

# Drought legacies mediated by trait trade-offs in soil microbiomes

BIN WANG <sup>1,†</sup> AND STEVEN D. ALLISON<sup>1,2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697 USA

<sup>2</sup>Department of Earth System Science, University of California, Irvine, California 92697 USA

**Citation:** Wang, B., and S. D. Allison. 2021. Drought legacies mediated by trait trade-offs in soil microbiomes. *Ecosphere* 12(6):e03562. 10.1002/ecs2.3562

**Abstract.** Soil microbiomes play a key role in driving biogeochemical cycles of the Earth system. As drought frequency and intensity increase due to climate change, soil microbes and the processes they control will be impacted. Even after a drought ends, microbiomes and other systems take time to recover and may display a memory of previous climate conditions. Still, the mechanisms involved in these legacy effects remain unclear, making it difficult to predict climate and biogeochemical rates in the future. Here, we used a trait-based microbiome model (DEMENTpy) to implement trade-off-mediated mechanisms that may lead to drought legacy effects on litter decomposition. Trade-offs were assumed to follow the Y-A-S framework that defines three primary life-history strategies of microorganisms: high growth Yield, resource Acquisition, and Stress tolerance. We represented cellular trade-offs between osmolytes required for drought tolerance and investment in enzymes involved in litter decomposition. Simulations were run under varying levels of drought severity and dispersal. With high levels of dispersal, no legacy effects were predicted by DEMENTpy following drought. With limited dispersal, severe drought resulted in a persistent legacy of altered community-level traits and reduced litter decomposition. Moderate drought resulted in a transient legacy that disappeared after two years, consistent with recent empirical observations in Southern California ecosystems. These results imply that greater movement along the trade-off between enzyme investment and osmolyte production resulted in stronger legacy effects. More generally, factors that shift the position of a microbiome in YAS space may alter the legacy outcome following drought. Our trait-based modeling study motivates additional empirical measurements to quantify YAS traits and trade-offs that are needed to make accurate predictions of soil microbiome resilience and functioning. Also, our study illustrates an emerging approach for representing trait trade-offs in microbiomes and vegetation that dictate ecosystem responses to drought and other environmental perturbations.

**Key words:** decomposition; DEMENTpy; disturbance; drought; history; legacy; microbiome; resilience; trade-off; trait-based model.

**Received** 2 February 2021; accepted 12 February 2021; final version received 6 April 2021. Corresponding Editor: Debra P. C. Peters.

**Copyright:** © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** wbwenwu@gmail.com

## INTRODUCTION

Drought of increasing severity and frequency both regionally and worldwide is an important environmental change affecting the Earth system (e.g., Borsa et al. 2014, Berdugo et al. 2020). The soil microbiome is a key driver of element cycling (e.g., Falkowski et al. 2008), so microbial responses are integral for evaluating drought

impacts on ecosystem biogeochemistry. Still, these responses are omitted or implicitly treated in global assessments of drought–biosphere interactions (e.g., Green et al. 2019).

Over a half-century of research has uncovered myriad physicochemical, physiological, and ecological mechanisms underlying microbial functional responses to drought disturbance in soil environments (e.g., Birch 1958, Schimel et al.

2007, Manzoni et al. 2012). Moreover, multiple studies have suggested that drought may have lasting effects on the soil microbiome and its functioning, even after drought conditions have ended (e.g., Evans and Wallenstein 2012, Meisner et al. 2015, Hawkes et al. 2017, Martiny et al. 2017, Hinojosa et al. 2019). This phenomenon, here termed drought legacy, has also been observed in forests and other biomes (e.g., Cuddington 2011, Anderegg et al. 2015, Conradi et al. 2020). Still, the mechanistic basis for microbial drought legacies remains unclear. Such a lack of mechanistic information hinders the ability to predict drought impacts on ecosystem processes.

Legacies likely originate from microbiome changes that persist after a drought disturbance. Microbiomes are complex adaptive systems, with their functioning emerging from both individual variation and within-community interactions. Also, plant responses to drought may impact this functional emergence and contribute to legacy effects (e.g., Kaisermann et al. 2017). Past laboratory- and field-based studies explained soil microbial drought legacies by framing compositional differences in terms of microbial functional groups with different life-history strategies. Notably, Hawkes and Keitt (2015) proposed a mechanism driven by shifts in relative abundance of moisture generalists vs. specialists, where generalists are functionally more stable than specialists with variations in moisture. Along a rainfall gradient in Texas, USA, high variability in historical rainfall was thought to select for dominance by generalist taxa, resulting consistency in moisture responses across sites (Hawkes et al. 2017, Waring and Hawkes 2018). Similarly, Evans and Wallenstein (2014) argued that soils with relatively stable moisture history had more moisture-sensitive taxa and hence larger changes in biomass and composition following drought (Evans and Wallenstein 2012).

Functional groupings are based on physiological traits and can help simplify complex microbiomes but may obscure important physiological and ecological details. For instance, microbial cells can re-direct resource allocation from exoenzyme production to osmolytes that confer desiccation resistance (e.g., Schimel et al. 2007), an intracellular metabolic strategy that displays

large inter-cellular variability (e.g., Manzoni et al. 2012). Without representing these physiological processes, models may have difficulty predicting microbial community responses to drought disturbance and the consequences for functioning. Addressing this challenge could help reconcile studies that report drought legacies of varying magnitudes with differing time frames, including those that observed no legacy (e.g., Rousk et al. 2013, Fuchslueger et al. 2016). A similar lack of mechanistic understanding also applies to warming-induced legacies in microbiome functioning (e.g., Karhu et al. 2014). Linking individual-level physiological variation to community-level shifts could help fill this gap in knowledge of microbial functioning with environmental change.

Trait-based approaches for dealing with ecological complexity can bridge the gap between community dynamics and physiological variation that may underpin drought legacies in microbiomes. Such approaches have been established previously in plant communities (e.g., McGill et al. 2006), and more recently, Malik et al. (2020) proposed a trait-based framework that emphasizes trade-offs among three primary life-history strategies of microorganisms—Y-A-S (Yield-Acquisition-Stress). On the empirical side, a manipulative experiment in a grassland ecosystem in Southern California attributed a drought legacy in litter decomposition to changes in bacterial composition and associated carbohydrate degradation traits (Martiny et al. 2017). This study illustrates the potential to establish trait-based linkages between microbial physiology and community shifts underlying legacies.

Based on the Y-A-S framework, drought disturbance should cause cellular physiology and microbial composition to shift toward drought tolerance at the expense of other traits, such as investment in exoenzymes. Persistence of this functional shift could result in a drought legacy that affects organic matter decomposition. With this reasoning, factors that shift microbiomes along the trade-off between enzyme investment and stress tolerance could alter the magnitude and duration of drought legacies. For instance, the intensity of drought, which directly modulates intracellular metabolic allocation to enzymes versus osmolytes (e.g., Csonka 1989,

Schimel et al. 2007), may determine movement along the trade-off and hence affect the legacy magnitude. In addition, microbial dispersal (e.g., Fukami 2015, Vila et al. 2019) may alter drought legacies through effects on community composition and dynamics that regulate drought tolerance trade-offs (Hawkes et al. 2017).

Theory-driven, trait-based models are well positioned to complement laboratory- and field-based studies and explore the mechanisms underpinning soil microbiome drought legacies. Individual-based models in particular offer the ability to bridge scales from individual cells through communities to ecosystems by explicitly simulating intracellular metabolic processes, ecological dynamics of microbial communities, and emergent functioning (Allison 2012). Such an approach can overcome some of the limitations of aggregated models that treat microbes as a single biomass pool or a few discrete functional groups (see a review by Wieder et al. 2015). In addition, trait- and individual-based models are appropriate for testing the null hypothesis that representing legacies would have little impact on biogeochemical model predictions (Rousk et al. 2013).

The goal of our study was to test the consequences of resource-based trade-offs for drought legacies in soil microbiomes. Our approach applied a modeling framework for soil microbial systems—DEMENTpy—that represents emergent trade-offs among resource acquisition and drought tolerance traits at both the physiological level and the community level as proposed in the Y-A-S framework. This individual- and trait-based model represents physiological processes and microbial interactions in a spatially explicit context. Specifically, we asked the following questions: (1) How does drought intensity affect the magnitude and duration of drought legacy for the process of litter decomposition? (2) How does microbial dispersal affect the magnitude and duration of drought legacy? (3) What are the underlying changes in enzyme investment and drought tolerance traits? We tackled these questions by applying DEMENTpy to a grassland ecosystem in Southern California. Our study exemplifies how trait-based investigations into microbiome legacies can link resource-based trade-offs with element cycling in response to climate change.

## METHODS

### *Model description*

DEMENTpy (DEcomposition Model of ENzymatic Traits in Python; GitHub Repository: <https://github.com/bioatmosphere/DEMENTpy>) is a spatially explicit, trait- and individual-based model. Starting from continuous physiological traits, DEMENTpy bridges across soil microbiome scales from individual cells through communities to systems (see Appendix S1: Fig. S1 for model structure). Its mechanistic modeling framework is built upon its predecessor DEMENT (e.g., Allison 2012, Allison and Goulden 2017, Wang and Allison 2019). DEMENTpy initiates a microbial community composed by randomly drawing values from uniform distributions of microbial traits and assigning them to a large number of hypothetical taxa (see a list of traits in Appendix S1: Fig. S1B and more details in Appendix S1). Community dynamics are simulated by explicitly modeling demographic processes of cell metabolism and growth, mortality, and reproduction for each taxon population at a daily time step. Microbial taxa secrete exoenzymes (constitutive and inducible) that degrade different organic compounds at rates that depend on temperature and moisture. To address questions related to drought response, the current version of DEMENTpy represents explicit osmolyte production (constitutive and inducible). Drought tolerance of each taxon is determined by normalizing the inducible osmolyte rate of production to a value from 0 to 1. This formulation establishes a mechanistic connection between osmolyte production and drought tolerance (Schimel et al. 2007) in contrast to the previous model version which instead directly introduced a drought tolerance parameter and imposed a corresponding penalty on carbon use efficiency (Allison and Goulden 2017).

DEMENTpy tracks intracellular metabolism of assimilated monomer carbon derived from exoenzymatic degradation of substrates (Appendix S1: Fig. S1C; see Appendix S1 for substrate degradation and other demographic processes). After growth respiration, assimilated carbon is directed to enzyme production, osmolyte production, and associated maintenance respiration, which are treated as simultaneous processes without prescribing an order. The

carbon remaining after constitutive and inducible metabolite production accumulates toward biomass (denoted as yield). We assume that constitutive osmolyte production varies across taxa independently of water potential, reflecting microbial allocation to maintain water potential balance across the cell wall (e.g., Csonka 1989, Potts 1994). By contrast, inducible production of osmolytes occurs when water potential falls below a threshold. Mortality of microbial cells is simulated both deterministically by accounting for mass balance and stochastically based on death probability dependent on drought tolerance and water potential. More details on model structure, processes, formulae, and parameters are included in Appendix S1.

### *Modeling experiments*

We applied DEMENTpy to a grassland ecosystem at Loma Ridge, Southern California (Allison et al. 2013), and parameterized the model with 100 different hypothetical bacterial taxa on a 100 by 100 spatial grid with decomposing grass litter containing ten different substrates (see parameter values in Appendix S1: Table S1 and substrates in Appendix S1: Table S2). DEMENTpy was forced with daily weather data from the year 2011, which is designated as the ambient scenario (Appendix S1: Fig. S2A). In addition to this ambient scenario, we conducted simulations to examine drought disturbance response and recovery in three phases (Appendix S1: Fig. S2). Two drought scenarios, denoted moderate and severe, were generated by reducing the water potential during the dry season by a factor of four and ten, respectively. These scenarios were created to test the sensitivity of microbial community responses and are not intended to mimic specific field conditions, although they do approximate seasonal variation in moisture availability. After a community establishment phase and a successive drought period, ambient conditions were re-imposed to test for legacy effects on microbial communities and substrate decomposition. Simulations in default mode did not allow for microbial dispersal; once taxa disappeared from a default simulation, they could not return. We also ran simulations in dispersal mode to test how dispersal affects drought response and legacy effects. In contrast to the default mode, dispersal mode allows extinct taxa

to recolonize at the start of each model year. This mode accounts for the possibility that bacterial populations survive in local refugia or nearby wetter areas and then disperse on to fresh litter. Note that our simulations ran at the scale of individual litter particles; substrate input quantity and quality were held constant across drought scenarios and do not incorporate ecosystem-scale feedbacks to plant productivity.

### *Simulation protocol*

After assigning hypothetical taxa to random locations on a spatial grid with homogeneously distributed substrates, each simulation was run for 10 yr at a daily time step (spin-up: 3 yr; drought disturbance: 3 yr; recovery: 4 yr; Appendix S1: Fig. S2). Substrates, monomers, and enzymes were reinitialized uniformly on the spatial grid at the start of each new year at the same concentrations as the first year. At the start of each year, the microbial community on the spatial grid was randomly reinitialized with the same total microbial biomass. Two reinitialization methods were applied to differentiate the default and dispersal modes: For the default mode, microbial community composition was determined according to the fractional biomass of each taxon on the last day of the previous year (Appendix S1: Fig. S2C); in dispersal mode, the taxon frequencies were proportional to the cumulative biomass of each taxon over the entire previous year (Appendix S1: Fig. S2D). Simulations were repeated 40 times for each scenario under the two modes (default and dispersal) with 40 different random number generation seeds ( $5 \times 40 = 200$  runs in total). This sample size was determined by a convergence analysis of DEMENTpy's stochastic nature (Appendix S1: Fig. S3). We do not report simulations of moderate drought in dispersal mode because they were not relevant after analyzing the severe drought scenarios.

### *Data analysis*

Unless indicated otherwise, all analyses were conducted on the ensemble of 40 runs for each of the five scenarios. Datasets extracted from these simulations included taxon traits (enzyme investment and drought tolerance); a time series of taxon-specific allocation to enzymes (inducible plus constitutive), osmolytes (inducible plus



constitutive), carbon yield, and biomass; and a time series of compound-specific and total substrate concentrations. Taxon-specific allocations to enzymes, osmolytes, and yield were aggregated to derive community-level allocation. Community-level traits of enzyme investment and drought tolerance were calculated from biomass-weighted taxonomic traits (see Appendix S1 for calculation method). Because the system stabilized within 3 yr (Appendix S1: Fig. S2), results up to year 9 (3rd year of recovery from drought disturbance) are presented. In addition, 95% confidence intervals are shown for most variables except for microbial community composition and community carbon allocation, for which only one out of the 40 simulations is shown.

## RESULTS

### *Microbial community dynamics under the ambient drought scenario*

The system became relatively stable after 2 yr, with seasonal dynamics in the microbial community repeating across years (Appendix S1: Fig. S2). Seasonal dynamics of community composition and biomass reflected a joint control by climate and substrates. Starting in the wet season that was replete with substrates, the microbial community established and grew in biomass. As substrates were degraded and depleted, microbial cells began to starve and die. Declining water potentials after the start of the dry season induced more death. Together, these two processes resulted in declining microbial biomass from a peak around  $20 \text{ mg}\cdot\text{C}\cdot\text{cm}^{-3}$  (Fig. 1A) and drove the composition toward taxa with higher drought tolerance and lower enzyme investment (Appendix S1: Fig. S4A). Hence, community-level enzyme investment decreased (Fig. 2A), and drought tolerance increased across the dry season (Fig. 2B). Similar seasonal and inter-annual dynamics were observed for the community with dispersal but with higher biomass (peaking around  $30 \text{ mg}\cdot\text{C}\cdot\text{cm}^{-3}$ ) and taxonomic diversity (Figs. 1D and 2C,D; Appendix S1: Fig. S4B).

### *Responses to drought disturbance of varying severity*

Total microbial biomass declined significantly under drought, with the greatest declines of

nearly 50% under the severe scenario, resulting in a peak biomass less than  $10 \text{ mg}\cdot\text{C}\cdot\text{cm}^{-3}$  (Fig. 1B,C). Severe drought also more drastically altered microbial community composition compared to moderate drought. Community taxonomic richness and functional capacity shifted dramatically after 2 yr of drought perturbation. Compared to the ambient scenario, drought tolerance increased significantly across seasons from 0.62 up to 0.92 under the moderate scenario and up to 0.97 under the severe scenario (Fig. 2A,B). However, the community-averaged enzyme investment only declined significantly in the severe scenario across the dry season and did not change substantially in the moderate scenario except late in the dry season (Fig. 2A,B). These trait changes reflected differences in community-level carbon allocation between enzymes and osmolytes and thus yield (Fig. 3A; Appendix S1: Fig. S5A). Under the moderate drought scenario, the percentage of assimilated carbon allocated to osmolytes ranged between 65% and 85%, compared to the ambient range of 50–70%, whereas enzyme allocation was consistently lower (10% on average) compared to the ambient scenario (20% on average). However, the resulting yield was similar, ranging between 0 and 30%, although some days in the ambient scenario were higher (reaching at most 40%) early in the dry season. Under the severe scenario, the allocation to osmolytes was even higher and allocation to enzymes even lower, and the community yield approached zero more often. These differences in community resource allocation resulted in reduced degradation of substrates over the grid, with the two drought scenarios showing different rates of decomposition (average of 57.4% and 85.7%, respectively; Fig. 4A,B).

After ambient conditions were re-imposed for 2 yr (i.e., by year 9), new stable microbial communities assembled (Fig. 1B,C and Appendix S1: Fig. S2C). Compared to the ambient scenario, communities that re-assembled following drought had different levels of drought tolerance and enzyme investment. Drought tolerance remained significantly higher under both moderate drought (0.90) and severe drought (0.96) scenarios, even after drought disturbance ended (Fig. 2A). In contrast, enzyme investment under the moderate scenario became similar to the

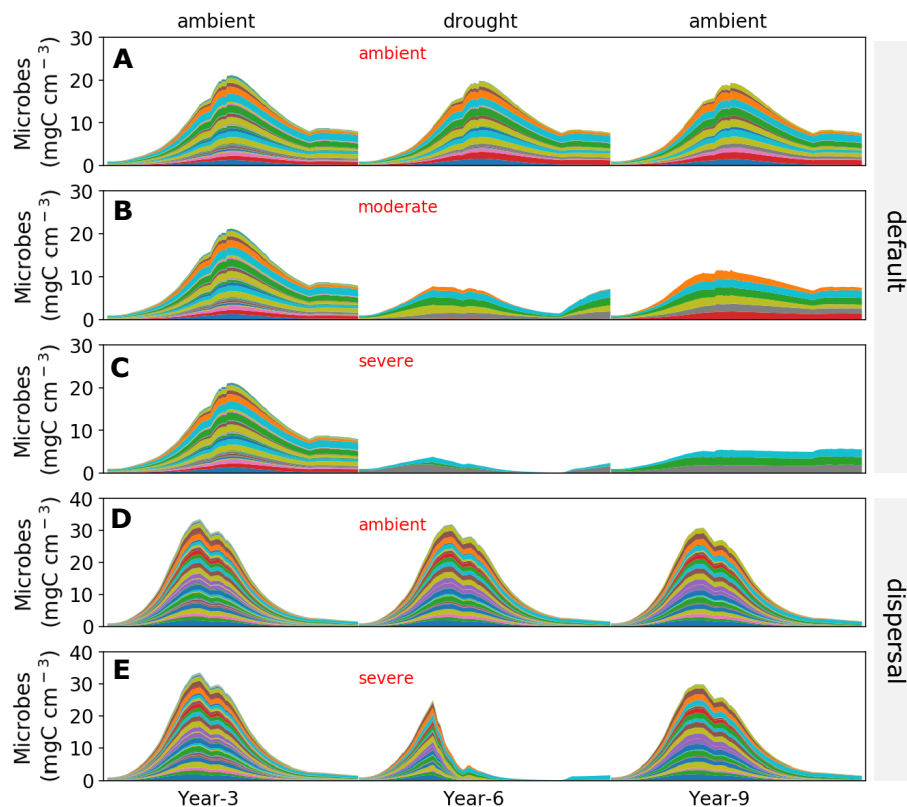


Fig. 1. Microbial community dynamics in ambient and drought simulations with and without dispersal. (A–C) Dynamics without dispersal under ambient, moderate, and severe drought scenarios, respectively. (D, E) Dynamics with dispersal under ambient and severe drought scenarios, respectively. Colored bands represent biomass of hypothetical taxa ( $\text{mgC}\cdot\text{cm}^{-3}$ ) averaged over the  $100 \times 100$  spatial grid. Data shown are only for years 3, 6 (the 3rd year under drought), and 9 (the 3rd year after drought). See Appendix S1: Fig. S2 for the full 10-year dynamics under the ambient scenario of both default and dispersal mode.

ambient community, whereas enzyme investment following severe drought remained significantly different (Fig. 2B). During the dry season by year 9, only the community that had experienced severe drought showed a clearly lower allocation to enzymes compared to the ambient community (Fig. 3B; Appendix S1: Fig. S5B). The resilience of enzyme investment in the moderate drought community meant that decomposition rates converged on ambient levels by year 9 (Fig. 4A). In contrast, substrate mass loss remained lower by 47.7% on average (Fig. 4A) in year 9 of the severe drought scenario, although the magnitude of decline was dampened compared to the antecedent drought period. Prior to year 9, the reductions in mass loss associated with transient microbial communities (year 7)

were significant for both drought scenarios (average declines of 18.0% and 55.5%, respectively).

#### *Responses to severe drought disturbance with dispersal*

With dispersal of taxa from the previous year's microbial pool, the direct responses to severe drought were similar to the default mode, though with differing magnitudes and seasonal patterns. Compared to ambient conditions, the microbial community showed both lower total biomass and reduced taxonomic richness with drought disturbance, though the values were higher with dispersal than in the default mode (Fig. 1E). Community-average enzyme investment and drought tolerance differed between severe drought and ambient scenarios but with a

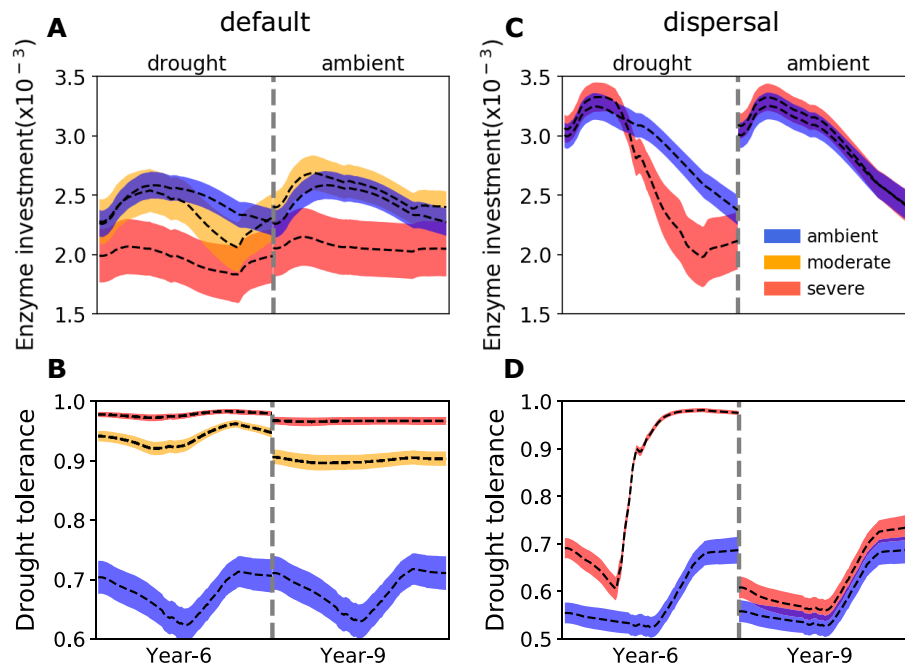


Fig. 2. Seasonal dynamics of community-level enzyme investment and drought tolerance of microbial communities under different drought scenarios. (A, B) Enzyme investment and drought tolerance during year 6 (3rd year under drought) and year 9 (3rd year after drought) under three drought scenarios (ambient, moderate, and severe) without dispersal, respectively. (C, D) The same for communities with dispersal under two drought scenarios (ambient and severe). Dashed lines and color bands are means and 95% confidence intervals ( $n = 40$ ).

different seasonal pattern predicted for dispersal compared to default mode. With the onset of the dry season, enzyme investment declined sharply from a peak of 0.0033 down to 0.0020, and drought tolerance increased sharply from 0.60 to 0.97, with differences from the ambient scenario increasing over time (Fig. 2C,D). These changes reflected the community allocating more assimilated carbon to produce osmolytes and less to enzymes, which resulted in zero yield when drought was most severe during the dry season (Fig. 3C; Appendix S1: Fig. S5C). All of these changes resulted in significantly lower substrate decomposition (year 6; an average decline of 56.3%; Fig. 4A).

When ambient conditions were re-imposed, recovery from drought was rapid with dispersal compared to the default mode. Two years after drought ended, the communities became similar in the drought and ambient scenarios (Fig. 1E), a stark contrast to the default mode (Fig. 1C). This compositional similarity coincided with similar community enzyme investment (Fig. 2C) and

drought tolerance (Fig. 2D), which resulted in the same community-level allocation of assimilated carbon among enzymes (30–60%), osmolytes (40–60%), and thus yield (0–30%; Fig. 3D; Appendix S1: Fig. S5D). These communities ultimately had almost exactly the same composition and substrate decomposition rates (Fig. 4B). In fact, in contrast to the default mode, the transient community did not even show significant differences in the 1st year following drought (year 7; Fig. 4B). Based on this clear lack of legacy effects following severe drought, we did not find it relevant to run simulations of the moderate scenario with dispersal.

## DISCUSSION

By representing physiological mechanisms in a trait-based model, we tested the relationships between drought legacy and drought severity and dispersal in simulated litter microbiomes. Drought legacy effects on litter decomposition ranged from persistent through transient to

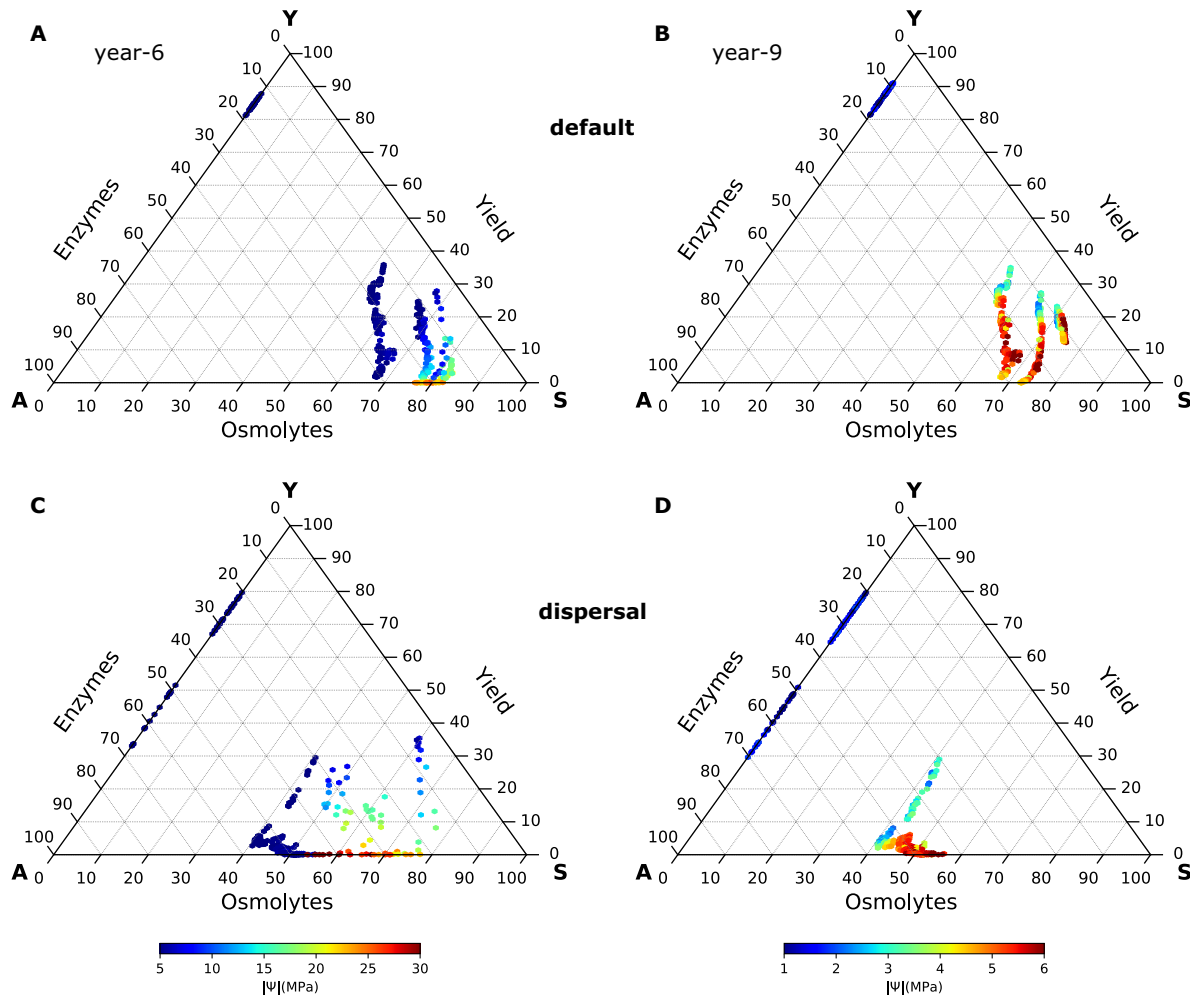


Fig. 3. Ternary plots of community-level allocation of assimilated carbon among enzymes, osmolytes, and growth yield over time under different dispersal scenarios. (A, B) Enzyme–Osmolyte–Yield trade-off of communities during year 6 (3rd year under drought) and year 9 (3rd year after drought), respectively, of the default mode (without dispersal). (C, D) The same for the dispersal mode. Yield, enzymes, and osmolytes correspond to Y (Yield), A (resource Acquisition), and S (Stress) strategies labeled, respectively, at the triangle vertices (Malik et al. 2020). See Appendix S1: Fig. S5 for a version with points differentiated by drought scenario instead of water potential.

nonexistent and depended on drought severity and microbial dispersal (Fig. 4). This variation in legacy magnitude and duration emerged from a clear mechanistic basis—trade-offs between enzyme production and drought tolerance, in line with the Y-A-S strategy framework. These results are relevant for understanding the resilience of microbial systems—weaker legacies correspond to higher resilience of soil microbiome functioning in response to historical drought.

Our analysis of how resource-based trade-offs drive legacy mechanisms and microbial system resilience will help more accurately quantify carbon cycle feedbacks to drought in the Earth system.

#### *Transient legacy under moderate drought*

The severity of drought disturbance influences legacy magnitude and duration by determining the extent to which a microbial community can



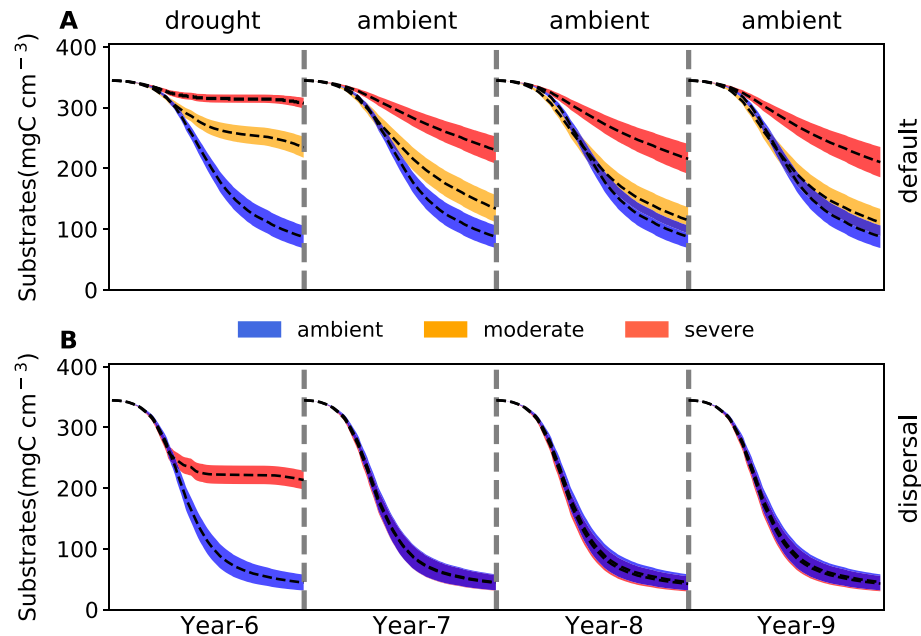


Fig. 4. Changes in substrate concentrations as litter decomposes during and after drought perturbation. (A) Total substrates on the spatial grid during years 6 (last year of drought) to 9 under three different scenarios (ambient, moderate, and severe drought) without dispersal. (B) The same for simulations with dispersal under ambient and severe drought scenarios. Dashed lines and colored bands are means and 95% confidence intervals ( $n = 40$ ), respectively. See Appendix S1: Fig. S6 for an example illustration of the underlying substrate-specific changes.

adapt (Fig. 4A). Our drought disturbance lasted long enough for communities to reach a stable state. However, our simulations focused on exploring underlying mechanisms and only represent a subset of actual drought disturbances in terms of frequency, intensity, and duration. At the drought intensities we analyzed, legacies ranged from transient to persistent. Weaker disturbances might result in no legacy at all.

Drought of lower severity had a transient negative effect on decomposition post-disturbance, but eventually the legacy effect disappeared (Fig. 4A), a pattern that we dub transient legacy. This transient legacy pattern is consistent with results from an experiment in which microbial communities were transplanted across a rainfall manipulation at Loma Ridge, CA. Here, the drought legacy effect on litter decomposition disappeared after one year (Martiny et al. 2017; ). It is noteworthy that our model-predicted recovery from drought was driven by a community with the same functioning but different composition and biomass. However, with a total biomass

difference varying from 50% to almost zero (Fig. 1B), microbial biomass is probably not a major driver of the legacy pattern, consistent with findings from Loma Ridge (Martiny et al. 2017) and another reciprocal transplant study across a climate gradient in Southern California (Glassman et al. 2018). Rather, the transience of the legacy mainly resulted from convergence in community enzyme investment despite lingering differences in community composition and drought tolerance (Fig. 2A,B). Such a compositional but not functional change in an ecosystem after disturbance—which has been observed before (e.g., Ives and Carpenter 2007, Fukami 2015)—supports the notion of functional similarity in the soil microbiome (Allison and Martiny 2008, Louca et al. 2018). This transient legacy mechanism may allow for resilience of microbial and other systems following moderate perturbation.

#### *Persistent legacy under severe drought*

A strong drought disturbance can push a community to reach an even higher drought

tolerance by sacrificing more investment in enzyme production (including a loss of relatively more drought-intolerant taxa), thereby forming a community not only compositionally but also functionally different (Fig. 2A,B). These conditions can lead to a persistent legacy (Fig. 4B). A similar long-term legacy in soil heterotrophic respiration has also been observed in microcosm and field transplant experiments (Hawkes et al. 2017). This persistent legacy is consistent with the idea of alternative stable states with different functioning in ecological systems (Scheffer et al. 2001). Disturbance-driven alternative stable states have been reported across an array of systems; for example, in a bacterial community experiencing antibiotic perturbation (Cairns et al. 2020), in gut microbiota experiencing transient osmotic perturbation (Tropini et al. 2018), and in tropical (e.g., Staver et al. 2011) and boreal forests (Herzschuh 2020), as well as in small pond systems (Chase 2003). Conceptually, a persistent legacy means the loss of system resilience with severe disturbance (Scheffer et al. 2001). However, this loss of resilience may lead to a new microbial community state that is more resistant to future disturbances.

#### *Disappearance of legacy under severe drought with dispersal*

Importantly, dispersal can reduce legacies in organic matter decomposition (Fig. 4B). By reintroducing taxa from the previous year's microbial pool, we found that even with severe drought, dispersal can rescue taxa from extinction and completely mitigate the effect of environmental selection on the microbial community (Fig. 1E). By restoring drought tolerance and enzyme investment traits (Figs. 2C,D, 3D), dispersal can overwhelm the drought legacy in organic matter decomposition (Fig. 4B). This result suggests that dispersal can increase microbial systems' resilience to drought disturbance (Allison and Martiny 2008) in stark contrast to the persistent legacy induced by severe drought disturbance without dispersal (Fig. 4A). We note that there are many dispersal factors that influence community dynamics but were not represented in our model. For instance, dispersal timing (e.g., priority effects) and magnitude both matter for community response to perturbation (e.g., Fukami 2015, Vila et al. 2019). Furthermore,

even an unsuccessful invasion by a single species that interacts only briefly with the resident community can induce an alternative stable state with distinct functioning (Amor et al. 2020). Variation in dispersal processes could therefore drive compositional and functional changes to varying extents (e.g., Fukami 2015), resulting in varying magnitudes of decomposition legacy. For example, in a field transplant experiment with passive dispersal, Hawkes et al. (2017) did not observe mitigation of a historical rainfall legacy in soil respiration. Given this result, we recognize that our exploration of dispersal mechanisms and intensities is incomplete; our study was mainly aimed at drought tolerance trade-offs and not meant to be exhaustive.

#### *A mechanistic conceptual framework*

We propose to organize legacy scenarios based on the Y-A-S framework, as illustrated in Fig. 5. Drought legacies are ultimately determined by the trajectory of a community in a conceptual space defined by enzyme investment, drought tolerance, and yield. Factors that affect cellular metabolic and community-level trade-offs between enzyme and osmolyte production may influence the magnitude and/or duration of a drought legacy. For instance, when drought selects for a community with higher drought tolerance but ultimately similar enzyme investment (e.g., moderate drought scenario; Fig. 4A), a transient legacy occurs. However, when more severe drought selects for higher drought tolerance at the expense of enzyme investment (Fig. 4A), a persistent legacy with impaired substrate decomposition can occur. In contrast, when the community does not shift in strategy space (e.g., with dispersal present; Fig. 4B), even transient legacies may not occur.

Trade-offs in microbiomes and the biosphere more generally are often complex (e.g., Berezovsky and Shakhnovich 2005, Ferenci 2016). Some trade-offs may be context-specific, and even positive relationships between costly traits may be observed under certain conditions (Moreno-Gómez et al. 2020, Tikhonov et al. 2020). These principles may apply to the relationship between enzyme investment and drought tolerance which may depend on drought intensity, dispersal, metabolic plasticity, and evolutionary history. For instance, a fourth legacy

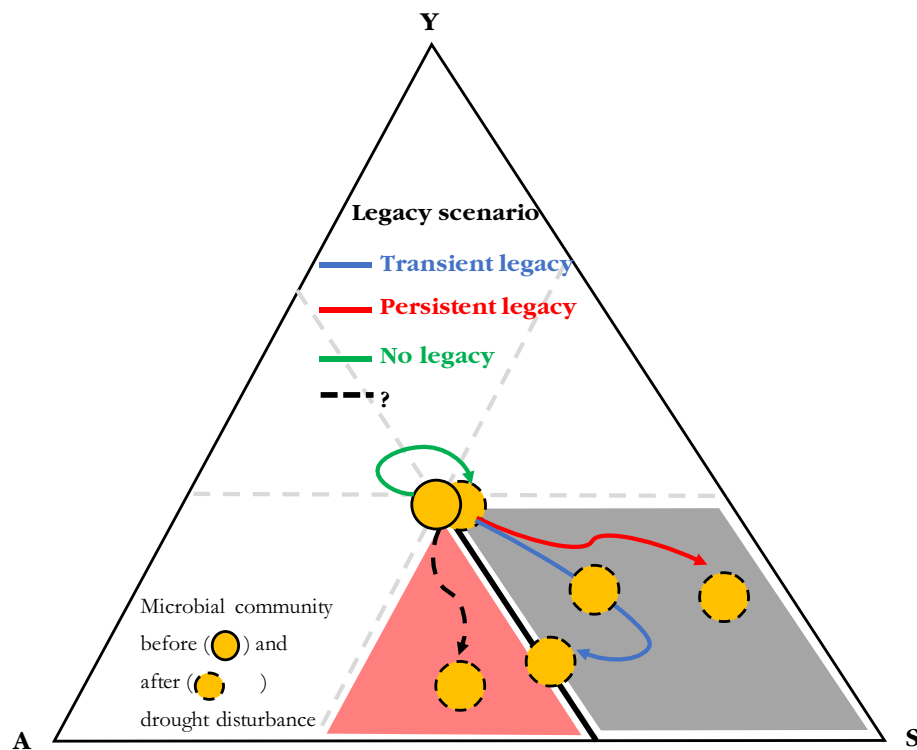


Fig. 5. Overlay of drought legacy scenarios in YAS-constrained space. Drought legacy is contingent on the trajectory of a microbial community in the YAS space after drought disturbance. There will be no legacy if a community does not move at all (green trajectory) or if it moves along the thick black line. If an altered community remains in the gray region, a persistent legacy will occur. However, if the community eventually leaves the gray region and returns to the thick black line, a transient legacy can occur. We also propose that a community could move into the red region with both increased drought tolerance and enzyme investment (but at the expense of growth yield). Note: The positioning of the starting community in the center of the space (filled yellow circle) is for illustration purposes only; real communities may start anywhere in the YAS space.

scenario may exist with both increased osmolyte and enzyme investment that trade off against lower yield (the red region in Fig. 5). Going forward, our study could be extended by broadening the range of drought and dispersal scenarios and modifying the trade-off assumptions in DEMENTpy to gain a more complete picture of the mechanisms underlying drought legacies.

## CONCLUSIONS

Our study revealed how hypothesized trade-off-mediated mechanisms of community-level trait change can lead to drought legacies in soil microbiomes. Confirming these mechanisms with empirical data could increase confidence in predictions of litter and soil organic matter

decomposition in response to drought and other environmental changes. Legacies of impaired decomposition, even when transient, may enhance carbon sequestration in soil systems, but may also allow fuels to accumulate for the next fire season, thereby increasing fire risk (e.g., Pellegrini et al. 2018). Additionally, impaired decomposition can inhibit nutrient turnover and availability, thereby influencing plant productivity and interactions with microbes (e.g., Kaisermann et al. 2017). These and other cascading changes arising from microbiome legacies could initiate more complex ecosystem feedbacks. Evaluating these implications requires a holistic approach that integrates microbial and vegetation processes across ecosystem to Earth system scales. Such an approach is crucial for predicting

biogeochemical rates in the context of projected global climate change that may induce legacy effects. Trait-based models of both microbial and vegetation dynamics are proving essential in achieving this predictive understanding.

## ACKNOWLEDGMENTS

We thank Dr. Christine Hawkes at North Carolina State University and Dr. Sarah Evans at Michigan State University for friendly but critical reading of and suggestions to the manuscript. The two anonymous reviewers are acknowledged for constructive comments. This research was funded by the NSF Ecosystem Studies Program (DEB-2016482) and the US Department of Energy Office of Science, BER, under award numbers DE-SC0016410 and DE-SC0020382.

## LITERATURE CITED

- Allison, S. D. 2012. A trait-based approach for modelling microbial litter decomposition. *Ecology Letters* 15:1058–1070.
- Allison, S. D., and M. L. Goulden. 2017. Consequences of drought tolerance traits for microbial decomposition in the DEMENT model. *Soil Biology and Biochemistry* 107:104–113.
- Allison, S. D., Y. Lu, C. Weihe, M. L. Goulden, A. C. Martiny, K. K. Treseder, and J. B. Martiny. 2013. Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology* 94:714–725.
- Allison, S. D., and J. B. Martiny. 2008. Resistance, resilience, and redundancy in microbial communities. *Proceedings of the National Academy of Sciences of the United States of America* 105:11512–11519.
- Amor, D. R., C. Ratzke, and J. Gore. 2020. Transient invaders can induce shifts between alternative stable states of microbial communities. *Science Advances* 6:eaay8676.
- Anderegg, W. R. L., et al. 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349:528–532.
- Berdugo, M., et al. 2020. Global ecosystem thresholds driven by aridity. *Science* 367:787–790.
- Berezovsky, I. N., and E. I. Shakhnovich. 2005. Physics and evolution of thermophilic adaptation. *Proceedings of the National Academy of Sciences of the United States of America* 102:12742–12747.
- Birch, H. F. 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil* 10:9–31.
- Borsa, A. A., D. C. Agnew, and D. R. Cayan. 2014. Ongoing drought-induced uplift in the western United States. *Science* 345:1587–1590.
- Cairns, J., R. Jokela, L. Becks, V. Mustonen, and T. Hiltunen. 2020. Repeatable ecological dynamics govern the response of experimental communities to antibiotic pulse perturbation. *Nature Ecology and Evolution* 4:1385–1394.
- Chase, J. M. 2003. Community assembly: when should history matter? *Oecologia* 136:489–498.
- Conradi, T., K. Van Meerbeek, A. Ordóñez, and J. C. Svenning. 2020. Biogeographic historical legacies in the net primary productivity of Northern Hemisphere forests. *Ecology Letters* 23:800–810.
- Csonka, L. N. 1989. Physiological and genetic responses of bacteria to osmotic stress. *Microbiological Reviews* 53:121–147.
- Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. *Biological Theory* 6:203–210.
- Evans, S. E., and M. D. Wallenstein. 2012. Soil microbial community response to drying and rewetting stress: Does historical precipitation regime matter? *Biogeochemistry* 109:101–116.
- Evans, S. E., and M. D. Wallenstein. 2014. Climate change alters ecological strategies of soil bacteria. *Ecology Letters* 17:155–164.
- Falkowski, P. G., T. Fenchel, and E. F. Delong. 2008. The microbial engines that drive Earth's biogeochemical cycles. *Science* 320:1034–1039.
- Ferenci, T. 2016. Trade-off mechanisms shaping the diversity of bacteria. *Trends in Microbiology* 24:209–223.
- Fuchslueger, L., M. Bahn, R. Hasibeder, S. Kienzl, K. Fritz, M. Schmitt, M. Watzka, and A. Richter. 2016. Drought history affects grassland plant and microbial carbon turnover during and after a subsequent drought event. *Journal of Ecology* 104:1453–1465.
- Fukami, T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1–23.
- Glassman, S. I., C. Weihe, J. Li, M. B. N. Albright, C. I. Looby, A. C. Martiny, K. K. Treseder, S. D. Allison, and J. B. H. Martiny. 2018. Decomposition responses to climate depend on microbial community composition. *Proceedings of the National Academy of Sciences of the United States of America* 115:11994–11999.
- Green, J. K., S. I. Seneviratne, A. M. Berg, K. L. Findell, S. Hagemann, D. M. Lawrence, and P. Gentile. 2019. Large influence of soil moisture on long-term terrestrial carbon uptake. *Nature* 565:476–479.
- Hawkes, C. V., and T. H. Keitt. 2015. Resilience vs. historical contingency in microbial responses to environmental change. *Ecology Letters* 18:612–625.
- Hawkes, C. V., B. G. Waring, J. D. Rocca, and S. N. Kivlin. 2017. Historical climate controls soil respiration

- responses to current soil moisture. *Proceedings of the National Academy of Sciences of the United States of America* 114:6322–6327.
- Herzschuh, U. 2020. Legacy of the Last Glacial on the present-day distribution of deciduous versus evergreen boreal forests. *Global Ecology and Biogeography* 29:198–206.
- Hinojosa, M. B., V. A. Laudicina, A. Parra, E. Albert-Belda, and J. M. Moreno. 2019. Drought and its legacy modulate the post-fire recovery of soil functionality and microbial community structure in a Mediterranean shrubland. *Global Change Biology* 25:1409–1427.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58–62.
- Kaisermann, A., F. T. de Vries, R. I. Griffiths, and R. D. Bardgett. 2017. Legacy effects of drought on plant–soil feedbacks and plant–plant interactions. *New Phytologist* 215:1413–1424.
- Karhu, K., et al. 2014. Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature* 513:81–84.
- Louca, S., et al. 2018. Function and functional redundancy in microbial systems. *Nature Ecology Evolution* 2:936–943.
- Malik, A. A., J. B. H. Martiny, E. L. Brodie, A. C. Martiny, K. K. Treseder, and S. D. Allison. 2020. Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. *ISME Journal* 14:1–9.
- Manzoni, S., J. P. Schimel, and A. Porporato. 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. *Ecology* 93:930–938.
- Martiny, J. B. H., A. C. Martiny, C. Weihe, Y. Lu, R. Berlemont, E. L. Brodie, M. L. Goulden, K. K. Treseder, and S. D. Allison. 2017. Microbial legacies alter decomposition in response to simulated global change. *ISME Journal* 11:490–499.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:178–185.
- Meisner, A., J. Rousk, and E. Bååth. 2015. Prolonged drought changes the bacterial growth response to rewetting. *Soil Biology and Biochemistry* 88:314–322.
- Moreno-Gómez, S., D. J. Kiviet, C. Vulin, S. Schlegel, K. Schlegel, G. S. van Doorn, and M. Ackermann. 2020. Wide lag time distributions break a trade-off between reproduction and survival in bacteria. *Proceedings of the National Academy of Sciences of the United States of America* 117:18729–18736.
- Pellegrini, A. F. A., et al. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553:194–198.
- Potts, M. 1994. Desiccation tolerance of prokaryotes. *Microbiological Reviews* 58:755–805.
- Rousk, J., A. R. Smith, and D. L. Jones. 2013. Investigating the long-term legacy of drought and warming on the soil microbial community across five European shrubland ecosystems. *Global Change Biology* 19:3872–3884.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Schimel, J., T. C. Balser, and M. Wallenstein. 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88:1386–1394.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334:230–232.
- Tikhonov, M., S. Kachru, and D. S. Fisher. 2020. A model for the interplay between plastic tradeoffs and evolution in changing environments. *Proceedings of the National Academy of Sciences of the United States of America* 117:8934–8940.
- Tropini, C., et al. 2018. Transient osmotic perturbation causes long-term alteration to the gut microbiota. *Cell* 173:1742–1754.
- Vila, J. C., M. L. Jones, M. Patel, T. Bell, and J. Rosindell. 2019. Uncovering the rules of microbial community invasions. *Nature Ecology & Evolution* 3:1162–1171.
- Wang, B., and S. D. Allison. 2019. Emergent properties of organic matter decomposition by soil enzymes. *Soil Biology and Biochemistry* 136:107522.
- Waring, B., and C. V. Hawkes. 2018. Ecological mechanisms underlying soil bacterial responses to rainfall along a steep natural precipitation gradient. *FEMS Microbiology Ecology* 94(fiy001).
- Wieder, W. R., et al. 2015. Explicitly representing soil microbial processes in Earth system models. *Global Biogeochemical Cycles* 29:1782–1800.

## DATA AVAILABILITY

All data and code underlying the analyses and illustrations in this manuscript (Python-based step-by-step analysis presented in Jupyter Notebook) are accessible at: <https://github.com/bioatmosphere/microbiome->



drought-legacy. The version of DEMENTpy code used in this study is available at: <https://github.com/bioatmosphere/DEMENTpy/releases/tag/v1.0>.

### SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3562/full>