure 1**). As a result, resource supply declines disproportionally to water content. The reduction in diffusion as soils dry is well understood from soil physics, but explicitly considering physical transport processes in soil biology has lagged (Dwivedi et al. 2017, Evans et al. 2016, Manzoni et al. 2014, Smith et al. 2017).

Distinguishing between direct physiological stress and indirect diffusion-driven substrate limitation as drivers of reduced microbial activity is tricky. One approach is to use gas-phase substrates. Stark & Firestone (1995) used $^{15}NH_3$ to separate moisture controls on nitrification, the oxidation of ammonium to nitrate, and showed that, down to a water potential of −0.5 MPa, reduced diffusion accounted for at least 50% of the reduction in nitrification.

The importance of transport in regulating microbial responses to moisture stress is suggested by a meta-analysis of moisture effects on microbial activity. Manzoni et al. (2012) found a linear decrease in relative microbial activity with decreasing water potential, leading to thresholds at which activity ceases (−13.8 MPa in mineral soils and −36.5 MPa in surface plant residues). They concluded that although the threshold in residues may reflect microbial physiology, the threshold in mineral soils must be constrained by reduced diffusion—the consistency and insensitivity to site history suggest it is likely driven by physical, rather than biological, processes. This finding is also consistent with the argument framed by Schimel & Schaeffer (2012) that microbial access to soil carbon is the primary control on whether that carbon is decomposed (and respired to CO_2), although the fate of the carbon—how it is allocated by microbes to growth versus other processes—may be controlled by the composition of the microbial community.

The ability of the soil to support transport also influences soil food webs. The smallest microbial predators (protozoa, nematodes, tardigrades, and phage) depend on cilia and flagella to swim through water-filled pores (Geisen et al. 2014). As soils dry, their ability to find their microbial prey declines, and microbial mortality decreases. Predators require relatively large pores to move through the soil, larger than are needed for molecules to diffuse; hence, as soils dry, predation likely slows before microbial activity or even growth decline. For example, at a water potential of −0.1 MPa, relatively large pores remain water filled (~3 μm diameter); this would be small enough to constrain the movement of soil fauna. At −1 MPa, only pores smaller than 0.3 μm remain water filled (Papendick & Campbell 1981). Soil mesofauna, such as mites and collembola, move through air spaces and so may remain active in drier soils, but as bacteria primarily live in fine pores (Foster 1988, Mummey et al. 2006), they may be somewhat protected from predation in dry soils.

By functioning simultaneously as a resource, solvent, and transport medium, water creates complex microbial responses driven by a combination of effects on resource availability, organismal physiology, community dynamics, and food web dynamics. As soils dry, these effects become increasingly extreme.

2. ORGANISMAL RESPONSES

2.1. Osmotic Acclimation

Microbial responses to water stress are complex (Wood 2015). To retain water as soils dry and Ψm declines, microbes must reduce their internal solute potential (Ψs) by accumulating solutes (osmolytes) (Csonka 1989, Killham & Firestone 1984, Wood 2015). Microbes preferentially accumulate organic molecules that reduce Ψs without disrupting cell metabolism (so-called compatible solutes); these include proline, glycine betaine, trehalose, and glutamate. Inorganic ions, notably K^+, are harmful at high concentrations; cells use these after they have exhausted their ability

to synthesize or take up compatible solutes (Killham & Firestone 1984). Bacteria are classically thought to rely on nitrogenous osmolytes such as proline and glycine betaine, whereas fungi use polyols and simple carbohydrates such as glycerol, erythritol, and mannitol (Witteveen & Visser 1995). When grown in culture, microbes show a range of strategies for accumulating osmolytes—from not accumulating any, to producing them in response to reduced water potentials, to maintaining high levels of compounds in their cytoplasm (Harris 1981, Killham & Firestone 1984).

As studies have begun to analyze microbial osmolyte accumulation in situ, however, the patterns observed in pure culture studies have not stood up well. Although Warren (2014) found known osmolytes in dry soils, other researchers have not. For example, Boot et al. (2013) analyzed the accumulation of amino acids in the microbial biomass of a California grassland where essentially no rain falls between April and October. They found no evidence that amino acids acted as osmolytes; glutamate levels were consistently 2–3% of the total microbial biomass. The other putative osmolytes—proline and glycine betaine—were absent (Boot et al. 2013). They further concluded that in California grasslands, no plausible concentration of osmolytes would keep microbes hydrated. In these soils, Ψm can drop below −30 MPa (Barnard et al. 2014), which is likely beyond microbes' ability to osmoregulate: At even 1 M solute concentration, Ψs is only approximately −5 MPa (Davis et al. 2000, Harris 1981). Additionally, Boot et al. (2013) argued that, as soils dry, diffusion and substrate supply would become limiting before moisture became stressful. Hence, osmolytes might be both unaffordable and ineffective. Similar conclusions were drawn by Kakumanu et al. (2013) who found that as drying became more intense, extractable organic carbon increased but known osmolytes actually decreased.

Perhaps it is not surprising that soil-based studies show different patterns than culture-based studies—organisms that do not synthesize osmolytes are unlikely to grow in salty culture media. Given that the majority of microorganisms in soil have never been cultured, including whole lineages (Becraft et al. 2017), it seems possible that the classic osmolytes are not representative of dominant microbial drought acclimation strategies. Rather, soil microbes appear more likely to survive dehydrating and to rehydrate, recover, and regrow (Meisner et al. 2017).

2.2. Resource Use

Water stress alters microbial resource use in a variety of ways. Dry soils can reduce microbial access to soluble resources, and drought stress can reduce the efficiency with which microorganisms use resources. But drying can also increase access to gaseous and volatile substrates.

2.2.1. Carbon use and growth efficiency. As soils dry, diffusion rates decline and semisoluble materials precipitate. This combination means that as water stress increases, microbes become resource limited, and it should limit their ability to use physiological acclimation strategies, such as synthesizing compatible solutes, that cost energy and require carbon.

If microbes must use an active physiological acclimation strategy to survive and remain functional under stress, as opposed to avoiding stress by entering dormancy (see Section 2.4), one might expect them to reduce their growth efficiency—microbes under stress would be expected to allocate fewer resources to reproduction and more to survival (Schimel et al. 2007). With reduced growth efficiency, biomass should decline in dry soils. Few studies have addressed this directly; however, one study that came close used ^{13}C-acetic acid vapor to measure microbial carbon use efficiency (CUE) (Herron et al. 2009). The authors assessed the fraction of ^{13}C converted into microbial carbon, although this likely included osmolytes and extracellular materials. CUE did not change as the soil dried until moisture had dropped to 0.05 g H_2O/g soil, at which level

Ψm had dropped below −0.6 MPa. At that moisture, total microbial respiration had declined by approximately 30%, and estimates of growth efficiency based on ^{13}C immobilization versus gross nitrogen mineralization diverged, suggesting disruption of cellular processes.

2.2.2. Volatile substrates. In contrast to organisms that rely on water-soluble substrates, organisms that rely on volatile or gaseous substrates, most notably methanotrophs that obtain energy from oxidizing methane gas, benefit from modest soil drying (Borken et al. 2006, Dijkstra et al. 2011, Fest et al. 2017). For these organisms, as soil dries, substrate availability increases because substrate is supplied by gaseous diffusion through air-filled pores (**Figure 1**). Increased substrate supply as soils dry may balance increasing physiological stress and so reduce their overall sensitivity to drought. For example, Gulledge & Schimel (1998) found that in an Alaskan boreal forest, CH_4 consumption was maximal at 30% of water holding capacity (WHC), whereas CO_2 production did not peak until at least 60% of WHC. Fest et al. (2017) showed that when throughfall was reduced in a eucalypt forest, soil water content decreased by 15%, but air-filled porosity increased by 20%; the net effect was to increase soil methane uptake by more than 50%. This study, however, observed limited evidence of moisture stress under dry conditions—only a hint was found in the data that methanotroph activity dropped even under the driest conditions (<20% water-filled pore space). The conclusion that moderate soil drying does not stress methane oxidizers was reinforced by Stiehl-Braun et al. (2011), who used ^{14}C-CH_4 and autoradiography to evaluate the location of CH_4 oxidation. Drought roughly halved volumetric soil moisture but increased CH_4 consumption. Notably, drought expanded the zone of consumption deeper into the soil profile but did not visibly reduce consumption in the surface soil, as might be expected if drying inhibited activity.

2.3. Microbial Extracellular Polymers: Enhancing the Microenvironment

Microbes may improve function and survival under harsh conditions by enhancing their local microenvironment. One way to do this is to produce extracellular polymeric substances (EPS); these are primarily polysaccharides but also contain DNA, proteins, and other materials released from live or dying cells (More et al. 2014). EPS act as sponges, delaying drying, and may retain water even at low Ψm. EPS cannot, however, prevent Ψm from equilibrating with the bulk soil and so, ultimately, cannot prevent physiological stress. But as soils dry, the EPS gel may connect microorganisms and substrates and so support activity at low Ψm (Holden 2011, Tecon & Or 2017, Wolfaardt et al. 1999). If drought reduces microbial activity by collapsing diffusion and limiting substrate supply, synthesizing EPS should be a useful drought acclimation strategy (Chenu & Roberson 1996, Manzoni & Katul 2014, Or et al. 2007).

As with most things related to soil, the specific nature of the materials found in any location or soil type is likely to depend partially on the nature of the organisms that produced the EPS and partially on the nature of the mineral phase—different types of compounds bind preferentially to different clay minerals (Lin et al. 2016).

2.4. Dormancy

Many microorganisms go dormant when conditions become unfavorable (Jones & Lennon 2010). Endospores, formed by several *Firmicutes* groups (Filippidou et al. 2016), may be the epitome of stress survival mechanisms (Nicholson et al. 2002), but there are other forms of dormancy. Dormancy is an effective evolutionary strategy for surviving resource and physical stressors

(Jones & Lennon 2010), particularly when stress occurs regularly, such as in Mediterranean ecosystems that regularly go without rain for six months or more.

The distinction between actual dormancy and mere starvation or stasis, however, may be unclear. Dormancy carries a cost—microbes must invest in dormancy, spending carbon to create structures that enhance long-term survival. However, as soils dry, many microbes may just tough it out and run out of resources, or they may simply dehydrate. One would expect that either mechanism would reduce survival relative to that possible with true dormancy, but this remains a poorly studied area of soil biology.

3. COMMUNITY RESPONSES

3.1. Biomass

Stress alters communities, shifting dominance and relationships. But, in soil, the first question about how moisture influences microbes is simple: How does drought stress influence the total size of the microbial mass?

3.1.1. Seasonal patterns. One might predict that microbial biomass would decline as soils dry: Stress, reduced rhizosphere inputs, and limited substrate supply should all reduce microbial survival. However, this is not always the case—microbial biomass often remains stable or even increases through months-long dry periods (Aponte et al. 2010, Landesman & Dighton 2010, Parker & Schimel 2011, Schaeffer et al. 2017). Rather, a decline in biomass sometimes occurs with the start of the wet season, even while activity spikes (Butterly et al. 2009, Parker & Schimel 2011, Schaeffer et al. 2017). Why? It must be that, although growth rates may be very low during the dry season, death rates are even lower. As microbial and consumer activity increase with the onset of rains, however, microbial biomass can decline.

3.1.2. Experimental dry–rewet cycles. Seasonal patterns, however, do not necessarily match findings from studies that focus on responses to either individual dry–wet events or multiple dry–wet cycles. Studies regularly show some immediate decline in biomass following rewetting. Following a single dry–rewet cycle, Wu & Brookes (2005) noted that microbial biomass had declined by 44% in a silty-clay loam soil from the Rothamsted permanent pasture plots. In a British grassland, following a single dry–rewet event, microbial biomass declined (Gordon et al. 2008), although microbial nitrogen showed a spike immediately following rewetting.

Despite an immediate drop that sometimes follows a dry–rewet cycle, biomass of microbes may recover (Saetre & Stark 2005), as may populations of protozoa. The overall upshift in microbial activity, growth, and food web dynamics might explain why in some ecosystems (such as California grasslands) microbial biomass increases under drought but then declines during the wet season (Schaeffer et al. 2017).

3.2. Community Composition

As with overall biomass, the composition of the bacterial community (as indicated by membrane lipids or DNA) may change relatively little with drought and rewetting, even among soils that have experienced substantially divergent antecedent conditions (Barnard et al. 2014, Butterly et al. 2009, Evans & Wallenstein 2012, Kakumanu et al. 2013). But when seasonal shifts do occur, the drivers of these shifts are difficult to sort out. Are seasonal shifts caused by changes in moisture and temperature that act directly on the microbes? Or does the environment

influence microbes through plant phenology and associated seasonality in carbon inputs to soils? Photosynthesis, root exudation, and litter production are all sensitive to drought, so climate and weather influence microbial communities through multiple pathways (Bardgett et al. 2008).

Analyzing microbial community change during drought and rewetting is challenging because of the constraints inherent in microbial community analysis approaches. DNA analyses, for example, may capture relic DNA from long-dead organisms (Carini et al. 2016). Ribosomal RNA (rRNA) reflects only live organisms, but comparisons across taxa are fraught because cellular rRNA levels and ratios of rRNA:DNA vary enormously across taxa (Blazewicz et al. 2013); even some dormant cells may contain high numbers of ribosomes. Perhaps the most reliable tool for assessing community response is stable isotope probing that analyzes only DNA from organisms that have incorporated a tracer—if that tracer is applied during rewetting, the method can reliably analyze populations that have replicated following rewetting (Dumont & Murrell 2005). Of course, this method does not indicate what happened during the dry phase—which organisms survived and which died?

The simplest hypothesis for drought effects on microbial communities is that patterns are driven by death—organisms die from physiological stress or starvation. This leaves other organisms dominating the community at a time when activity and growth are limited; death also releases material from microbial cells (necromass) into the soil, and this material is available to support the growth of other organisms when the soil is rewet. But, how much mortality occurs? If cells die, is it during the dry phase or during the rewetting that is inherently part of the analysis (Wu & Brookes 2005)? How would you even distinguish between them? Problems exist with the simple logic that microbial death drives community shifts, however—if death is the driver, microbial biomass should decline. As noted above, this does not always occur.

It might not be the overall composition of the community that shifts with drying and rewetting but which organisms are active (usually considered to mean actively growing and often defined based on rRNA) (Blazewicz et al. 2013). The active organisms are a subset of the whole community (Barnard et al. 2014). In California annual grassland soil following rewetting, *Acidobacteria* and *Verrucomicrobia* increased, whereas *Actinobacteria* and *Firmicutes* decreased (Barnard et al. 2014). *Acidobacteria* dominated the DNA in that soil but showed little seasonal pattern in their total proportion of the bacterial community (Barnard et al. 2013). In contrast, *Acidobacteria*'s contribution to the rRNA pool (the active community) crashed during the dry season, even though it was the second most dominant phylum during the wet season. At the class level, *Rubrobacteridae* in the *Actinobacteria* were dominant with more than 50% of the rRNA reads; that proportion increased through the dry season (Barnard et al. 2013). Fungi appear to survive drought more successfully than do bacteria (Evans & Wallenstein 2012).

Placella et al. (2012) observed somewhat different results using rRNA following experimental rewetting—*Actinobacteria* had high levels of rRNA shortly after rewetting, whereas *Bacilli* peaked several hours later and *Proteobacteria* rRNA took several days to substantially increase. Interestingly, in the same soil, bromodeoxyuridine (BrDU) incorporation into newly synthesized DNA showed the reverse pattern—*Alphaproteobacteria* (particularly *Sphingomonadaceae*) and *Bacteroidetes* were fast responders (31.6% and 29.4% of new DNA sequences 12 h after rewetting, respectively), whereas *Actinobacteria* increased substantially only after 48 h (when it comprised 28% of the labeled DNA) (D. Roux-Michollet, J.P. Schimel, P.A. Holden, unpublished observations). An analogous but more extensive study (Aanderud et al. 2015) assessed rapidly responding bacteria by ^{18}O-stable isotope probing; across a range of ecosystems, the dominant fast-responding bacteria were the *Sphingomonadaceae* (in the *Alphaproteobacteria*), which accounted for 38% of ^{18}O-labeled DNA sequences.

It seems possible that *Actinobacteria* maintain a level of potential activity such that they can upregulate function quickly following rewetting, whereas other groups are able to start replicating and actively growing more quickly. The nature of microbial response to drought and rewetting thus remains complex, given the multiple ways in which we may measure and assess activity and growth with microorganisms (Blazewicz et al. 2013).

Several articles have suggested that microbial community dynamics drive the pulses of CO_2 following rewetting. For example, Placella et al. (2012) is titled "Rainfall-Induced Carbon Dioxide Pulses Result from Sequential Resuscitation of Phylogenetically Clustered Microbial Groups," and the running head of Aanderud et al. (2015) is "Rare Bacteria Generate Pulses of Activity." But, of course, it is possible, even perhaps likely, that causality goes the other way around, as shown by Göransson et al. (2013), who tracked the timing of respiration versus bacterial growth after wetting a dry soil; respiration began within minutes, whereas growth (measured by leucine incorporation) did not begin for at least 12 h. This finding suggests that the mobilized carbon fuels the microbial community shifts, and as discussed above, the pulse of available carbon seems driven by chemical and physical processes; the microbial community dynamics respond to that pulse in carbon availability. From the perspective of soil biogeochemistry, it may therefore be incidental or even irrelevant which organisms actually metabolize and respire the carbon. The fate of carbon likely depends not on who metabolizes it but on what they do with it. Only if organisms allocate the carbon differently, producing materials with different long-term fates (e.g., proteins versus cell walls versus EPS), would it alter the long-term fate of that carbon (Schimel & Schaeffer 2012). Understanding the balance between the physicochemical and the biological drivers that control soil microbes response to moisture remains an important area of research if we are to improve our understanding of the connections between microbial community and biogeochemical dynamics.

4. ECOSYSTEM RESPONSES

4.1. Carbon Cycling

A key metric of how shifting moisture can alter ecosystem dynamics is the alteration of how soil systems process carbon. The stresses associated with being dry and the processes that occur on rewetting can alter the availability of soil carbon and its fate. Understanding these changes requires considering both the dry period itself and the rewetting.

4.1.1. Dry conditions. As soils dry, total microbial activity and respiration decline (Carbone et al. 2011, Davidson et al. 1998, Wu et al. 2011). However, the magnitude of the respiration decrease varies; in some cases even substantial reductions in soil moisture have only limited effects on respiration (Lu et al. 2017). Reflecting the variation in experimentally determined moisture responses, a number of response curves have been incorporated into models to predict the response of soil respiration to varying moisture (Bauer et al. 2008) (**Figure 2**). It is well recognized, however, that as soils become saturated, microbial activity declines due to oxygen limitation (Davidson et al. 2012).

One question has been which mechanisms are responsible for reduced microbial activity under conditions of moisture limitation. It had often been assumed that microbial activity declines because of microbial physiological responses to moisture stress (Orchard & Cook 1983, Schimel et al. 2007). Yet, it seems unlikely that physiological stress alone can adequately explain whole-profile or across-soil patterns in respiration. These patterns seem too coherent to be easily explained by varying microbial physiology; groups of microorganisms show wildly varying responses to soil moisture (Harris 1981, Griffin 1981), whereas the actual response patterns of microbial activity

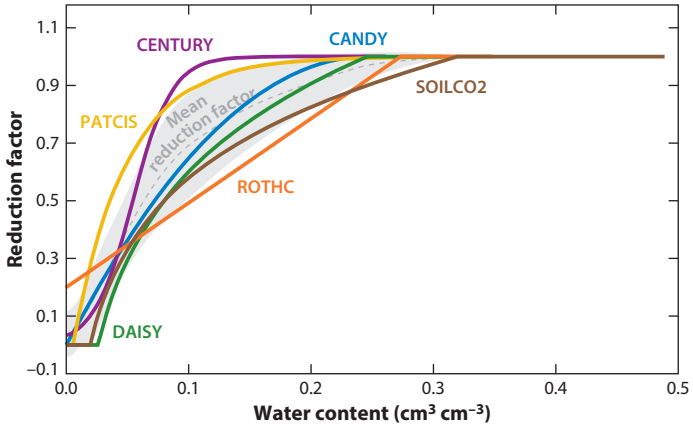

Figure 2

Soil moisture reduction functions of soil heterotrophic respiration as represented in six different carbon models dependent on the volumetric water content. The gray shaded area represents the standard variation. Figure adapted from Bauer et al. (2008) with permission.

relative to water potential show regular, defined patterns with distinct thresholds of water potential at which microbial activity ceases(Manzoni et al. 2012) (**Figure 3**).

One process that may influence how carbon cycling responds to altered moisture is depolymerization by extracellular enzymes, because depolymerization is the critical first step in making plant detritus available for microbial use (Henry 2012, Schimel & Bennett 2004). However, enzyme activities do not show consistent responses to moisture (Alster et al. 2013, Sardans et al. 2008), perhaps because actual enzyme responses can result from changes in either the amount of enzyme present or the activity of individual enzyme molecules. Separating these can be difficult because modern assays measure potential enzyme activity using artificial substrates under optimal conditions (including adequate moisture) rather than field conditions (German et al. 2011); therefore, we have good reason to suspect that enzyme potential measurements may not reliably reflect in situ activity (Schimel et al. 2017). Extracellular enzymes are small and in intimate contact with substrate, and thus need thinner water films and smaller water-filled pores to function than do larger microbial cells; hence, enzyme activity might continue even as cellular metabolism declines with soil drying (Geisseler et al. 2011). Enzyme activity continuing even after microbial respiration declines might account for the increase in extractable organic matter pools when soils are dry (Schaeffer et al. 2017). However, this hypothesis has not been adequately tested.

4.1.2. Rewetting. It has long been recognized that rewetting a dry soil causes a pulse of CO_2 (the Birch effect) (Birch 1958, Göransson et al. 2013, Kim et al. 2012). The CO_2 pulse can be many times greater than the basal level of respiration. However, the mechanism that drives the Birch effect remains unclear. Does it result from microbes respiring osmolytes that are suddenly a lethal liability? Does it result from microbes metabolizing the corpses of those that died during the drought or were killed by rewetting? Or does rewetting mobilize stable soil carbon that is then respired by surviving microbes?

Which mechanism is responsible for the Birch effect will influence long-term carbon dynamics, particularly as drying and rewetting intensify with climate change (Dai 2012). If the carbon released is microbial (osmolytes or dead cells), that carbon would be within a rapidly turning over, active carbon fraction (Parton et al. 1988). Additionally, if the carbon comes from microbes

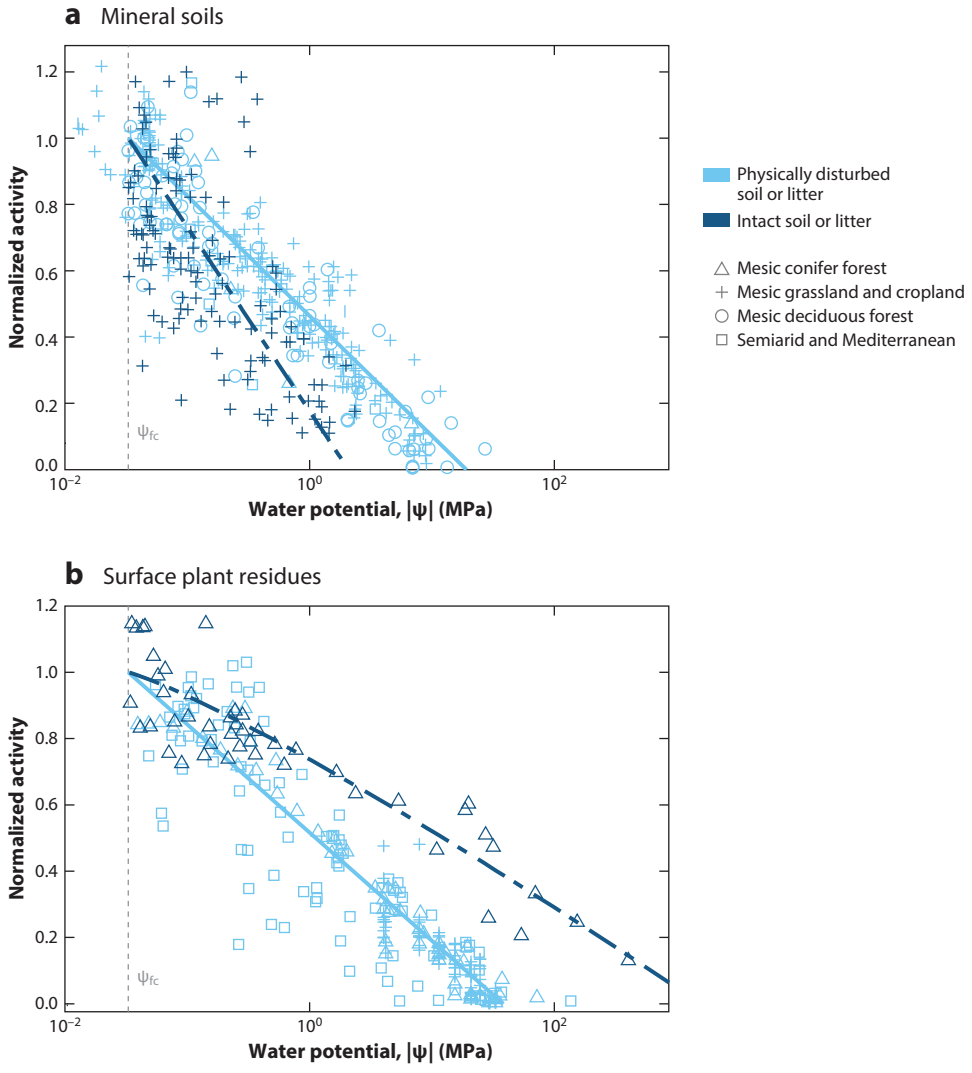

Figure 3

Microbial community-level responses of respiration, expressed as a fraction of maximum, as a function of water potential ψ in (*a*) mineral soil and (*b*) surface plant residues (i.e., forest floor, leaf litter layer, or crop residues). ψ_{fc} represents ψ at field capacity. Light blue lines represent physically disturbed soil or litter; dark blue lines represent incubations of intact soil or litter samples. Figure adapted from Manzoni et al. (2012) with permission.

killed by the stress of dry–rewet cycles, it could suggest a loss of microbial capabilities and hence a potential reduction in future carbon losses. Thus, if the Birch effect carbon release is primarily from microbial materials, dry–wet cycling might reduce long-term carbon loss from soil. In contrast, if the Birch effect results from mobilizing otherwise stable old carbon pools, it would fuel microbial growth, possibly priming the loss of additional stable soil carbon. With this mechanism, dry–wet cycles could act to mobilize stable soil carbon and reduce long-term soil carbon storage.

A general, but confusing, pattern emerges from rewetting experiments: Studies on single pulses often conclude that the carbon is lost from the microbial biomass (e.g., Fierer et al. 2003, Kieft et al. 1987). In contrast, studies evaluating multiple wet–dry cycles often conclude that the overall carbon loss over time is too large to be attributed purely to biomass loss—the carbon must come from stable soil carbon (Miller et al. 2005, Xiang et al. 2008). Reconciling these different perspectives has remained a challenge, likely because multiple mechanisms are at play (Borken & Matzner 2009), and the real question ought to be about the balance among mechanisms.

Fierer et al. (2003) used a pulse-chase ^{14}C approach to discern the source of the CO_2 pulse that results after rewetting. They added ^{14}C-glucose to moist grassland soil then dried the soil, rewet it, and measured the enrichment of both CO_2 and extractable organic carbon. The CO_2 respired was roughly 50% more ^{14}C enriched than overall microbial biomass, whereas extractable dissolved organic carbon was only 15% to 30% as enriched as the biomass. They concluded that "the rewetting pulse is generated from microbial biomass C, but without significant microbial cell lysis" (Fierer et al. 2003, p. 804).

In contrast, Miller et al. (2005) ran a chaparral soil through multiple dry–wet cycles over 110 days; it released almost twice as much CO_2 as soils incubated at constant optimum moisture. More additional carbon was released than was initially present in the microbial biomass, excluding biomass as a possible ultimate source of CO_2.

Analogous results were found in a grassland soil, where multiple dry–wet cycles increased both CO_2 release and microbial biomass (Xiang et al. 2008), particularly in deep soils, where both increased by more than fivefold. This work led the authors to conclude, "Thus, it isn't possible that the 'extra' CO_2 could have come from C lost from microbial biomass as a result of stress" (Xiang et al. 2008, p. 2287). Other studies have also found that dry–wet cycles have limited effects on overall microbial biomass. For example, Mikha et al. (2005) found that biomass carbon in a silt loam mollisol was unaffected by dry–wet cycles, although microbial biomass nitrogen actually increased through three cycles.

How can we reconcile the conclusions of Fierer et al. (2003) and Xiang et al. (2008)? It seems likely that the answer lies in the finding of a flush of unenriched extractable organic carbon by Fierer et al. (2003). If, in each cycle, carbon is immediately lost from the microbial biomass and material is simultaneously mobilized from the soil matrix, that mobilized material may be taken up by microbes and used to replace lost biomass carbon (and to fuel additional growth). Hence, through multiple cycles, the carbon mobilized may ultimately be from stable soil carbon, but within each cycle the carbon comes immediately from microbial biomass.

Total respiration, however, is not always increased over basal levels at optimal moisture by pulsing; for example, Yu et al. (2014) found that following addition of pea straw to a loamy sand (i.e., a soil with presumably limited ability to stabilize soil carbon), respiration in all pulsing treatments was reduced relative to a constantly moist treatment. An additional complexity is that in some studies rewetting pulses changed little through multiple cycles (Miller et al. 2005, Xiang et al. 2008). In other studies, however, the size of pulses declined across cycles (e.g., Yu et al. 2014) or the net effect of multiple cycles was to decrease overall respiration (Mikha et al. 2005, Shi & Marschner 2015).

Such discrepancies seem to depend on the dynamics of bioavailable carbon. Shi & Marschner (2015) noted that the carbon flush in the first wet phase of a dry–wet cycle can constrain the amount respired during later cycles; they argued that given a finite pool of carbon that can be mobilized by rewetting, if more is consumed in the first cycle, naturally, less carbon would be available in later cycles. This argument is logical but does not always apply; in some studies, rewetting pulses do not diminish (Miller et al. 2005, Xiang et al. 2008).

I hypothesize that two factors regulate the pattern of rewetting pulses. First is a soil's texture and ability to stabilize biodegradable organic matter (Abramoff et al. 2018, Bailey et al. 2017,

Schmidt et al. 2011); second is a soil's history of physical disturbance (particularly tillage). Clay-rich soils maintain large pools of stable organic matter (OM) that can fuel multiple respiration pulses (Butterly et al. 2010); physical disturbance might deplete such OM pools. These patterns might explain why a deep clay loam Pachic Argixeroll in California showed large respiration pulses from 600–800-year-old carbon during a laboratory dry–wet cycling experiment (Schimel et al. 2011): In situ, slow percolation might not be as effective at mobilizing carbon as pouring water on a sample in the laboratory. In contrast, coarse textured and tilled soils showed weaker rewetting pulses (Mikha et al. 2005, Shi & Marschner 2015, Yu et al. 2014).

4.1.3. Mechanism of carbon mobilization. The mechanisms of carbon mobilization upon rewetting remain unclear. One possibility is aggregate slaking—as water is drawn into an aggregate, air inside is pressurized enough to crack the aggregate open, exposing organic matter to attack (Le Bissonnais 1996, Mikha et al. 2005). However, slaking does not stand up well as a primary mechanism driving the respiration pulse. Mikha et al. (2005) found rewetting pulses without significant shifts in aggregate distributions. Schimel et al. (2011) found that rewetting deep, poorly aggregated soils still mobilized large amounts of carbon. Slaking could explain a large first pulse in a series of dry–wet cycles, but presumably the bulk of easily slaked aggregates would be broken up during that first event and so one would expect later cycles to release less CO_2 (Denef et al. 2001). As noted, however, this is often not the case. An additional argument against the aggregate slaking explanation is from Navarro-García et al. (2012), who found that grinding aggregates before dry–wet cycling increased respiration and microbial biomass, but increases only peaked after several cycles. They postulated that disrupting aggregates exposed particulate organic matter that had to be broken down by exoenyzmes before it could be respired. Disrupting soil structure is likely important at the whole-profile scale in changing pore distributions as well as water percolation and storage, but mobilizing organic matter appears to be a microscale effect, perhaps associated with shifts in hydration of organic coatings on minerals or shifts in ionic strength that might alter organic matter–mineral binding (Kleber et al. 2007).

Whatever the specific mechanism that mobilizes carbon, it is sensitive to the soil's extent and history of drought. Williams & Xia (2009) dried soils to defined moisture levels, rewet them, and then extracted simple organic molecules. The drier the soils were before rewetting, the more material was extracted, with amounts more than doubling when soils were dried to −45 MPa. Soils with a history of drought stress, however, released less carbon. Most of the materials released were not classic microbial compounds (simple amino acids, sugars, etc.), reinforcing the conclusion that the organic materials mobilized are soil, rather than microbial, compounds.

Most work on dry–wet cycling has been done in the laboratory, which raises questions about its direct relevance to in situ conditions. In laboratory studies, drying is often much more rapid than occurs in a natural soil profile, yet the speed of drying is important in regulating the microbial response to drying—slower drying allows microbes to sense the developing drought and to synthesize osmolytes if they are capable of doing so (Warren 2016). Pouring water on disturbed soil might also mobilize more carbon than would natural rewetting (Smith et al. 2017). If the assumption is that the released carbon is a microbial response to a rapid increase in water potential (dumping osmolytes or dying) (Kieft et al. 1987), how a soil is rewet might be irrelevant. However, if carbon is mobilized from physical protection, the rate and nature of rewetting could be critical in regulating whether carbon is mobilized. The natural slow percolation of water through soil pores might drive less mass transport of organic molecules between sources and microbes (Smith et al. 2017, Tecon & Or 2017). Such phenomena might explain why so much carbon that is easy to mobilize in the laboratory can be centuries old. Linking the extensive laboratory research on dry–wet cycling to real-world conditions in whole soil is critical.

4.2. Nitrogen Cycling

Drought reduces overall microbial activity, and this reduction applies to nitrogen-cycling as well as carbon-cycling processes. However, as soils dry, the effects on nitrogen cycling can differ from those on carbon cycling—resulting from microbial and elemental stoichiometry patterns that influence nitrogen mineralization–immobilization dynamics. Just as with respiration, nitrogen mineralization often increases when dry soils are rewet (Leitner et al. 2017, Saetre & Stark 2005). The material mobilized by rewetting is rich enough in nitrogen that as microbes regrow they have surplus nitrogen and so mineralize nitrogen. Potential nitrogen-rich substrates that could fuel such a flush would include bacterial osmolytes, microbial necromass (Liang et al. 2017), and nitrogen-rich but clay-protected small molecules (Kleber et al. 2007). Fungi, conversely, produce nitrogen-free osmolytes, such as trehalose and polyols (Davis et al. 2000), and so should stimulate immobilization on rewetting.

A critical step in the nitrogen cycle is nitrification, which regulates whether nitrogen becomes vulnerable to leaching or denitrification. Nitrification is sensitive to soil drying, being constrained by NH_4^+ diffusion in dry soils (Stark & Firestone 1995). But even in ecosystems that as a whole appear nitrogen limited, rewetting creates a flush of available nitrogen, which can make an ecosystem appear nitrogen saturated (Homyak et al. 2014). As California soils dry in the summer, NH_4^+ becomes the dominant nitrogen form, but nitrification switches on rapidly following rewetting (Parker & Schimel 2011). NH_3 oxidizers appear to switch on before NO_2^- oxidizers (Placella & Firestone 2013), allowing NO_2^- to accumulate and drive a pulse of NO flux following rewetting (Homyak et al. 2016). Hence, drying–rewetting dynamics appear to have disproportional effects on nitrogen losses and trace gas dynamics relative to their effects on carbon cycling.

4.3. Large-Scale Biogeochemical Dynamics

Moisture regulates soil respiration and can act as a master variable: Drying can dampen respiratory responses to warming. For example, across a range of Alaskan forest sites, respiration increased with warming following a general Q_{10} relationship but only up to 17°C (Gulledge & Schimel 2000) (**Figure 4**). Above this temperature, respiration rates were low and insensitive to temperature. The break occurred because, in Alaska, rain is always cool and evaporation limits heating; soils could warm only above 17°C if they were dry enough to be water stressed. Although such sharp threshold responses have rarely been reported, a decreasing temperature sensitivity as soils dry is common (Conant et al. 2004, 2017) as are complex interactions between temperature and moisture sensitivity (Davidson et al. 1998, Sierra et al. 2015).

We know surprisingly little about the overall dynamics of drying and wetting in situ in microbial systems because it is difficult to simultaneously document the physical distribution of water through the soil profile and the processes responsible for driving biogeochemical fluxes following rewetting (Castanha et al. 2018, Collins et al. 2014). Particularly, identifying soil chemical changes is difficult in dry soils because most chemicals are water soluble and unmeasurable without extraction. However, a novel technique for sampling soil solution with minimal physical disturbance is microdialysis (Inselsbacher et al. 2011), which uses a small flow-through dialysis membrane to sample materials free to diffuse through the soil solution; using microdialysis, it is possible to follow hour-by-hour dynamics of materials in soil solution following rewetting (Leitner et al. 2017) (**Figure 5**). In the immediate post-rewetting period, simultaneous to a pulse of NO, inorganic nitrogen species become depleted in solution; however, roughly one day following the rewetting, a pulse of ammonification is seen—a time when microbial growth is rapid (Göransson et al. 2013, Placella et al. 2012).

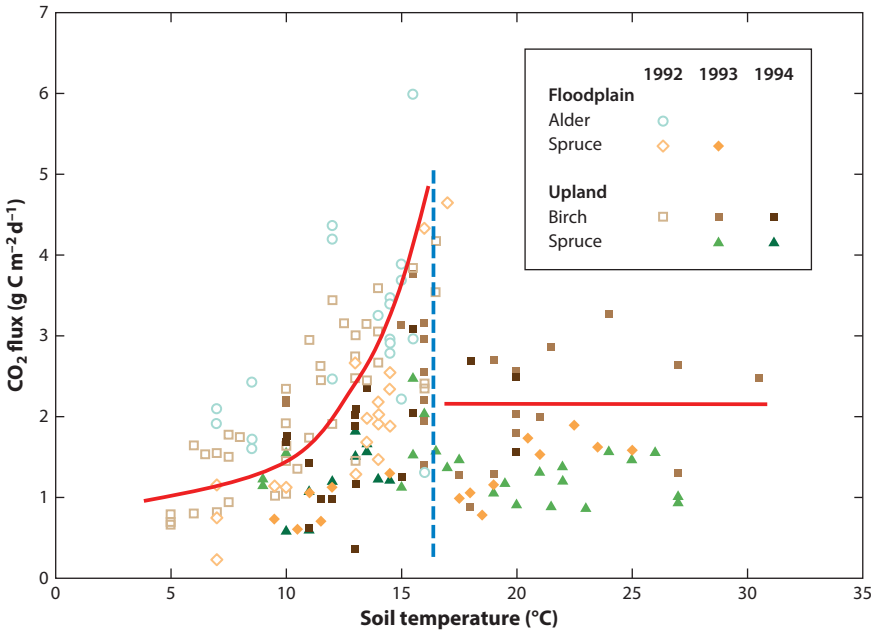

Figure 4

Temperature response of respiration measured in a range of Alaskan taiga forest stands from 1992 to 1994. The red lines represent the temperature responses below and above 17°C. The dashed blue line illustrates the sharp threshold between these temperature regimes. Figure adapted from Gulledge & Schimel (2000).

Improving our understanding of how drought and dry–wet cycles drive whole-soil biogeochemical processes is going to be critical to improve our understanding of how these processes will respond to the changing climate, which we anticipate will create more drought and more erratic soil moisture regimes. To build new generations of Earth System models that can capture changing climate and weather patterns, addressing dry soil and rewetting dynamics will be critical.

4.4. Modeling the Effect of Drought on Soil

Classical carbon and nitrogen cycling models (e.g., CENTURY, ROTHC) assume microbial communities and processes are in quasi steady state with their environment (Schimel 2001). Such models deal with moisture effects on microbial processes by using reducing functions to account for less-than-perfect conditions (Parton et al. 1987). They include no effects of rewetting or of moisture history. In other words, soils have no memory—if they are wet now, they are wet. That they were dry 10 minutes before does not matter. But drying–rewetting events are the epitome of non-steady state; hence, classical models do poorly under these conditions (Li et al. 2006).

Several perspectives have driven how moisture is represented in soil models. Some focus on water potential—in other words, water is a resource required to maintain physiological activity (Manzoni et al. 2012). Others have focused on developing integrated metrics that capture the balance of water versus oxygen as a control over respiration. For example, Linn & Doran (1984) showed that microbial activity was maximal at 60% water-filled pore space; this is the moisture content at which soil micropores are filled with water while macropores are drained, balancing substrate supply against effective soil aeration (McCulley et al. 2005, Moyano et al. 2013, Skopp et al. 1990).

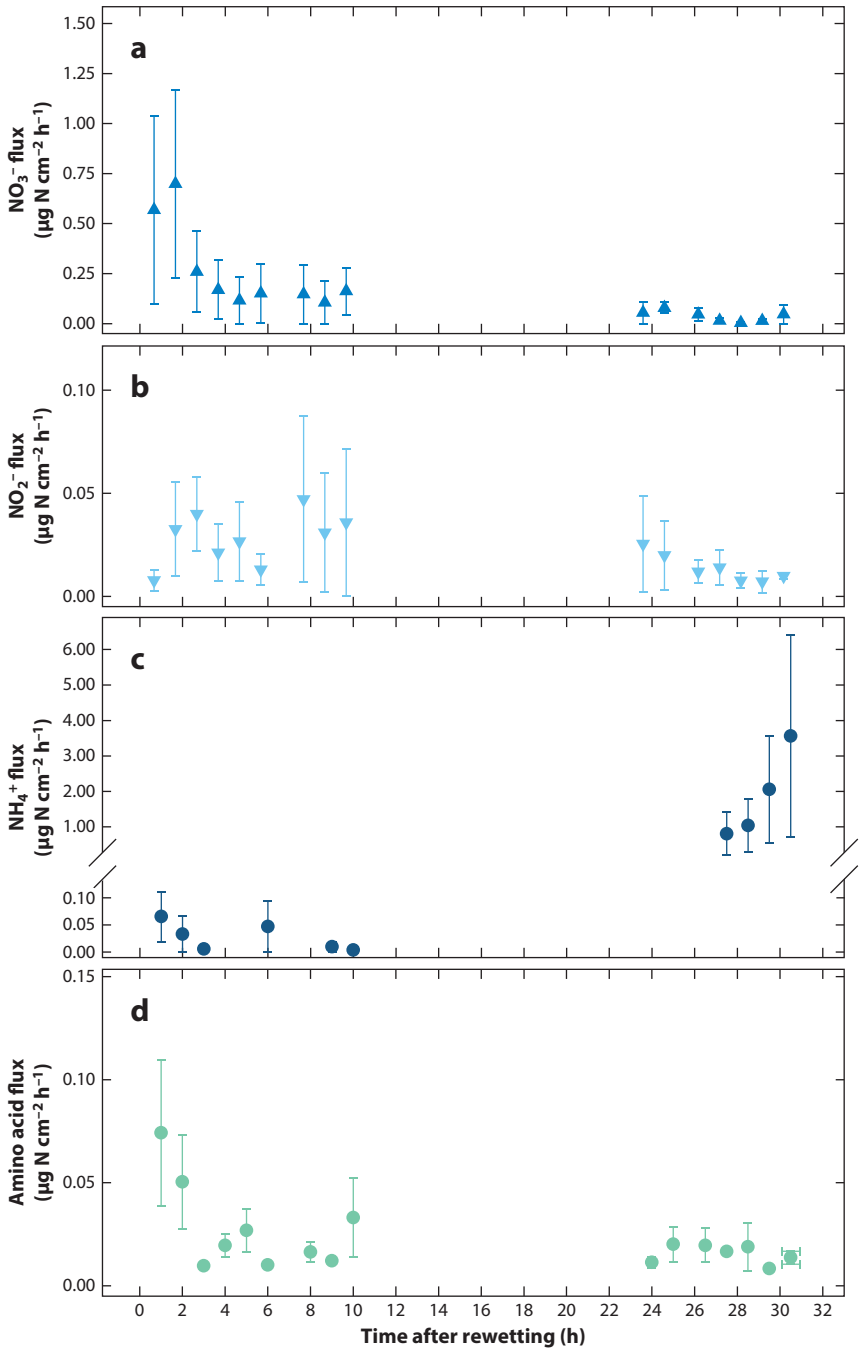

Figure 5

Diffusive fluxes of (*a*) NO_3^-, (*b*) NO_2^-, (*c*) NH_4^+, and (*d*) the sum of 17 amino acids determined in situ with microdialysis after wetting a California grassland soil. Figure adapted from Leitner et al. (2017) with permission.

New approaches to modeling have been exploring explicit approaches to capturing biogeochemical processes (Abramoff et al. 2018, Lawrence et al. 2009, Li et al. 2010, Manzoni et al. 2016, Sulman et al. 2014). One approach to capturing rewetting pulses in a first-order model is to create an empirical rewetting pulse function (Li et al. 2010); this substantially improved DAYCENT's ability to capture dry–wet cycles. However, any such function derives from a specific set of conditions that might not apply under different circumstances. Lawrence et al. (2009) modeled dry–wet cycles by assuming that extracellular enzymes remain active in dry soil and that reaction products accumulate, waiting for adequate water to support diffusion of products to active cells. This assumption, however, is not supported by measurements that showed reducing sugars did not accumulate in dead roots that had been sampled from the field and incubated dry in the laboratory (Homyak et al. 2018). In contrast, Manzoni et al. (2016) integrated both enzymatic breakdown and diffusion to estimate how soil drying and rewetting regulate soil processes. The essential behavior that allows these models to capture dry–wet dynamics is that they separate the generation of small molecules from their uptake and metabolism; thus, they accumulate during dry periods but are rapidly consumed on wetting. The specific mechanism may not be critical, as long as the carbon is mobilized from appropriate pools and with appropriate dynamics. Getting the linkages among processes right remains a critical area to integrate climate, soil hydrology, and soil biogeochemical processes.

5. SYNTHESIS AND RESOLUTION

Water is the ultimate resource for life. Yet, few terrestrial ecosystems do not experience episodic drought, times when moisture limits microbial activity, organic matter decomposition, and nutrient mineralization. The mechanisms by which moisture regulates soil processes, however, are complex. Water is an essential physiological resource for microbial cellular function, and water's role as a resource has often been perceived as its primary role in controlling microbial activity in soil. That is largely why moisture effects have been modeled following the normal form for potentially limiting resources—increasing to a maximal response level (**Figure 3**).

Increasingly, however, it appears that water's role as a resource might actually be the least important of its three roles in regulating soil processes. Rather, water is critical as both a solvent and a transport medium; these roles appear critical in regulating how soil moisture regulates biogeochemical processes. The majority of organic substrates in soil are water soluble, and their metabolism is regulated by the movement of chemicals in solution from sources to microbes (Schimel & Schaeffer 2012).

Microbial community responses to dry conditions and to subsequent wetting events are complex, and understanding these may prove key in deciphering the microbial ecology of soil (Tecon & Or 2017). But organismal responses may actually not be very important in regulating how soil organic matter is processed through dry and rewetting cycles. Rather, as soil microbes are generally carbon starved, whatever biodegradable carbon becomes accessible will be rapidly metabolized. Hence, the diversity and community composition may be more a response to the shifts in moisture and carbon availability than an independent driver of the processes. As physical transport appears to be a main factor regulating organic matter dynamics under drought and rewetting, the factors regulating carbon mobilization are critical yet remain poorly understood.

After working through what we know (and think we know) about how soil microbes and microbial processes respond to drought and rewetting, the answers to a number of major questions remain that are either uncertain or simply unresolved. Answering the following questions will improve our understanding of soil ecology—in fact, it might transform it.

FUTURE ISSUES

1. What is the balance of direct physiological stress versus resource supply as drivers of microbial dynamics through drought and dry–wet cycles?
2. How much microbial mortality occurs during the dry season versus during rewetting?
3. Does a causal connection between the microbial community shifts that occur with drought and rewetting and the associated carbon fluxes exist? Are microbial community dynamics drivers of the abiotic resource pulses, or are microbes effectively responders to these pulses?
4. What are the origins and chemical nature of the organic matter respired by soil microbes on rewetting?
5. How will altered dry–wet cycles influence ecosystem-scale carbon storage?

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