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PERSPECTIVE

Drought impacts on microbial trait distribution and feedback to soil carbon cycling

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Abstract

1. Quantifying the impact of drought on microbial processes and its consequences for soil carbon cycling is hindered by the lack of underlying mechanistic understanding. Therefore, there is a need to scale up the physiological response to changing water status from individual soil microbes to collective communities across different ecosystems.
2. Here we propose the use of a framework that incorporates trait-based ecology to link drought-impacted microbial processes to rates of soil carbon decomposition and stabilisation. We briefly synthesise existing knowledge on the effects of drought on microbial physiology at the individual to community scale, before integrating this understanding within a framework incorporating life-history strategy, ecological strategy and biochemistry.
3. This framework highlights a dynamic allocation to high yield (Y), resource acquisition (A) and stress tolerance (S) pathways as environmental conditions change. Y-A-S strategies represent sets of traits that tend to correlate due to physiological or evolutionary trade-offs. This framework enables assessment of microbial processes along two key environmental gradients of water and resource availability, both of which are constrained by drought.
4. The variable chemistry of biomass and necromass produced under different physiological strategies in response to drying–rewetting impacts organic matter decomposition and stabilisation in soils, and should also be considered when quantifying soil carbon balance. We highlight that diversion of resources away from microbial growth can alter soil organic matter chemistry and its persistence depending on the kind of microbial compounds produced.
5. To advance such a framework, we highlight avenues of research that would enable the further identification and quantification of traits linked to Y-A-S strategies and the physiological outcomes at the community level under drought and rewetting, and conclude by hypothesising how ecosystem-level changes might feedback on to the soil carbon cycle. A scalable understanding of microbial drought-response mechanisms affecting soil carbon cycling will transform the way microbial physiology is represented in ecosystem studies.

KEYWORDS
drought, drying–rewetting, microbial traits, soil carbon, water stress

1 | INTRODUCTION

Climate change-induced extremes of precipitation patterns are becoming more severe and frequent (Dai, 2012), disrupting biogeochemical cycling in terrestrial ecosystems (de Vries et al., 2020; Sippel et al., 2018; Xu et al., 2019). Soil drying represents a distinct physiological burden to microbes. As soils dry, water films form on soil particles, concentrating aqueous pore water constituents (dissolved nutrients, solutes, toxicants), restricting diffusion of substrates and extracellular enzymes, and increasing interactions between microbial populations (Or et al., 2007; Schimel, 2018). Drought can also impart changes in plant and microbial communities that can lead to changes in plant litter chemistry and the chemical composition of microbial necromass, both of which are key resources for soil microbes. The lingering impact of drought can be observed following rewetting, which leads to microbial resuscitation, and growth, and which, in turn, determines soil carbon fluxes (Barnard et al., 2020).

Far from being passive passengers in soils undergoing drought, soil micro-organisms possess a wide range of metabolic strategies and adaptive traits to preserve intracellular turgor pressure and cellular integrity in the face of fluctuating environmental conditions (Bouskill, Wood, Baran, Ye, et al., 2016; Malik, Swenson, et al., 2020). These pathways can be energy intensive (Oren, 1999), and require reallocation of intracellular carbon reserves (Bonny et al., 2021), leading to selection for distinct microbiomes, reduced growth yields and a feedback to soil biogeochemistry. How drought shapes the distribution of microbial communities, and the composition and stability of soil organic matter remains a significant gap in our knowledge. However, bridging this gap could be achieved by an improved understanding of microbial functions under fluctuating environmental conditions, as seen through the lens of traits.

The use of trait-based approaches to improve understanding of microbial feedbacks to ecosystem-scale processes is gaining popularity, as it allows one to distil complex microbial data into simpler ecological units that can be categorically linked to pools and fluxes. Traits can be defined as the phenotypic, morphological, behavioural and physiological characteristics of micro-organisms (Martiny et al., 2015). Herein, we review the literature from the perspective of a microbial trait-based framework to synthesise a mechanistic understanding of the microbial functional response to drought and its impacts on soil carbon cycling processes. We focus on a recently proposed framework which uses traits to define three main microbial life-history strategies: high yield (Y), resource acquisition (A) and stress tolerance (S) along two axes of environmental variation – abiotic stress and resource availability (Malik, Swenson, et al., 2020). Studying microbial functions as traits, assigning Y-A-S life-history strategies to dominant populations in the community, and linking them to organic matter decomposition and stabilisation will enable upscaling of microbial activity to soil carbon cycling processes (Figure 1a).

We provide a mechanistic understanding of the direct and indirect effects of drought on microbial populations and the consequences for community-level functions, and soil carbon storage. The manuscript is split into three main sections: a review of the existing literature, the integration of this information into a Y-A-S framework, and some predictions on the consequences of microbial response to drought and rewetting on soil carbon balance. Our literature review begins by discussing findings from laboratory experiments characterising the metabolic response of isolates undergoing drought-like stress. While lacking in environmental relevance, experiments at the scale of single cells or simple populations can provide a clear temporal representation of how microbes respond to and adapt to rapid fluctuations in their environment. Such understanding can be useful in deriving traits at the community scale for identifying population response to stress; however, incorporating this information into a trait-based framework requires a coherent linkage to natural systems (Bell, 2019). We demonstrate concordance between different scales by highlighting traits identified within isolates to mechanisms emerging from studies of complex communities responding to soil drying. Relative to the isolate experiments, the field studies suffer from a low signal-to-noise ratio because of the inherent complexities of soil microbial communities and the matrix they inhabit. As such, the underlying mechanisms behind community-level functional changes in drought-impacted soils can be multifactorial and complex, caused not only due to physiological changes within community members but also due to changes in community membership (Hall et al., 2018). Regardless of the mechanisms that drive changes in community-level functions, community-aggregated traits enable linking of cellular level microbial functions to ecosystem-scale process rates. We integrate the cellular level understanding within a trait-based biogeochemical framework and examine the role of drought- and rewetting-impacted microbial communities in the carbon cycle.

2 | RESPONSES TO DROUGHT STRESS FROM THE ISOLATE TO SOIL COMMUNITY SCALE

Micro-organisms, including bacteria, fungi and archaea, must maintain a positive intracellular turgor pressure relative to their external environment, which is typically achieved through the synthesis or transport and accumulation of solutes within the cytoplasm (Bois et al., 2006; Bremer & Krämer, 2019; Oren, 1999). An increase in external solute concentration (hyperosmotic shock) can result in water efflux from the cytoplasm and a drop in turgor pressure. Conversely, the rapid decline of external osmolarity (hypoosmotic shock) can result in a swift influx of water, and elevation in turgor pressure. Given the importance of turgor pressure for cell growth

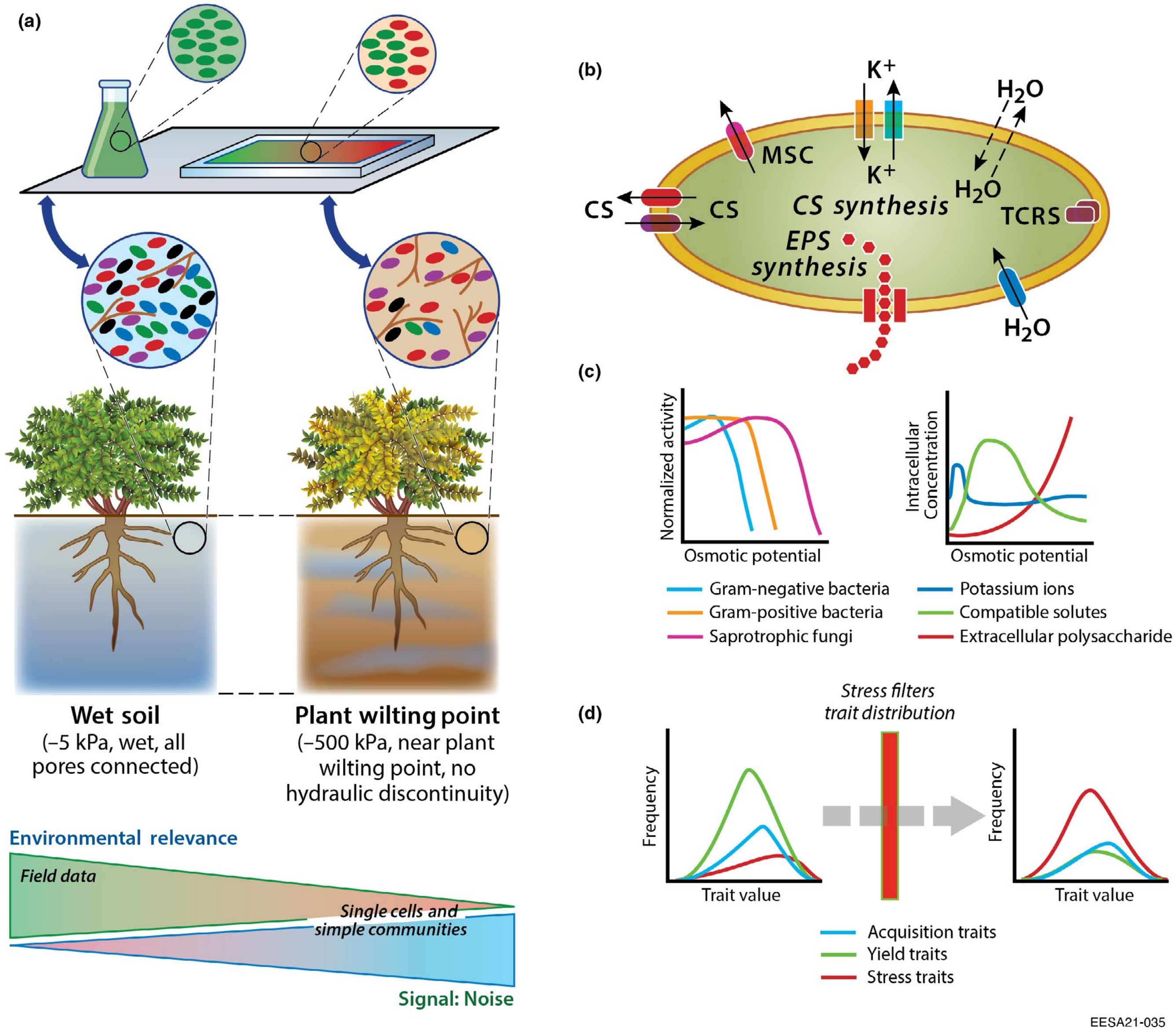

FIGURE 1 Multiscale depiction of the microbial response to drought stress. (a) Characterising the below-ground response to drought requires a strong understanding of community transition at the field scale. However, a low signal-to-noise ratio in soil necessitates downscaling to elucidate mechanisms in stressed isolates. Thus, critical mechanistic understanding can be gleaned from single or interacting laboratory cultures. (b) Microbial cells possess a range of traits to maintain turgor pressure during fluctuations in osmotic potential. As described in the text, changes in the external environment can be sensed using two-component regulatory systems (TCRS), and a response may occur through the accumulation of cations (e.g. K^+), the accumulation or synthesis of compatible solutes (CS) and synthesis of extracellular polysaccharides (EPS). As stress passes, bacteria can remove CS through specific and general mechanosensitive channels (MSC). (c) Microbes also show characteristic response to stress on the basis of cellular structure (e.g. cell wall or hyphal morphology) and the uptake or synthesis of different solutes. (d) At the field scale, microbial stress can be detected by measuring the frequency distribution of different traits across spatial or temporal scales

and division (Ferjani et al., 2003; Rojas, 2018; Rojas et al., 2014), microbes have evolved a number of pathways to regulate their intracellular environment, and maintain intracellular turgor pressure under fluctuating external osmolality. A comprehensive summary of osmosensing and osmoregulatory mechanisms, and cellular homeostasis is beyond the scope of the current manuscript; however, the reader is referred to a number of excellent reviews on these topics (Bremer & Krämer, 2019; Cox et al., 2018; Rojas, 2018; Wood, 2011). Here we briefly review some of the microbial strategies that embody our definition of a microbial trait, and permit upscaling beyond isolate studies to wild populations as traits emblematic of global stress responses (Figure 1a).

The microbial cell wall serves as the initial barrier to acute environmental fluctuations, and diversity in cell wall morphology give rise to characteristic differences in the sensitivity of broad microbial groups (e.g. Gram-positive and -negative bacteria, and fungi) to changing osmotic potential (Figure 1c, Manzoni et al., 2012). Many non-halophilic microbial species employ a 'salt-out' strategy to deal with hyperosmotic shock (Figure 1b; Bremer & Krämer, 2019; Kempf & Bremer, 1998). As the osmotic potential of a solution declines, changes to external solute concentrations stimulate two-component sensing systems (Zschiedrich et al., 2016), which, in turn, upregulate transporters (Pilizota & Shaevitz, 2012) specifically involved in the rapid accumulation of potassium ions (K^+) to limit water loss (Dinnbier et al., 1988; Whatmore et al., 1990). The accumulation of Na^+ ions has also been identified to a limited extent in soils (Malik, Martiny, et al., 2020). However, this short-term strategy can upset the ionic balance of the cell, and is quickly superseded by the synthesis or accumulation of compatible solutes and efflux of cations (Figure 1c; Dinnbier et al., 1988). Compatible solutes are highly-water soluble organic compounds, which include glucosyl, glycerol, glycine betaine, ectoine, proline, and trehalose. They restore cellular hydration, maintain intracellular macromolecular structure and allow cellular function to continue under stress (Bremer & Krämer, 2019; Wood et al., 2001). The genetic capacity to produce these compounds is found across a diverse range of bacteria (Crits-Christoph et al., 2018) and fungi (Jennings & Burke, 1990; Welsh, 2000), and the transcription of genes related to compatible solute synthesis is tightly controlled by external osmotic potential (Csonka, 1989; Kempf & Bremer, 1998). As a consequence, the cytoplasmic concentrations of osmolytes increase as a function of external osmolarity (Cayley & Record, 2003).

Consistent with these isolate studies, the production of a range of non-structural carbohydrate and amino acids under drought conditions has been identified in soil microbial communities across temperate, Mediterranean and tropical ecosystems (Bouskill, Wood, Baran, Ye, et al., 2016; Lebre et al., 2017; Malik, Martiny, et al., 2020; Roy Chowdhury et al., 2019; Warren, 2014). Evidence for osmolyte production comes from metabolite profiling and identification of genes for osmolyte synthesis under drought treatment. Observations of increased abundance or transcription of osmolyte transporter genes in drier soils suggest osmolyte transport and accumulation. Furthermore, as with the isolate studies, the most common osmolytes identified in soils globally were trehalose, ectoine, proline and glycine betaine (Bouskill, Wood, Baran, Ye, et al., 2016; Lebre et al., 2017; Malik, Martiny, et al., 2020; Roy Chowdhury et al., 2019; Warren, 2014). Other studies within dry soils have failed to measure appreciable concentrations of osmolytes in response to drying (Boot et al., 2013; Kakumanu et al., 2013). This could be attributable to experimental or analytical approaches in analysing rapid changes in osmolyte concentrations (Warren, 2014), but might also represent an adaptation of microbial communities within very dry soils towards dormancy rather than osmolyte production.

An additional drought adaptation is the secretion of extracellular polymeric substances (EPS) and the formation of biofilms (Bouskill, Wood, Baran, Hao, et al., 2016; Lebre et al., 2017; Malik, Martiny, et al., 2020). These biofilm structures retain moisture and concentrate resources enabling micro-organisms to maintain metabolic activity under reduced external water potential and limited substrate diffusion. In addition, antibiotic compounds have also been measured in increased abundance under drought (Bouskill, Wood, Baran, Hao, et al., 2016), which suggest that they act as signalling molecules to facilitate intra- and interspecies communication associated with biofilm formation in soil communities.

However, reliance on compatible solute synthesis, or EPS production, as an ecological stress response is an energetically expensive strategy (Oren, 1999), and would likely become increasingly unfavourable as soils dry and substrate diffusional rates are constrained (Manzoni et al., 2014). Acquisition of compatible solutes from the surrounding environment requires significantly less energetic expenditure (Lycklama a Nijeholt et al., 2018; Oren, 1999), and might therefore be a more favourable ecological strategy. Indeed, studies have shown that cells preferentially take up external osmolytes rather than synthesise new ones (Kempf & Bremer, 1998; Wood et al., 2001). However, due to the formation of water films under drought, and constraints on diffusion, the supply and accessibility of compatible solutes is unlikely to match demand, and dormancy might become the favoured strategy (Manzoni et al., 2014).

Under prolonged stress, or conditions of starvation, cells can also enter a reversible dormant or persistent state (Figure 1c; Harms et al., 2016; Lennon & Jones, 2011; Song & Wood, 2021). Dormancy is a broadly distributed trait, and occurs through various phenotypic pathways, including spore formation (Stephenson & Lewis, 2005), a low replicative state (Gray et al., 2019; Keep et al., 2006) or an inert state (Hoare et al., 2008). Osmotic stress has previously been shown to induce dormancy in bacterial cultures (Sachidanandham & Yew-Hoong Gin, 2009), which can be resuscitated as the external environment becomes more favourable to growth and reproduction. Alternatively, cells can exit dormancy due to a quorum sensing mechanism, such as the secretion of resuscitation promoting factor that remodels the cell envelope to facilitate growth (Keep et al., 2006). Such mechanisms might be at play during the entry into and resuscitation from dormancy in soil environments under drought (Blazewicz et al., 2014; Gonçalves et al., 2016; Malik, Martiny, et al., 2020; Placella et al., 2012; Song et al., 2019).

An added, and understudied, dimension here is the role of cell–cell interactions. The aforementioned formation of water films that occur as soils dry could lead to greater interactions between endemic populations. A recent study showed an increase in cell-to-cell transfer of a plasmid in *Pseudomonas putida* populations as water potential declines (Tecon et al., 2018). Given the broad distribution of secondary metabolisms, and osmoregulatory as well as antagonistic (e.g. antibiotic production) traits (Crits-Christoph et al., 2018), interactions between different populations under drought could promote the survival of drought-intolerant populations, through the acquisition of compatible solutes released by drought-tolerant populations. Indeed, given sufficient spatial separation, cells can coexist and enable survival of competitors (Kim et al., 2008). In this respect, cheating could emerge as an important strategy to survive drought stress, whereby cells specialise in the rapid acquisition of exported osmolytes to maintain metabolism and circumvent the energetic costs of synthesising osmolytes. Such an ecological strategy would be similar to the producing-cheater paradigm suggested for the acquisition of organic monomers while avoiding the need to produce extracellular enzymes (Allison & Vitousek, 2005; Kaiser et al., 2015).

As external osmolarity declines and stress passes, or at the onset of hypoosmotic conditions, compatible solutes are rapidly removed from the cell to prevent lysis, which would occur as water rushes back into the cell (Figure 1b). Cells lose these solutes through the opening of different types of mechanosensitive channels. Bacteria possess a range of these channels (Booth et al., 2007), which differ in their substrate specificity, their electrophysiological properties and the width of opening. Some channels show substrate specificity under hypoosmotic conditions, exporting specific compounds (e.g. glutamate), while other channels export a broad range of solutes (Cox et al., 2018). Rich in carbon and nitrogen, a number of studies have suggested that compatible solutes might serve as an energy source post-stress. There is some evidence that this could be the case; bacteria can use osmolytes such as trehalose as the sole source of energy and carbon (Argüelles, 2000). However, in general, bacteria tend to separate osmotic regulation from energy generation, but the rapid export of osmolytes from the cell does not preclude the subsequent uptake and catabolism of a portion of these compatible solutes, which seems to be the case in soils following rewetting (Fierer & Schimel, 2003) that causes a rapid CO_2 release often referred to as the Birch effect (Barnard et al., 2020; Birch, 1958).

3 | MICROBIAL RESPONSES TO DROUGHT-INDUCED CHANGES IN RESOURCES

Drought impacts microbial functions directly not only by acting as a stressor but also by limiting substrate supplies due to diffusional constraints limiting flow and transport as water films in soil become disconnected (Manzoni et al., 2012; Schimel, 2018). Lower moisture levels affect communities by reducing substrate supply by interrupting previously connected hydrological flow paths that facilitated diffusion and mass transfer, by reducing substrate dissolution, and substrate desorption from mineral surfaces, and impairing motility and, therefore, dispersal (Schimel, 2018; Stark & Firestone, 1995). Consequentially, to decipher the ecosystem-level response of drought and the underlying microbial processes, we need to also study changes in microbial resources, and their diffusional, transport and uptake constraints.

Production of extracellular degradative enzymes under drought conditions is likely reduced due to the lower return of the breakdown products as a result of diffusional constraints (Li & Sarah, 2003; Sardans & Peñuelas, 2005). However, some studies have demonstrated increased potential enzyme activity in soil communities due to increased abundance of certain microbial groups such as Actinobacteria that can tolerate desiccation and produce degradative enzymes (Bouskill, Wood, Baran, Hao, et al., 2016). Other studies have found that soil micro-organisms employ a strategy of maintaining active exoenzymes in their proximity to conserve access to labile organic nitrogen during dry periods (Piton et al., 2020). It is also likely that exoenzymes continue to operate under dry conditions that reduce metabolic activity, such that the breakdown products accumulate and are available for use when higher moisture levels return (Lawrence et al., 2009; Zeglin et al., 2013), while soil drying can also alter the turnover rate of enzymes (Alster et al., 2013). Iron acquisition pathways have also been identified to increase in abundance under drought, which has been linked to an elevated demand for iron in drier soils because of oxidation. Oxygen permeation increases in drier soils, precipitating out poorly soluble ferrous iron (Fe^{2+}), potentially leaving soil microbes iron limited (Bouskill, Wood, Baran, Hao, et al., 2016; Malik, Swenson, et al., 2020; Xu et al., 2021). Biofilm formation in communities through production of exopolysaccharides (EPS) or capsules is an adaptation to retain moisture under drought but these structures also concentrate resources enabling micro-organisms to maintain metabolic activity under limited substrate diffusion.

In addition to causing physiological stress and disrupting substrate flows, drought can alter the quantity and quality of plant-derived organic matter, due to drought-related changes in the composition and physiology of plants and other primary producers (Allison et al., 2013; Suseela & Tharayil, 2018). Drought-tolerant plant species can often produce more recalcitrant foliar and root litter, which would impact microbial resource acquisition strategies (Henry et al., 2005; Morecroft et al., 2004). Drought-related changes in microbial composition and physiology are likely to change the microbial necromass and metabolic products that would impact the stabilisation and turnover of these compounds ultimately leading to changes in soil carbon balance. Such feedbacks have rarely been studied in the relation to the response of microbial processes on soil carbon cycling.

4 | A MICROBIAL FRAMEWORK TO PREDICT SOIL CARBON BALANCE IN RESPONSE TO DROUGHT

Drought-induced changes in microbial physiology will have consequences for below-ground carbon cycling and could alter the soil carbon balance. Based on our current understanding of the microbial response to drought, as reviewed above, we present a conceptual model to quantify and predict soil carbon balance. The model includes the direct and indirect effects of drought as well as the ecosystem feedbacks that are generated due to the complex interactions of above-ground and below-ground processes (Figure 2). Microbial intracellular resource reallocation requires trade-offs under dynamic conditions. Such trade-offs can also alter the chemistry of the microbial necromass produced and the metabolites and enzymes released or exported into the soil. Such variation in microbial physiology under stress that leads to resource reallocation and changes in organic matter chemistry are the key microbial pathways influencing soil carbon decomposition and stabilisation.

Regardless of the stress response mounted by micro-organisms to maintain metabolism and grow in dry conditions, or simply enable survival, the increased investments in stress tolerance traits are likely to negatively impact growth due to cellular level trade-offs (Figure 1d, Malik, Swenson, et al., 2020). Reducing microbial growth yield will, in turn, impact community biomass with consequences for ecosystem-level biogeochemistry (Malik, Swenson, et al., 2020; Schimel et al., 2007). For example, the increased carbon and energy demand attributable to stress tolerance could increase mineralisation rates and lower soil carbon. Such relationships have been widely evidenced by drought-induced reduction in the activity and size of soil microbial biomass (Allison et al., 2013; Hicks et al., 2018; Hueso et al., 2012; Malik, Martiny, et al., 2020; Manzoni et al., 2012; Waring & Hawkes, 2015).

The reduction in microbial biomass can also be attributed to drought-induced constraints on substrate flow (Bouskill, Wood, Baran, Hao, et al., 2016; Schimel, 2018) and changes in the chemistry of plant litter and microbial necromass (Allison et al., 2013; de Vries et al., 2018; Malik, Swenson, et al., 2020). However, direct evidence for both remains elusive. Substrate diffusional constraints, brought about by reduced hydrological connectivity, will decrease microbial growth and result in allocation of biomass carbon to alternative resource acquisition strategies (such as the decomposition of more complex organic matter). This is likely to lower soil carbon as energy demands increase for alternative resource acquisition strategies (Figure 2). Drought-induced changes in plant and microbial community composition and physiology will feedback onto the chemistry of soil organic matter, which will alter its decomposability, stabilisation rates and persistence leading to changes in soil carbon pools. Impact of these factors on soil carbon balance is likely to be context dependent.

How these interdependent factors act to regulate microbial trait distribution, community biomass, chemistry of soil organic matter and carbon cycling rates (Figure 2) remains difficult to quantify. The feedback between microbial metabolic response to drought, and the soil carbon cycle remains an area of significant uncertainty, both from an empirical standpoint, but also for models seeking to predict carbon-climate feedbacks. These uncertainties are exacerbated by dry–wet cycles that eventually determine the magnitude of drought-induced change in soil carbon. An increasing frequency of drought-precipitation cycles are likely to result in a nonlinear relationship between soil moisture and carbon fluxes (Moyano et al., 2013) as the microbial community adapts to drought and trait-expression changes. In the sections below, we elaborate on the different pathways of microbial influence on soil carbon in response to drought and present hypothetical predictions which may be useful to develop future experiments.

5 | TRAIT TRADE-OFFS AND THE FEEDBACK OF DROUGHT-IMPACTED MICROBIAL PHYSIOLOGY ON THE SOIL CARBON CYCLE

A microbial trait-based framework is an appealing mechanism for scaling from microbial physiology to ecosystem-level processes (Hall et al., 2018; Wallenstein & Hall, 2012). The Y-A-S theoretical framework can be used to assess and quantify the microbial impact on soil carbon cycling processes along two key drought-impacted environmental gradients: resource and water availability (Malik, Swenson, et al., 2020). The framework incorporates physiological stress response (S strategy)

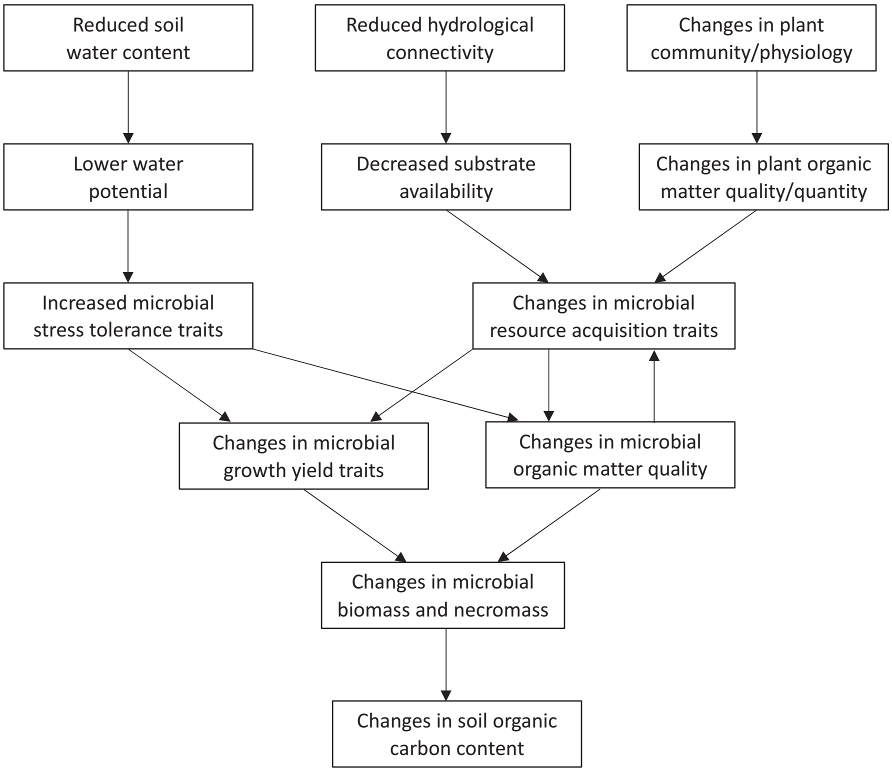

FIGURE 2 Conceptual model of the direct and indirect effects of drought on long-term soil carbon balance. Three key routes of influence on microbial functions have been considered with feedback to soil carbon cycling. There are major uncertainties in many of these responses, which is signalled by the lack of a clear trend in those effect traits

and changes in resource acquisition (A strategy) induced by droughts in soil microbial communities (Figure 1d). Here we provide Y-A-S predictions in two major soil categories based on the literature reviewed in the preceding sections that could be applied globally (Figure 3; Table 1).

For the sake of intelligibility, we recognise two broad classes of soils: (a) those with simpler and accessible resources that are mostly plant derived such as rhizosphere, organic soil, or the surface litter layer; and (b) those soils with more complex, mineral-associated resources that are predominantly microbial in origin, such as bulk or mineral soil. The two scenarios differ in microbial access to substrate, whereby microbes in mineral soils are more likely to experience limitation in substrate diffusion than those in organic soils which provide resources with higher accessibility and degradability (Manzoni et al., 2012). As a consequence, the microbial trait distribution within organic soils should trend towards a transporter-mediated, uptake-optimised A strategy, while mineral soils would select for a depolymerisation-optimised A strategy with higher extracellular enzyme production to mine resources.

The S strategy that microbes employ in response to drought depends on the soil water potential which is influenced by drought intensity and frequency. We suggest a cascade of physiological response depending on the water potential (Figures 1c and 3), starting with osmolarity maintenance using inorganic ions followed by organic osmolytes as water potential declines. Further drying and reduction in water potential will pose severe carbon and energy demands on cells, which will likely lead to shifts in community composition, selecting for drought-tolerant taxa, and biofilm formation through EPS production as a collective community response to the hydraulic discontinuity induced by drought near plant wilting point (Figure 3). Under extreme drought, which will cause microbial metabolic impairment, microbes would prefer to avoid cellular damage through dormancy. Dormancy is a favourable strategy under very dry conditions or even under moderately dry conditions when in carbon-poor soils but the recovery to a metabolically active state on rewetting will be delayed. Such a stress avoidance mechanisms would mean very low carbon turnover in consistently dry soils.

Based on the principle of trait trade-offs which underpin the Y-A-S life-history strategy framework, we hypothesise that an increased investment in A and/or S strategies will reduce investment in the Y strategy (reduced investment in growth and biomass synthesis), which leads to a decrease in soil carbon accumulation through lower microbial necromass stabilisation in the mineral matrix. By contrast, A and S strategies have increased investment in synthesis of non-structural compounds that are mineralised through respiration and lost relatively quickly.

6 | DROUGHT IMPACT ON THE CHEMISTRY OF MICROBIAL NECROMASS AND ON THE SOIL CARBON CYCLE

There is a general consensus growing around a paradigm shift concerning carbon stabilisation in soils. Recent studies and synthesis efforts hypothesise that most plant-derived organic matter is processed by soil microbes over relatively short time-scales (months to years), and microbial necromass and metabolic products interact with the mineral matrix or become part of aggregates, creating stable complexes that persist over multi-decadal time-scales (Schmidt et al., 2011; Sokol et al., 2019). Theses microbial-derived products are important sources of CO_2 efflux upon wet-up (Figure 4a; Barnard et al., 2020; Blazewicz et al., 2014; Fraser et al., 2016) but have only recently been considered while estimating the ecosystem implications of drought. Factors controlling the size and composition of the necromass pool would therefore be important in determining the stabilisation of the microbial-processed mineral-associated or aggregate-occluded organic matter (Buckeridge et al., 2020; Dong et al., 2021; Throckmorton et al., 2012). Here we consider how variable physiological strategies due to changes in water status and resource availability can impact the size and composition of the necromass generated.

We hypothesise here that microbial allocation towards a Y strategy would increase microbial necromass and the stabilisation of necromass-derived organic matter in soil; selection for an A or S strategy is more likely to favour increased mineralisation and the loss of soil carbon. This is because the chemical structure of the microbial compounds produced determines the short-term decomposition rates, stabilisation in the soil mineral matrix or occlusion in aggregates (Buckeridge et al., 2020; Dong et al., 2021; Kallenbach et al., 2016; Newcomb et al., 2017). For example, if microbes synthesise osmolytes in response to soil drying, the allocated carbon is likely to be lost as CO_2 following the rapid mineralisation of these simpler sugars and amino acids upon rewetting. By contrast, if microbes respond to drought stress through EPS production, which persists in soils for much longer (Schimel & Schaeffer, 2012; Sher et al., 2020), the carbon lost post-wet-up is likely smaller. Furthermore, the higher investment in degradative enzymes instead of only transporters for uptake of available substrates in the vicinity is likely to result in higher carbon sequestration because extracellular enzymes can be more persistent by virtue of their complex protein structure or ability to form complexes in association with soil minerals. Therefore, in addition to identifying trade-offs in microbial traits away from growth (Y-strategy) that might stabilise carbon within soil, to maintenance activities (A and S strategy), which can lead to carbon loss, the chemical structure of the microbial compounds produced, and their role in the soil carbon cycle, should also be characterised.

7 | FLUCTUATING DRYING–REWETTING CYCLES AND THE SOIL CARBON CYCLE

In many ecosystems, single drought events are likely an exception, and communities are subject to multiple cycles of soil drying and wetting. The episodic nature of such drying and rewetting poses a significant stress to soil microbial communities, one which can lead to a greater loss of soil carbon than that lost through single events (e.g. prolonged summer dry downs, Figure 4a,b). The extent of carbon lost, as CO_2, is largely dependent on a

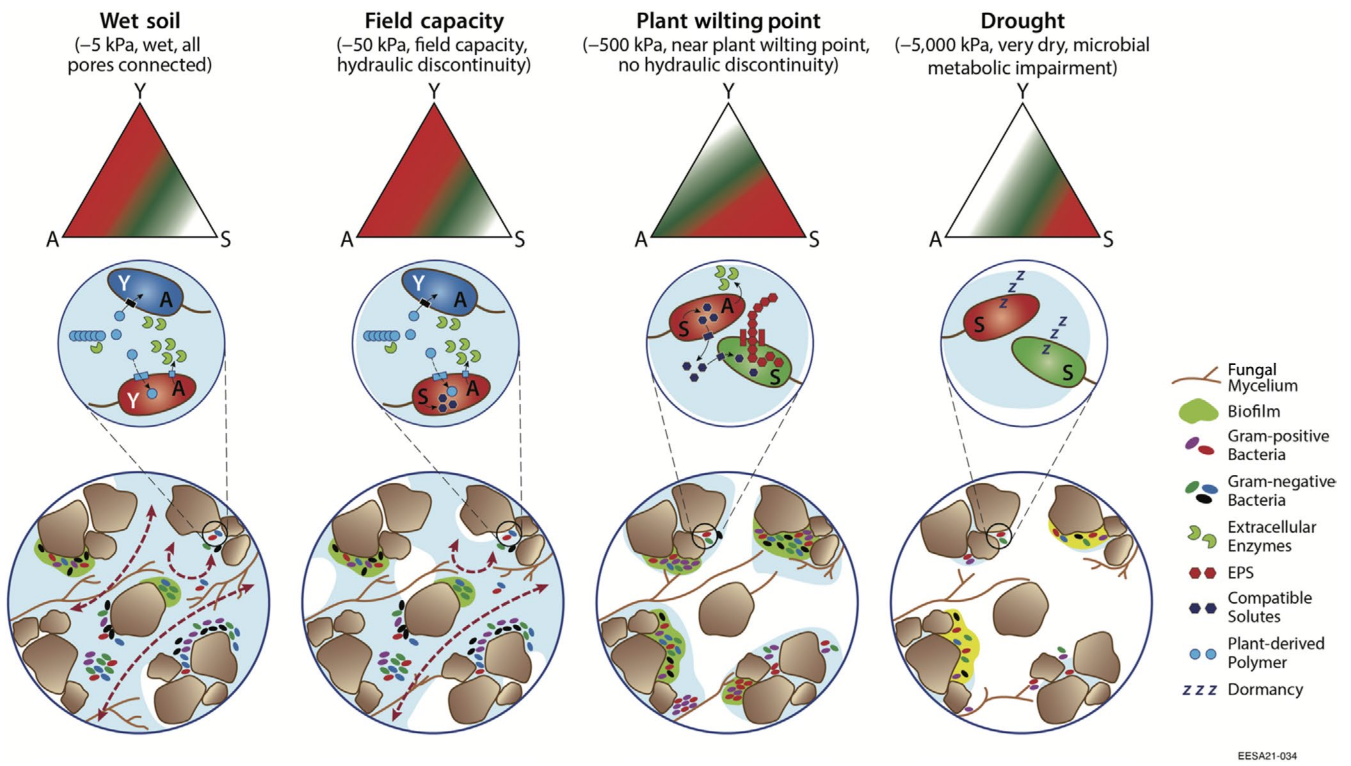

FIGURE 3 The Y-A-S framework as applied to soils undergoing drying. This illustration depicts the changes in porewater connectivity, community composition (large circles), microbial metabolism (magnified microbial cells), and concomitant shifts in trait distribution and resource allocation (triangles) under drier and drier conditions. The colours displayed in the triangles represent the hypothetical allocation of cellular resources to different traits (i.e. yield, acquisition and stress), whereby red shows greater allocation and upregulation of pathways, green lower allocation and white no allocation. Further details of trait responses are provided in Table 1

TABLE 1 Water status-dependent trait distribution. The table provides details of Y-A-S predictions across varying soil water potential in two main soil categories: organic and mineral soils. The water potentials are only indicative

Water status	Wet soil	Field capacity	Plant wilting point	Severe drought
Water potential	−5 kPa	−50 kPa	−500 kPa	−5000 kPa
Soil conditions and hydrology	All pores connected, with gas diffusion	Some hydraulic discontinuity	No hydraulic connectivity, thin water films form	Absence of water, microbial metabolic impairment
Organic soil (simpler and accessible resources mostly plant derived)	YA Growth-optimised Y strategy, uptake-optimised A strategy	YA Substrate diffusional constraints small, uptake-optimised A strategy, Growth-favoured Y strategy	S Osmolyte or EPS biofilm strategy	S Dormancy and sporulation strategy
Mineral soil (complex, mineral associated resources mostly microbially processed)	YA Growth-optimised Y strategy, Depolymerisation-optimised A strategy	A Substrate diffusion and transport hindered; large investment in A strategy	S EPS biofilm strategy, osmolyte strategy if resources available, otherwise dormancy	S Dormancy and sporulation strategy

series of interdependent factors, including the mean annual precipitation of a region, soil properties, the extent of dry-down and the frequency of dry–wet cycles (Fierer & Schimel, 2002; Smith et al., 2017; Zhang et al., 2020). The carbon released under fluctuating drying–rewetting cycles has been shown to be principally microbial in origin (Barnard et al., 2020), which might stem from a declining carbon use efficiency following resource allocation away from growth and towards stress traits. The turnover of the resulted osmolytes on rewetting likely contributes significantly to strong CO_2 pulses (Warren, 2014). However, rewetting reverses the diffusional constraints that persist under drought, permitting dispersal of substrates and biochemical compounds, including extracellular enzymes released before, and during soil drying (Bouskill, Wood, Baran, Ye, et al., 2016; Sowerby et al., 2005). Thus, allocation to growth yield or resource acquisition pathways could be regulated under fluctuating dry–wet cycles (Figure 4c).

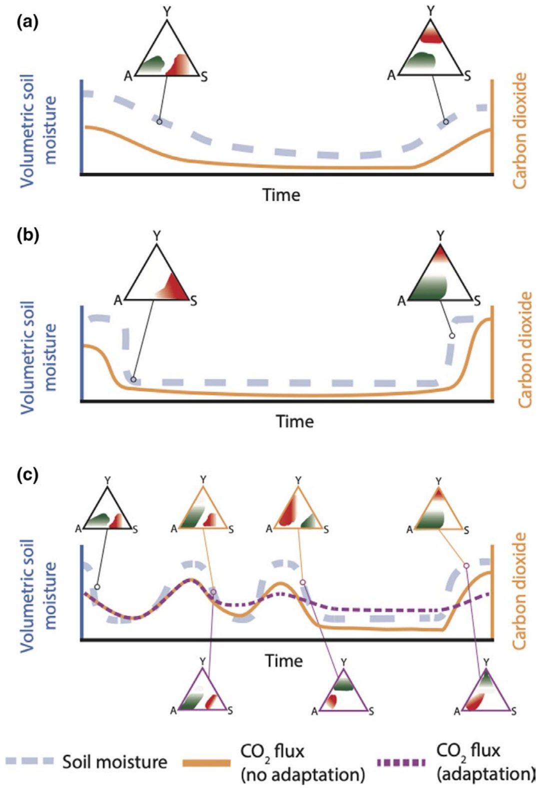

FIGURE 4 Hypothetical scenarios linking the rate and frequency of soil drying and rewetting to soil CO_2 fluxes, and microbial trait allocation (see Figure 3 for an explanation of the colours within the Y-A-S triangles). Panel (a) depicts microbial trait variation and CO_2 dynamics under a moderate drying and rewetting cycle that permits a metabolic response to drought (including compatible solute production). Panel (b) replicates the same scenario but with a strong dry-down and rapid rewet. Panel (c) depicts fluctuating dry–wet conditions and addresses the question of how soil carbon fluxes might change with associated microbial physiological adaptation to historical conditions. In this case, the distribution over time is provided for the endemic community (trait triangles framed in orange) and the adapted community (trait triangles framed in purple). The different scenarios outlined here are described in greater detail in Table 2

The reactivation and increased production of extracellular enzymes post-drought also suggests that pre-existing or stable carbon stocks could be vulnerable to changes in the frequency of drought-precipitation cycles under a changing climate (Alster et al., 2013; Smith et al., 2017).

The legacy of drought is also an important factor shaping the microbial response to current drought (Brangarí et al., 2021; Canarini et al., 2021; Smith et al., 2017). The microbial respiratory response to rewetting can be broadly divided into two different life strategies. The first involves the rapid resumption of respiration concomitant with wet-up, and is generally associated with dry ecosystems or those that regularly experience prolonged dry periods (Jones et al., 2019; Meisner et al., 2013). A second strategy can be characterised by a longer lag time prior to discernible activity and respiration, and is usually associated with humid ecosystems that rarely experience drought (Bouskill, Wood, Baran, Hao, et al., 2016). The stress imposed by fluctuating dry–wet conditions can also select for more drought-tolerant microbial taxa, which has the added effect of shifting the respiratory strategies from the rapid production of CO_2 upon wet-up to a slower, lagged response under frequent wet–dry cycles (Brangarí et al., 2021; Meisner et al., 2015). Such shifts, encompassing changes to community composition (and consequential changes in trait distribution), and the depletion of substrate, can dampen the CO_2 release to subsequent wet–dry cycles (denoted by the purple line in Figure 4c; Baumann & Marschner, 2013; Shi & Marschner, 2017).

An understudied aspect of such dampening is the role played by adaptation and acclimation. Acclimation to a frequently experienced stressor can change selective pressures, and shape species physiology, and interspecies interactions (Rodríguez-Verdugo & Ackermann, 2021; Rodríguez-Verdugo et al., 2019). Such changes, in the case of soil drying, can result in the more efficient use of carbon, altering the community carbon use efficiency (Leizeaga et al., 2021). Furthermore, studies of communities within arid and semi-arid ecosystems that experience drought on an annually recurring basis have measured little to no accumulation of osmolytes under stress (Boot et al., 2013; Kakumanu et al., 2013). This suggests little allocation of resources to metabolic stress pathways following a frequently experienced stress, with communities likely favouring more energy-saving strategies, including desiccation and dormancy. This restricts the accumulation of biomass, and the pool of labile compatible solutes, that can be mineralised upon soil rewetting (Brangarí et al., 2021), altering the trait space with implications for carbon cycling rates (Figure 4c).

8 | HYPOTHESIS TESTING THROUGH MODELLING APPROACHES

The increasing frequency and duration of drought (Büntgen et al., 2021; O'Connell et al., 2018; Schwalm et al., 2017) necessitates a greater consideration of the role microbial communities play in the future stability of carbon and nutrient cycling under a changing climate. While multiscale empirical data are critical for identifying and quantifying traits, the incorporation of these data into microbial-centric trait-based models (Allison, 2012; Bouskill et al., 2012; Cheng et al., 2018; Manzoni et al., 2014) represents an important avenue for testing hypotheses arising from such experiments.

While accurate parameterisation of distinct traits across multiple taxonomic groups has been a significant challenge to the application of these models, trait-derived data from genome or metagenomic sequencing show increasing promise for the parameterisation of certain traits (Cheng et al., 2018). Microbial generation times and optimal growth temperatures are two such traits that can be predicted from isolate genomic or metagenomically assembled genomic data (Sauer & Wang, 2019; Weissman et al., 2021). When combined with existing physiological trait data, including the energetic cost of synthesising and accumulating compatible solutes (Oren, 1999), it becomes feasible to develop simple models that represent the emergent response to soil moisture as a function of physiological traits and the cost benefits of resource allocation.

TABLE 2 Predictions of integrated long-term soil carbon balance under different hypothetical scenarios of fluctuating dry–rewetting events in soil as shown in Figure 4. We also provide details on the likely factors that impact the microbial response and the consequent feedback to soil carbon cycling

Hypothetical scenario	Microbial response	Predictions of long-term soil carbon (C) response
Consistent drought conditions followed by a gradual rewetting event (Figure 4a)	Stress response through intracellular osmolyte production followed by gradual increase in activity and growth	Low C loss due to the gradual nature of moisture changes, increased flux following rewetting linked to metabolism of osmolytes
Consistent drought; rapid onset followed by a strong rewetting event (Figure 4b)	Stress response through EPS and/or dormancy followed by high activity and growth	Medium C loss, high flux on rewetting linked to metabolism of necromass and resource remobilisation
Drought conditions followed by wetting in quick succession: no physiological adaptation (Figure 4c)	Stress response through osmolyte production followed by export of osmolytes, increased resource mobilisation	Very large C loss: osmolytes quickly metabolised on rewetting, substrate limitation after multiple cycles
Drought conditions followed by wetting in quick succession: physiological adaptation (Figure 4c)	Alternative response due to physiological adaptations to repeated droughts or to depletion of labile carbon	Large C loss: adaptation or community shifts could lower the impact of future dry–wet cycles

The adoption of these models could expedite a departure from static relationships governing carbon turnover with soil moisture as one would find within earth system models (e.g. Lawrence et al., 2011). Furthermore, the generation of trait parameters from genomic or classical methods can spur the development and adoption of dynamic energy budget models within microbial ecology (e.g. Cheng et al., 2019; Tang & Riley, 2015). These models characterise microbial metabolism as a molecular economy whereby the allocation of resources, be it towards yield, acquisition or stress, is weighed against requirements elsewhere. As such, the trade-offs that constrain cellular activity can be represented robustly, and this approach has previously been employed to improve model predictions of soil carbon response to warming (Tang & Riley, 2015). Given the complexity of metabolic responses to soil drying, dynamic-energy budget models offer an avenue for evaluating the role metabolic trade-offs play in underpinning the microbial drought stress response. Coupling empirical observations to microbial-centric biogeochemical models (Allison & Goulden, 2017), or ecosystem-scale models with a credible representation of microbial guilds (Bouskill et al., 2020), holds great promise for shedding further light on the microbial response to fluctuating environmental conditions, and the consequences for soil biogeochemistry.

9 | UNANSWERED QUESTIONS

We identify several outstanding questions and research areas discussed in this paper that might lessen the uncertainty surrounding the feedback of drought on the soil carbon cycle.

1. How do biotic interactions, plant–microbe and microbe–microbe, shape the ecosystem response to drought? Can cell–cell interactions, including the synthesis of compatible solutes, be competitive or mutualistic (e.g. through release of osmolytes which can be taken up by other community members)?
2. What are the substrate demands imposed on microbes through the variable metabolic responses to drought, and what is the quantitative impact on growth and carbon mineralisation rates?
3. How do substrate diffusional constraints arise due to reduced hydrological connectivity in dry soils, and what is the response of microbial communities to these constraints? Does this result in alternative resource acquisition strategies (e.g. decomposition of more complex organic matter)?
4. What are the drought-induced changes in microbial substrates as a result of changes in plant and microbial community composition? Do these changes in the substrate chemistry alter its decomposability and persistence thereby affecting soil carbon balance?
5. Does an increasing frequency of drought-precipitation cycles result in a nonlinear relationship between soil moisture and carbon fluxes? What is the role of microbial community adaptation to drought on creating such nonlinear relationships?

10 | CONCLUSIONS

A microbial trait-based understanding can be integrated into biogeochemical frameworks to quantify soil carbon decomposition and stabilisation rates under drought and in response to dry–wet cycles. Generalising the distribution of Y-A-S strategies in soils under drought is challenging; however, high-throughput culture-dependent and -independent approaches should facilitate such a task. Culture-based, mechanistic understanding of life-history strategies generated from laboratory experiments can be validated through omics-derived community-level indictors and linked to ecosystem process rates. Alternatively, hypotheses can be generated using field-based omics measurements, which can be validated using laboratory experiments. While the basis for identifying traits at the community level may emerge from observations at the isolate scale, the field scale also serves as a source of potentially new mechanisms that require further experimentation to confirm. For example, whether elevated antibiotic production under drought stimulates biofilm formation or an increasing iron demand under soil drying represent hypotheses that could be tested at the laboratory scale. This would serve to improve our mechanistic understanding of the microbial response to drought, but also increase the trait representation at the community scale. Such multiscale linkages will enable truly integrative ecological understanding of the consequences of microbial physiology on carbon cycling processes under drought.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

Both A.A.M. and N.J.B. conceived the ideas, reviewed the literature, led the writing of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This manuscript does not report any new data.

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