Viewpoints

The consequences of climate change for dryland biogeochemistry

Summary

Drylands, which cover >40% of Earth's terrestrial surface, are dominant drivers of global biogeochemical cycling and home to more than one third of the global human population. Climate projections predict warming, drought frequency and severity, and evaporative demand will increase in drylands at faster rates than global means. As a consequence of extreme temperatures and high biological dependency on limited water availability, drylands are predicted to be exceptionally sensitive to climate change and, indeed, significant climate impacts are already being observed. However, our understanding and ability to forecast climate change effects on dryland biogeochemistry and ecosystem functions lag behind many mesic systems. To improve our capacity to forecast ecosystem change, we propose focusing on the controls and consequences of two key characteristics affecting dryland biogeochemistry: (1) high spatial and temporal heterogeneity in environmental conditions and (2) generalized resource scarcity. In addition to climate change, drylands are experiencing accelerating land-use change. Building our understanding of dryland biogeochemistry in both intact and disturbed systems will better equip us to address the interacting effects of climate change and landscape degradation. Responding to these challenges will require a diverse, globally distributed and interdisciplinary community of dryland experts united towards better understanding these vast and important ecosystems.

Drylands make up > 40% of the planet's land surface and support *c.* 35% of the global human population, many of whose livelihoods rely on provisioning ecosystem services, such as food and fiber production (EMG, 2011; Prăvălie, 2016). Drylands also are increasingly recognized as dominant drivers of global biogeochemical cycling, including the long-term trend and interannual variability of both the terrestrial carbon (C) sink and atmospheric CO_2 concentrations (Poulter *et al.*, 2014; Ahlström *et al.*, 2015). In light of the local and global importance of drylands, observations suggesting that the structure and function of dryland ecosystems are highly sensitive to anthropogenic drivers of change are of great concern (Breshears *et al.*, 2005; Allen *et al.*, 2010; Reed *et al.*, 2012). Moreover, climate projections predict that warming, drought frequency and severity, and evaporative demand will

increase in drylands at faster rates than global means (Huang *et al.*, 2017; Scholes, 2020).

Despite their critical importance and sensitivity to change, our understanding and ability to predict climate change effects on dryland biogeochemistry and ecosystem functions lags severely behind mesic ecosystems (Schimel, 2010; Ferrenberg *et al.*, 2017; Hartley *et al.*, 2017; Renwick *et al.*, 2018). For example, hyper-arid and arid ecosystems account for *c.* 20% of the global land area, but < 1% of soil respiration observations (EMG, 2011; Warner *et al.*, 2019). Additionally, although drylands are key players in the global terrestrial C sink, the representation of dryland C cycling patterns in dynamic global vegetation models remains notably poor (MacBean *et al.*, 2021). These knowledge gaps may stem in part from a common public misconception that drylands are unproductive or even 'useless ecosystems' (Stafford Smith, 2008; Hoover *et al.*, 2020), an idea widely perpetuated in film, literature and popular culture (Beck, 2001; Tynan, 2020) and which has had implications for science, and the management and governance of dryland ecosystems (Mortimore *et al.*, 2009; Hunold & Leitner, 2011; Davis, 2016). As the need for increased research attention on drylands becomes clearer and more urgent, closing these long-neglected knowledge gaps has become a top priority for scientists and decision makers alike (Cowie *et al.*, 2011; Shukla *et al.*, 2019).

Here, we discuss two key challenges faced by scientists for evaluating dryland biogeochemical responses to climate change and for improving our capacity to predict ecosystem changes, which include (1) high levels of spatial and temporal heterogeneity in environmental conditions and (2) generalized resource scarcity. We also highlight (3) the implications of biogeochemical perspectives for developing effective dryland restoration and adaptation strategies and (4) the foundational importance of swift, collaborative action for successfully addressing dryland land-use change and degradation issues across the globe.

1. High spatial and temporal heterogeneity within and across dryland ecosystems make it challenging to predict biogeochemical responses to climate change. The expansiveness of drylands around the world and the patch-mosaic nature of dryland vegetation produce high heterogeneity in biogeochemical cycling across multiple spatial scales. As Earth's largest terrestrial biome, drylands are distributed across all continents and encompass enormous variability in soil-forming factors (i.e. parent material, topography, soil age, climate and organisms), which drive fundamental differences in C and nutrient cycling dynamics from local to continental scales (Fig. 1). The effects of dryland state factor variability are diverse, complex and far-reaching. Recent studies show, for example, that climate, local-scale topography and parent material can interact to strongly mediate soil respiration responses to rainfall pulses (Throop *et al.*, 2020) and that even seemingly subtle differences in soil texture can be a dominant driver of dryland
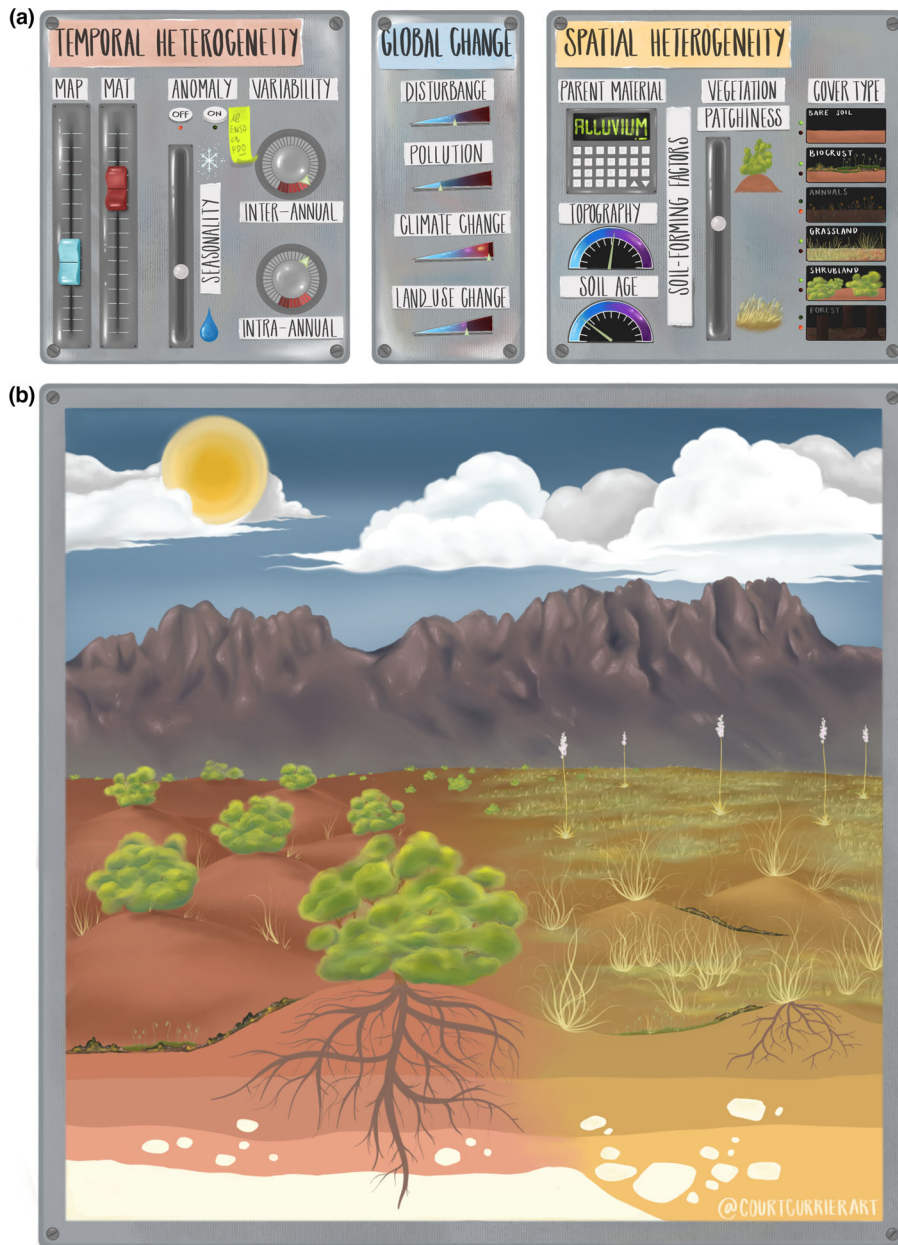
Fig. 1 Illustration of (a) the interacting abiotic and biotic factors that drive high spatial and temporal heterogeneity and multiple resource scarcity across dryland ecosystems imagined as the dials and controls of a machine. (b) A landscape divided (left–right) into two examples of the diverse dryland ecosystem types that can result according to the dial settings. Even under similar climatic conditions, for example, variability in physical soil properties (depicted here as red and yellow soils) can result from differences in soil forming factors, such as parent material or age, and lead to alternate plant cover types, with downstream consequences for biogeochemical cycling. The left side (red soil) illustrates a patchy shrubland with bare soil in shrub interspaces in addition to biological soil crusts, whereas the right side (yellow soil) represents a grassland developed on relatively deep soils, which also hosts biological soil crust communities. ENSO, El Niño Southern Oscillation; MAP, mean annual precipitation; MAT, mean annual temperature; PDO, Pacific Decadal Oscillation. Illustration by C. Currier.

soil C and nutrient availability (Osborne *et al.*, 2022). Layered on top of the inherent state factor heterogeneity represented across this vast biome, vegetation patchiness drives substantial differences in biogeochemical cycling at small spatial scales in drylands through a mixture of abiotic and biotic mechanisms. For example, plants can drastically modify microclimate conditions beneath their canopies relative to adjacent intercanopy soils by physically blocking solar radiation (Throop & Archer, 2007) and by altering moisture inputs and outputs through processes such as canopy interception and plant uptake (Breshears *et al.*, 1997; Barron-Gafford *et al.*, 2011). Plants also can create zones of nutrient enrichment and 'hotspots' of biogeochemical activity via litter inputs and root exudates as well as physically trapping litter transported across bare, interspace soils (Fig. 1; Schlesinger *et al.*, 1990; Aguiar & Sala, 1999; Throop & Belnap, 2019). Soil nitrogen (N) concentrations can vary by two to

three times between adjacent shrub and interspace soils, with cascading effects on elemental biogeochemical cycling (Schlesinger *et al.*, 1996). These N 'hotspots' found beneath shrub canopies can transfer N to the atmosphere at rates similar to those from fertilized agricultural fields (Eberwein *et al.*, 2020), driven by anaerobic processes such as denitrification (Krichels *et al.*, 2022), which are otherwise considered rare across dry and aerobic dryland environments.

In addition to high spatial heterogeneity, dryland biogeochemical cycling is sensitive to inter- and intra-annual fluctuations in temperature and precipitation (Fig. 1a). Variation in temperature and/or precipitation through time can result in pulse-dynamic biogeochemical cycling, generating complex temporal patterns in ecosystem processes, including primary production, trace gas emissions and even plant community composition (Austin *et al.*,

2004; Huxman *et al.*, 2004; Collins *et al.*, 2008). For example, precipitation is extremely variable within and among years across dryland types (Zhang *et al.*, 2021) and dryland soil surface temperatures can vary by 70°C in a single day (Tucker *et al.*, 2017). Under the low rainfall conditions characteristic of drylands, moisture from nonrainfall sources (e.g. fog, dew, adsorption from atmospheric water vapor) also can enable temporal pulses of biogeochemical cycling (McHugh *et al.*, 2015; Wang *et al.*, 2017). Building our understanding of biogeochemical dynamics across space and through time in drylands will be crucial for improving our ability to forecast climate change effects on ecosystem structure and function (MacBean *et al.*, 2021). This work will be particularly important in the most arid drylands, which have the greatest potential to provide insight into the ecological consequences of increasing aridity and which are currently the least well-studied (EMG, 2011; Warner *et al.*, 2019).

2. Generalized resource scarcity (e.g. low soil moisture and soil organic matter content) is common in drylands and predicted to result in high sensitivity to climate change, but we have a poor understanding of how biogeochemical processes are co-limited by multiple resources. The classic water-limitation model of drylands offers important insights into ecosystem function, but multiple resources (e.g. water, C, nutrients) often are scarce *simultaneously* in drylands, increasing the occurrence of co- and serial limitation (Austin, 2011; Choi *et al.*, 2022). High levels of spatial and temporal heterogeneity compound this complexity. Water, C and nutrient availability, for example, fluctuate widely with microhabitat conditions (e.g. shrub and interspace soils) and with the timing and nature of precipitation in drylands (Collins *et al.*, 2014). In this way, drylands present valuable research opportunities in the broader study of how resources interact to regulate ecosystem function. Nitrogen provides a good example of our incomplete understanding of how multiple resources interact across space and time. Although N is commonly cited as the least available and, therefore most limiting nutrient in drylands (Hooper & Johnson, 1999), N addition experiments do not provide strong or consistent evidence of increased ecosystem productivity or respiration. Instead, in some long-term experiments, drylands behave as if they were saturated with N – losing N during periods when N availability increases without a concomitant increase in biological N demand (Homyak *et al.*, 2016; Phillips *et al.*, 2021). This may reflect co- or serial limitation of N with other resources like water and/or C (Choi *et al.*, 2022). Improving our understanding of multiple resource dynamics by using multifactorial experiments with regression designs and isotope tracers, for example, may help improve our ability to predict and mitigate the biogeochemical consequences of climate change in drylands and across other diverse ecosystem types.

3. A deeper understanding of dryland biogeochemistry may help improve dryland restoration and adaptation efforts in the face of climate change. High heterogeneity and low resource availability make drylands vulnerable to disturbance and increase the likelihood of transitions to less-productive or novel ecological states (Bestelmeyer *et al.*, 2015). For these reasons, effectively restoring desired ecological structures and functions (e.g. soil stability, primary production, biodiversity) is highly challenging in drylands (Shackelford *et al.*, 2021). Grass and forb establishment post-seeding can be as low as 5% (James *et al.*, 2011). Likewise, the restoration of degraded biological soil crusts – communities of cyanobacteria, algae, lichens and bryophytes living in surface soils that play a central role in driving soil fertility and stability (Fig. 1b) – has proven difficult (Antoninka *et al.*, 2020). However, insights into biological soil crust community composition and functions, specifically the newly characterized 'cyanosphere', are providing promising directions toward effective soil crust restoration (Nelson & Garcia-Pichel, 2021). There also are emerging methods to restore select microbial components of ecosystems, such as inoculation with soil mycorrhizal fungi, yet our understanding of the factors that determine the success of this approach in drylands remains limited (Hoeksema *et al.*, 2010; Neuenkamp *et al.*, 2019).

Water availability often limits restoration success, yet understanding the individual and interactive roles of other potentially limiting resources, such as C and nutrients, may help increase recovery of plants and biological soil crusts in disturbed dryland areas. Incorporating concepts such as resource connectivity, the timing of concurrent resource availability, and the functional traits of vascular plants and soil organisms into restoration actions can further increase the likelihood of rehabilitating desired ecological outcomes (Young *et al.*, 2021). Examples of relatively straightforward actions stemming from biogeochemical insights include timing restoration efforts such as seeding around predicted rather than historic moisture availability or around periods of resource limitation for invasive species (Bradford *et al.*, 2018). Additionally, resource availability can be manipulated directly using artificial structures that collect eroded sediment, litter and nutrients, and seeds, which simultaneously enhance resource retention and concentrate plant propagules that can exploit these resources (Fick *et al.*, 2016; Peters *et al.*, 2020). Studies directly linking dryland microbial communities to ecological functions can inform management of soil communities that buffer the effects of global change (Delgado-Baquerizo *et al.*, 2017). Building our understanding of biogeochemical cycling in intact, disturbed and restored drylands will be a powerful tool for combating land degradation, which threatens the integrity of global drylands and the billions of people who rely on them (Reynolds *et al.*, 2007).

4. Improving our understanding of climate change consequences for dryland biogeochemistry and ecosystem functions requires decisive steps toward informing and engaging a larger, more diverse, and interdisciplinary community of experts. The challenge is large in scope: drylands are vast, heterogeneous and sensitive ecosystems that are expanding, and which play a critical role in local and global ecosystem functions. The challenge also is time-sensitive. Drylands are responding to rapid shifts in climate, with observable state changes across large regions such as the southwestern United States (Allen *et al.*, 2010; Bestelmeyer *et al.*, 2015; Guiterman *et al.*, 2022). The relative lack of research attention awarded to drylands may be the result, in part, of a false, culturally dominant discourse of drylands as desolate, empty spaces with limited inherent value (Beck, 2001; Hoover *et al.*, 2020; Tynan, 2020). However, efforts to draw attention to these knowledge gaps, improve predictive climate models, and support effective

management and restoration strategies in the face of climate change are currently in motion, including a 2019 Intergovernmental Panel on Climate Change (IPCC) special report on global desertification. Key actions that could capitalize on this moment are, first, to enhance education and outreach efforts, emphasizing the recruitment of students from the geographical and cultural cross-sections encompassed by drylands. Such efforts will help motivate a larger, more well-informed and stronger community of expert-stakeholders in future generations. A second set of actions is to unify, diversify and strengthen our existing community to support collaboration across international, disciplinary, and cultural boundaries. Dryland ecology is, by nature, an international endeavor, but, as in many fields, scientists are often siloed regionally and nationally. Expanded emphasis on international collaboration promises to enhance our understanding of variation in dryland patterns and processes. For example, the proposed United Nations International Year of Rangelands and Pastoralists (https://iyrp.info/) provides a vehicle to recognize the importance of dryland stewardship and to engage with people who live in drylands at a global level. Coordinated, distributed experiments, such as the Nutrient Network and emerging networks including RestoreNet and the International Drought Network, can simultaneously provide inclusivity and robustness to dryland ecosystem science (Yahdjian *et al.*, 2021). To produce actionable science, we will also benefit from a more thorough integration of basic and applied perspectives across a range of institutions and disciplines. Integrating diverse scientific approaches, harnessing and uniting existing research networks, supporting data synthesis efforts, and capitalizing on new technologies in drylands (e.g. remote sensing and a wide range of sensor networks) will all be critical. Finally, we should strive to engage those who live in, depend on, and steward drylands directly in long-term dryland ecosystem research, including students, land managers, dryland product consumers, Indigenous communities and the interested public (Galvin *et al.*, 2016). Co-production of knowledge between scientists, local inhabitants and the potential users of knowledge has the added benefit of increasing the utility, use and accessibility of research (Bremer & Meisch, 2017). Specific strategies for research co-production need to account carefully for different ways of knowing and power disparities between researchers and dryland inhabitants (Knapp *et al.*, 2019).

In conclusion, our community faces the urgently important task of strengthening our understanding and ability to forecast climate change effects in drylands. Focusing research attention on how climate change interacts with high levels of heterogeneity and low resource availability will create powerful opportunities to improve our knowledge of these scientifically undervalued systems. Moreover, taking on this challenge through coordinated, international, and locally inclusive education and outreach efforts will be fundamental to forecast the effects of climate change in varying social and ecological contexts in drylands, and to the design of adaptation and restoration strategies in the years ahead.

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Author contributions

All authors contributed equally to the ideas presented in this *Viewpoint* and helped with writing. Writing was led by BBO.

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