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Opinion

Microbial drought resistance may destabilize soil carbon

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Droughts are becoming more frequent and intense with climate change. As plants and microbes respond to drought, there may be consequences for the vast stocks of organic carbon stored in soils. If microbes sustain their activity under drought, soils could lose carbon, especially if inputs from plants decline. Empirical and theoretical studies reveal multiple mechanisms of microbial drought resistance, including tolerance and avoidance. Physiological responses allow microbes to acclimate to drought within minutes to days. Along with dispersal, shifts in community composition could allow microbiomes to maintain functioning despite drought. Microbes might also adapt to drier conditions through evolutionary processes. Together, these mechanisms could result in soil carbon losses larger than currently anticipated under climate change.

Highlights

Drought frequency and intensity are increasing with climate change.

Soil microbes cope with drought through physiological acclimation, dispersal, shifts in community composition, and evolutionary adaptation.

By acting as decomposers, microbes control the loss of carbon from soil.

Physiological, ecological, and evolutionary responses allow microbes to sustain losses of carbon from soils experiencing drought.

Climate change affects soil microbes

Around the world, climate change is impacting all forms of life, including **microbiomes** (see Glossary). As the engines of Earth's biogeochemical cycles [1], microbiomes can alter global carbon and nutrient cycling as the environment changes. Given that soils hold nearly 2000 Pg carbon [2], the climate responses of soil microbiomes could impact global carbon balance and future levels of greenhouse gases.

In addition to temperature, climate change alters rainfall, snow cover, seasonality, and the frequencies of extreme weather events [3]. Climate models predict a future with more frequent and intense droughts [4], and drylands occupy over 45% of the global land area, so knowing how microbes respond to dry conditions is valuable for managing and conserving terrestrial ecosystems across much of the planet [5]. Although microbial responses to drought have received increasing attention [6,7], we do not yet fully understand how this important global change might alter the carbon cycling functions of soil microbiomes [8]. This knowledge gap makes it difficult to predict the magnitude and direction of carbon–climate feedbacks in the Earth system. To improve these predictions, we need a comprehensive understanding of both plant and microbial community responses to drought across ecosystems.

Previous studies [9] show that microbiomes cope with drought through a wide array of mechanisms that fall into three main categories: **physiological acclimation**, community shifts, and evolution (Figure 1). Physiological mechanisms include changes in gene expression and metabolic pathways that facilitate microbial acclimation to desiccation and rewetting. Community shifts occur when drought selects for greater relative abundance of microbial taxa with adaptations for life under dry conditions. Dispersal contributes to community shifts by allowing drought-adapted taxa to migrate into dry locations. Evolution can lead to new microbial **traits** that confer drought resistance or tolerance [10].

Given this high potential for microbes to tolerate or avoid drought, I argue that drought-driven losses of carbon from soil will be larger than currently recognized. In most aerobic soils,

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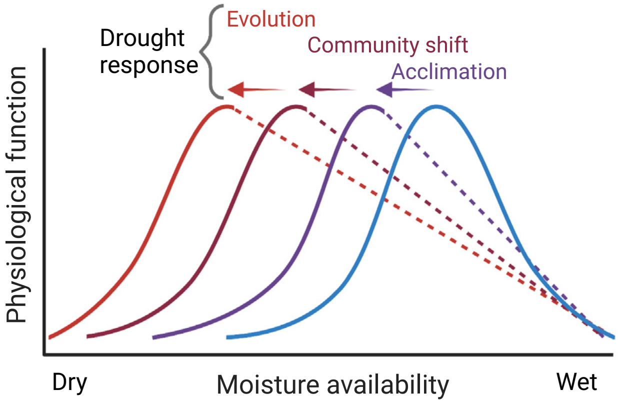


Figure 1. Physiological response curves may shift as microbiomes respond to drought. In the short term (minutes to days), physiological acclimation may help to sustain function, such as soil carbon decomposition. Over weeks to decades, community shifts and evolution could alter response curves to maintain functioning under dry conditions. Broken lines indicate potential variation in the breadth of the shifted response curves [58]. Figure created with BioRender.com.

heterotrophic microbes like bacteria and fungi are the primary gatekeepers for carbon loss [11]. If heterotrophic microbes bounce back from drought by acclimating, shifting, and adapting, they may sustain carbon losses from soil. Those losses would need to be offset by carbon inputs from resilient plants to avert a net decline in soil carbon stocks.

Soil carbon consequences of physiological response to drought

Physiological acclimation can allow microbes to survive, grow, and maintain carbon cycling in the face of drought [12] (Figure 2). In turn, these physiological responses may help heterotrophic microbes to sustain soil carbon losses. Soil microbial taxa vary widely in their rates of mortality under desiccating conditions in the laboratory [13], and there are clear moisture thresholds for microbial respiration in soils and litter. Some bacteria may respire down to water potentials of –10 MPa, and some fungi down to –60 MPa [14]. To retain cellular water under low ambient water potentials, microbes may produce osmolytes through constitutive and inducible pathways [15,16]. Osmolytes are low-molecular-weight compounds that are readily metabolized and could fuel decomposition of existing soil organic matter through priming effects [17].

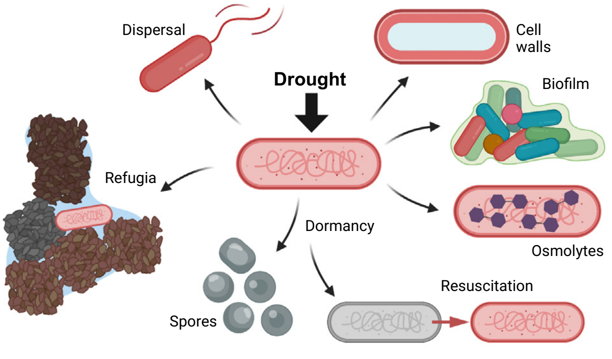


Figure 2. Physiological mechanisms of microbial response to drought. Drought tolerance strategies include protection from cell walls, biofilm formation, and production of osmolytes. Microbes may avoid drought by forming spores or going dormant during dry periods and resuscitating cellular activity upon wet-up. Microbes may also disperse to areas with greater water availability, such as water-filled soil pores that act as refugia. Figure created with BioRender.com.

Glossary

Environmental selection: the process by which environmental conditions such as moisture or temperature cause well-adapted taxa to increase in relative abundance (also called environmental filtering).
Heterotrophs: organisms that obtain energy by consuming reduced forms of carbon.
Legacy: a difference in community composition or functioning resulting from prior exposure to an environmental perturbation.
Microbiome: a community of microorganisms that may include bacteria, fungi, archaea, and viruses.
Physiological acclimation: change in metabolism or behavior that improves organismal performance without a change in genotype.
Trait: a phenotypic characteristic of an organism, population, or community.
YAS framework: an hypothesis that microbes fall into at least three life-history categories that trade off with one another due to resource limitation: high growth Yield, resource Acquisition, and Stress tolerance.

Microbes can also resist drought by producing extracellular metabolites and cell walls. For example, extracellular polymeric substances (EPS) form biofilms that reduce water loss [18]. As sticky polymers, EPS may contribute to soil aggregation and physical protection of organic matter [19]. In addition, thick cell walls may enable some microbes to prevent water loss even under low environmental water potentials [20]. Upon death, cell walls may contribute to necromass accumulation in soil [21], which could counter drought-induced carbon losses. Multiple drought tolerance mechanisms may coincide; for example, EPS and trehalose production both contributed to desiccation resistance of *E. coli* strains in the laboratory [16]. Overall, the potential for net carbon loss from soil is higher if microbes respond to drought by producing simple metabolites like osmolytes versus more complex EPS and cell wall materials (Figure 3, Key figure).

In addition to resisting or tolerating desiccation, some microbes employ strategies to avoid drought. Cells may go dormant by shutting down metabolism or forming spores that can survive extreme desiccation for decades or even centuries [22]. When dry conditions abate, dormant cells resume activity. Upon rewetting, some taxa activate within minutes, whereas other require days to ramp up growth and respiration [23]. These cycles of dormancy and resuscitation could allow higher decomposition rates during wet periods to offset lower rates during drought. Known as the Birch effect [24], this pattern of respiration pulses following wet-up may result in greater carbon release than observed under stable moisture conditions in some soils [25].

Another drought avoidance mechanism is occupation of refugia, or microsites in the soil with higher water potential. Such microsites may occur at the interfaces of soil particles, deep in the soil profile, or in topographic locations with higher water availability [26]. Multiple traits could facilitate microbial strategies of microsite occupation. Flagella or other motility mechanisms could

Key figure

Direct and indirect feedbacks of trait-based microbial strategies on soil carbon decomposition

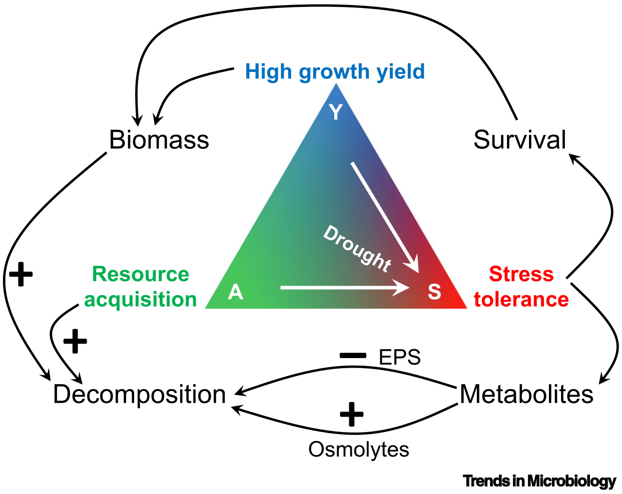


Figure 3. Investment in drought tolerance may trade off against resource acquisition, which could reduce decomposition. Alternatively, drought tolerance strategies could help to maintain decomposer biomass and generate easily decomposed metabolites, resulting in losses of soil carbon. Abbreviation: EPS, extracellular polymeric substances.

allow microbes to navigate toward high-water microsites as soils dry down. Conversely, dispersal traits, such as production of spores and volatile organic compounds that attract arthropod vectors, could be important in allowing microbes to migrate out of refugia and recolonize soils following wet-up [27].

A broad range of life history traits can influence microbial strategies for drought survival at the population scale. For example, microbial taxa that grow quickly under wet conditions could build up large populations and disperse widely, enabling some cells to reach wet refugia during drought. Such taxa might have very low resistance to desiccation, instead coping with changing moisture availability through boom-and-bust cycles of population growth and death [28].

While there are many mechanisms of microbial drought response, it remains unclear which are most important in a field setting. The physiological costs of different strategies likely vary in magnitude and resource demands [20]. Strategy costs and benefits may influence microbial survival, growth, and functioning under drought in ways that depend on the ecological context. In ecosystems where moisture levels fluctuate over days to weeks, tolerance strategies such as EPS production may be effective at maintaining consistency in extracellular water potential. Conversely, avoidance strategies like dormancy may be more effective in places with extended drought periods, such as deserts or Mediterranean climates.

Soil carbon consequences of ecological response to drought

At the community scale, microbial taxa that cannot acclimate to drought may be replaced as better-adapted taxa migrate in and become more dominant [29]. Through this process of **environmental selection**, drought often alters soil microbiome composition [6,30]. In leaf litter, drought reduces bacterial populations and alters bacterial and fungal community composition [31–33]. Sheik *et al*. [34] observed similar changes in response to warming-induced drought in a tall grass prairie soil. Other studies confirm that drought favors fungi over bacteria, and the relative abundances of taxa shift within these broad groups [35]. For example, Actinobacteria become more dominant with drought whereas Proteobacteria decline in terms of both relative abundance and activity [36]. Relative to fungal co-occurrence networks, bacterial networks in grassland mesocosms were more sensitive to drought disruption [37].

Due to evolutionary trade-offs, drought-induced changes in microbiome composition may have consequences for soil carbon cycling. The **YAS framework** assumes that microbes trade off resource investments in growth yield, resource acquisition, and stress tolerance traits [38]. If microbes invest in drought tolerance, trade-offs with other YAS traits could affect soil carbon storage. Drought-tolerant microbes may have lower growth yield, which could reduce their biomass and decomposition ability [39]. They may also have fewer resources available to produce enzymes involved in the degradation of soil organic matter. However, if these trade-offs are weak or non-existent, a shift toward drought tolerance strategies may not limit soil carbon decomposition.

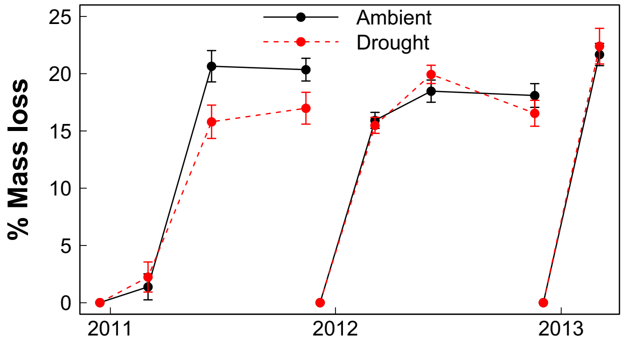
Empirical evidence for drought-induced YAS trade-offs is mixed. Although drought can alter the frequencies of genes involved in soil carbon and nitrogen cycling [40,41], Alster *et al*. [42] did not observe trade-offs with drought tolerance in a laboratory experiment with fungal isolates grown at different moisture levels. In a parallel field experiment, they found good evidence for a trade-off between drought tolerance and growth yield, but little evidence for trade-offs with resource acquisition [43]. In a California grassland, experimental drought altered microbial abundance and community composition, resulting in lower rates of litter decomposition by drought-exposed microbiomes [44]. However, little impairment of litter decomposition was observed when desert-adapted microbiomes were transplanted to cooler, wetter sites along a climate gradient in southern California [45].

Even if drought reduces the microbiome capacity for soil carbon degradation in the short term, resilience in community composition could allow carbon losses to recover over time. Alternatively, if recovery is slow, there could be a **legacy** of prior exposure to drought. Kaisermann *et al*. [46] found evidence for drought legacy effects on microbiome composition and microbe-mediated plant growth. Conversely, there were no drought legacy effects on bacterial growth, fungal growth, or microbial community composition after at least 10 years of drought treatment at five European sites along a climate gradient [47]. In the California grassland system [44], there was a legacy of impaired decomposition, but it dissipated after 1 year (Figure 4). A complementary modeling analysis confirmed that moderate drought was unlikely to cause legacies of impairment that lasted beyond this timeframe [48]. These results suggest that legacy effects may not occur unless drought intensity is strong enough to alter microbiome composition through community shifts or evolution.

Some studies have found legacies of resilience to drought. Prior exposure to 16 years of drought caused a Mediterranean soil microbiome to retain higher bacterial alpha diversity following experimental drought treatment in a greenhouse experiment [35]. In Puerto Rican tropical forest soils previously exposed to drought, a second drought treatment had relatively little additional impact on the phylogenetic diversity of bacteria [49]. Canarini *et al*. [50] found that recurrent drought over 10 years altered microbial community composition more than 1 year of drought. At the same time, the 10-year drought treatment resulted in a strong legacy effect that buffered microbial community functioning relative to the 1-year drought.

Integrated consequences of drought responses for soil carbon

Collectively, previous empirical studies support the argument that drought can lead to substantial losses of soil carbon. Based on a meta-analysis, the proportion of carbon lost with drought and rewetting increases with soil carbon content, meaning that carbon-rich soils may be particularly vulnerable to drought impacts [8]. Multiple microbial mechanisms may contribute to this response. Drought selects for microbial taxa, such as Actinobacteria, with adaptive physiological traits. These taxa increase in relative abundance, resulting in altered microbiome composition that often, but not always, persists following drought. When it persists, a change in microbiome



Trends in Microbiology

Figure 4. Legacy of drought exposure inhibits microbiome functioning for 1 year. Microbiomes from ambient and drought plots in California grassland were transplanted onto sterilized grassland litter which decomposed in the field for 1 year. Microbiomes were then collected at the end of the year and inoculated onto fresh litter for two subsequent years. Microbiomes originating from drought plots decomposed significantly less litter mass, but only during the first year. Figure adapted from Martiny *et al*. [44].

composition often, though not always, results in legacy effects on ecological properties such as microbial biomass, extracellular enzyme activity, and plant growth. In some cases, these legacies impair ecosystem functioning (Figure 4), but in other cases, they can buffer functioning against ongoing or future drought disturbance [50].

The implication of these outcomes is that microbiomes display an array of responses to environmental selection by drought, only a subset of which impair functioning. Together with physiological acclimation and evolutionary adaptation, these ecological responses likely provide resistance and resilience of the soil microbiome's diversity and metabolic capacity in the face of drought [51]. In contrast to YAS predictions, there is limited empirical evidence that drought-induced shifts in microbiome composition reduce the potential for organic matter decay through resource allocation trade-offs. Although such trade-offs may occur, they may have offsetting impacts on carbon cycling; for example, a trade-off-induced decline in extracellular enzyme production could be offset by a greater total biomass of drought-tolerant microbial decomposers.

It is also possible that microbes have evolved drought-tolerance mechanisms that avoid trade-offs with resource acquisition traits. Rather than trading off, investment in carbon and nutrient acquisition could fuel the production of metabolites that confer drought tolerance. Under selection by drought, *de novo* mutations could introduce novel genetic variation that leads to evolutionary adaptation through broader exploration of trait space. Although experimental evolution studies with drought are limited, comparative genomic studies show that bacterial and fungal responses to drought are phylogenetically conserved [33], and there is longstanding evidence that microbes evolve within a few hundred generations in response to temperature change [52,53]. We need additional experiments to understand the rates and mechanisms of microbial evolution in response to changing drought frequency and intensity, along with subsequent rewetting.

Heterotrophic microbes are key determinants of soil carbon turnover, but the net carbon lost will depend on how steeply plant inputs decline as ecosystems become drier. Although drought often reduces plant productivity and may trigger legacy effects [54], the consequences for soil carbon balance are more uncertain. Following drought, trees may pump carbon below ground to recover root function [55]. Also, symbiotic microbes in the rhizosphere and phyllosphere may respond to drought in ways that benefit their plant hosts, boosting the drought resilience of plant inputs and soil microbiomes in tandem [56]. Yet, given that desertification often results in soil carbon loss [5], recovery of plant inputs may be insufficient to counter carbon losses driven by resilient microbes. Overall, the relative drought response of plant inputs compared to microbial decomposition remains uncertain (see Outstanding questions).

Concluding remarks and future perspectives

Although desiccation has direct negative impacts on microbial metabolism, multiple mechanisms may help to sustain soil carbon losses under drought. Physiological acclimation, shifts in community composition and life history strategy, as well as evolutionary adaptation, may all maintain heterotrophic functioning in soils that experience higher drought frequency and intensity. While stable functioning is often beneficial, in this case it could reduce soil carbon storage if plant carbon inputs decline more steeply with drought than heterotrophic losses. In a global modeling analysis, soils were predicted to lose more carbon if microbes adapted to climate warming [57]. The same might happen if microbes adapt to drought.

Still, accurately predicting the net impact of drought on soil carbon will require additional research. First, we need empirical measurements of heterotrophic sensitivity to drought, including the relative contributions of physiological, ecological, and evolutionary mechanisms to drought

Outstanding questions

What are the physiological costs of drought strategies? Quantifying the costs of desiccation tolerance and avoidance is essential for predicting which strategies are most relevant. Several techniques offer promise for quantification. Transcriptomics and metabolomics can provide semi-quantitative data on the metabolic pathways active under drought. Genome-scale metabolic models can leverage genomic sequences to predict metabolic rates as environmental conditions change.

How do microbes evolve in response to drought? Evolutionary processes such as mutation, horizontal gene transfer, and genetic drift likely contribute to microbial drought response. Still, the dominant mechanisms, rates of change, and consequences for phenotype remain largely unexplored, especially in comparison to other selective forces like warming. Likewise, it remains unclear how microbes adapt to long-term changes in drought frequency and intensity of precipitation events. Additional evolution experiments should be run in the laboratory and field to fill these knowledge gaps.

How do plant responses to drought compare with microbial responses? Although there are many studies of plant physiology, community shifts, and evolution in response to drought, the consequences for soil carbon inputs are not well understood. Drought may induce some plants to allocate more carbon below ground to acquire water, but if plant productivity declines due to water limitation, reallocation may not maintain carbon inputs to soil. Quantifying plant inputs versus microbial outputs of carbon is crucial for determining soil carbon balance under drought.

How do we predict soil carbon balance with drought? We need improved models that account for mechanisms of plant and microbial response to drought at the ecosystem scale. A hierarchical, multiscale approach can help to reconcile the vastly different scales of microbial, plant, and ecosystem processes. For instance, outputs from trait-based, microbial-scale models can generate moisture-response functions for use in ecosystem models.

resistance and resilience [58]. These data should be gathered at broad spatial scales, for example, along gradients, to assess dependence on environmental variation. Observations must also cover a range of temporal scales, from minutes to decades, to quantify rates of response to drought. Second, microbial, ecosystem, and plant ecologists should work together to assess relative drought impacts on plant inputs versus heterotrophic losses. Finally, we need updated models of drought impacts on soil carbon cycling from microbial to global scales [59,60]. Models are powerful tools for scaling up measurements and mechanisms to predict soil carbon balance. With well-crafted models in hand, scientists can make better predictions to guide policy and mitigation efforts as the climate changes.

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Declaration of interests

No interests are declared.

References

1. Falkowski, P.G. *et al.* (2008) The microbial engine that drives the Earth's biogeochemical cycles. *Science* 320, 1034–1040
2. Jobbágy, E.G. and Jackson, R.B. (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* 10, 423–436
3. IPCC (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, IPCC
4. Cook, B.I. *et al.* (2015) Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Sci. Adv.* 1, e1400082
5. Lal, R. (2001) Potential of desertification control to sequester carbon and mitigate the greenhouse effect. *Clim. Chang.* 51, 35–72
6. Bogati, K. and Walczak, M. (2022) The impact of drought stress on soil microbial community, enzyme activities and plants. *Agronomy* 12, 189
7. Malik, A.A. and Bouskill, N.J. (2022) Drought impacts on microbial trait distribution and feedback to soil carbon cycling. *Funct. Ecol.* 36, 1442–1456
8. Canarini, A. *et al.* (2017) Soil carbon loss regulated by drought intensity and available substrate: a meta-analysis. *Soil Biol. Biochem.* 112, 90–99
9. Schimel, J.P. (2018) Life in dry soils: effects of drought on soil microbial communities and processes. *Annu. Rev. Ecol. Evol. Syst.* 49, 409–432
10. Martiny, J.B.H. *et al.* (2015) Microbiomes in light of traits: a phylogenetic perspective. *Science* 350, 649
11. Moyano, F.E. *et al.* (2013) Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. *Soil Biol. Biochem.* 59, 72–85
12. Alvarez, H.M. *et al.* (2004) Physiological and morphological responses of the soil bacterium *Rhodococcus opacus* strain PD630 to water stress. *FEMS Microbiol. Ecol.* 50, 75–86
13. Chen, M. and Alexander, M. (1973) Survival of soil bacteria during prolonged desiccation. *Soil Biol. Biochem.* 5, 213–221
14. Manzoni, S. *et al.* (2012) Responses of soil microbial communities to water stress: results from a meta-analysis. *Ecology* 93, 770–782
15. Harris, R.F. (1981) Effect of water potential on microbial growth and activity. In *Water Potential Relations in Soil Microbiology* (Parr, J.F. *et al.*, eds), pp. 23–95, American Society of Agronomy
16. Zhang, Q. and Yan, T. (2012) Correlation of intracellular trehalose concentration with desiccation resistance of soil *Escherichia coli* populations. *Appl. Environ. Microbiol.* 78, 7407–7413
17. Warren, C.R. (2016) Do microbial osmolytes or extracellular depolymerisation products accumulate as soil dries? *Soil Biol. Biochem.* 98, 54–63
18. Roberson, E.B. and Firestone, M.K. (1992) Relationship between desiccation and exopolysaccharide production in a soil *Pseudomonas* sp. *Appl. Environ. Microbiol.* 58, 1284–1291
19. Miltner, A. *et al.* (2012) SOM genesis: microbial biomass as a significant source. *Biogeochemistry* 111, 41–55
20. Schimel, J. *et al.* (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88, 1386–1394
21. Schurig, C. *et al.* (2013) Microbial cell-envelope fragments and the formation of soil organic matter: a case study from a glacier forefield. *Biogeochemistry* 113, 595–612
22. Billi, D. and Potts, M. (2002) Life and death of dried prokaryotes. *Res. Microbiol.* 153, 7–12
23. Placella, S.A. *et al.* (2012) Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. *Proc. Natl. Acad. Sci. U. S. A.* 109, 10931–10936
24. Birch, H.F. (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10, 9–31
25. Miller, A.E. *et al.* (2005) Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biol. Biochem.* 37, 2195–2204
26. Howe, J.A. and Smith, A.P. (2021) 2 – The soil habitat. In *Principles and Applications of Soil Microbiology* (3rd edn) (Gentry, T.J. *et al.*, eds), pp. 23–55, Elsevier
27. Choudoir, M.J. and DeAngelis, K.M. (2022) A framework for integrating microbial dispersal modes into soil ecosystem ecology. *iScience* 25, 103887
28. Meisner, A. *et al.* (2017) Partial drying accelerates bacterial growth recovery to rewetting. *Soil Biol. Biochem.* 112, 269–276
29. Allison, S.D. and Martiny, J.B.H. (2008) Resistance, resilience, and redundancy in microbial communities. *Proc. Natl. Acad. Sci. U. S. A.* 105, 11512–11519
30. Ochoa-Hueso, R. *et al.* (2018) Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. *Glob. Chang. Biol.* 24, 2818–2827
31. Allison, S.D. *et al.* (2013) Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology* 94, 714–725
32. Matulich, K. *et al.* (2015) Temporal variation overshadows the response of leaf litter microbial communities to simulated global change. *ISME J.* 9, 2477–2489
33. Amend, A.S. *et al.* (2016) Microbial response to simulated global change is phylogenetically conserved and linked with functional potential. *ISME J.* 10, 109–118
34. Sheik, C.S. *et al.* (2011) Effect of warming and drought on grassland microbial communities. *ISME J.* 5, 1692–1700
35. Preece, C. *et al.* (2019) Effects of past and current drought on the composition and diversity of soil microbial communities. *Soil Biol. Biochem.* 131, 28–39
36. Bastida, F. *et al.* (2017) Differential sensitivity of total and active soil microbial communities to drought and forest management. *Glob. Chang. Biol.* 23, 4185–4203

37. de Vries, F.T. *et al.* (2018) Soil bacterial networks are less stable under drought than fungal networks. *Nat. Commun.* 9, 3033
38. Malik, A.A. *et al.* (2020) Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. *ISME J.* 14, 1–9
39. Killham, K. and Firestone, M.K. (1984) Proline transport increases growth efficiency in salt-stressed *Streptomyces griseus*. *Appl. Environ. Microbiol.* 48, 239–241
40. Berlemont, R. *et al.* (2014) Cellulolytic potential under environmental changes in microbial communities from grassland litter. *Front. Microbiol.* 5, 639
41. Nelson, M.B. *et al.* (2015) Nitrogen cycling potential of a grassland litter microbial community. *Appl. Environ. Microbiol.* 81, 7012–7022
42. Alster, C.J. *et al.* (2021) Exploring trait trade-offs for fungal decomposers in a Southern California grassland. *Front. Microbiol.* 12, 665
43. Alster, C.J. *et al.* (2022) Trait relationships of fungal decomposers in response to drought using a dual field and laboratory approach. *Ecosphere* 13, e4063
44. Martiny, J.B. *et al.* (2017) Microbial legacies alter decomposition in response to simulated global change. *ISME J.* 11, 490–499
45. Glassman, S.I. *et al.* (2018) Decomposition responses to climate depend on microbial community composition. *Proc. Natl. Acad. Sci. U. S. A.* 115, 11994–11999
46. Kaisermann, A. *et al.* (2017) Legacy effects of drought on plant-soil feedbacks and plant-plant interactions. *New Phytol.* 215, 1413–1424
47. Rousk, J. *et al.* (2013) Investigating the long-term legacy of drought and warming on the soil microbial community across five European shrubland ecosystems. *Glob. Chang. Biol.* 19, 3872–3884
48. Wang, B. and Allison, S.D. (2021) Drought legacies mediated by trait tradeoffs in soil microbiomes. *Ecosphere* 12, e03562
49. Bouskill, N.J. *et al.* (2012) Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. *ISME J.* 7, 384–394
50. Canarini, A. *et al.* (2021) Ecological memory of recurrent drought modifies soil processes via changes in soil microbial community. *Nat. Commun.* 12, 5308
51. Zhou, Z. *et al.* (2020) Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nat. Commun.* 11, 3072
52. Lenski, R.E. (2017) Experimental evolution and the dynamics of adaptation and genome evolution in microbial populations. *ISME J.* 11, 2181–2194
53. Romero-Olivares, A.L. *et al.* (2015) *Neurospora discreta* as a model to assess adaptation of soil fungi to warming. *BMC Evol. Biol.* 15, 198
54. Hoover, D.L. *et al.* (2021) Drought resistance and resilience: the role of soil moisture–plant interactions and legacies in a dryland ecosystem. *J. Ecol.* 109, 3280–3294
55. Hagedorn, F. *et al.* (2016) Recovery of trees from drought depends on belowground sink control. *Nat. Plants* 2, 16111
56. Lau, J.A. and Lennon, J.T. (2012) Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proc. Natl. Acad. Sci. U. S. A.* 109, 14058–14062
57. Wieder, W.R. *et al.* (2013) Global soil carbon projections are improved by modelling microbial processes. *Nat. Clim. Chang.* 3, 909–912
58. Evans, S.E. *et al.* (2022) Microbes, memory and moisture: predicting microbial moisture responses and their impact on carbon cycling. *Funct. Ecol.* 36, 1430–1441
59. Zhou, J. *et al.* (2021) A comparison of linear conventional and nonlinear microbial models for simulating pulse dynamics of soil heterotrophic respiration in a semi-arid grassland. *J. Geophys. Res. Biogeosci.* 126, e2020JG006120
60. Allison, S.D. and Goulden, M.L. (2017) Consequences of drought tolerance traits for microbial decomposition in the DEMENT model. *Soil Biol. Biochem.* 107, 104–113