Biocrusts mediate a new mechanism for land degradation under a changing climate

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Global concerns for desertification have focused on the slow recovery of extensive and expanding drylands following disturbance, which may be exacerbated by climate change. Biological soil crusts (biocrusts) are photosynthetic soil communities found in drylands worldwide, which are central to the stability and resilience of dryland ecosystems, but vulnerable to global change. Here we use multiple decade-long experiments to investigate the consequences of climate and land-use change on biocrusts and soil stability. Biocrusts recovered rapidly under ambient temperatures but warming interacted with the precipitation disturbance to halt recovery. Moreover, warming alone caused losses of mosses, lichens and soil stability. Our results present a new mechanism contributing to land degradation in drylands whereby warming drives a state shift in biocrust communities, which degrades soil stability. The synergistic effects of climate and land-use change co-occur globally and our results support projections of increased desertification and lowered dryland resilience under warming.

Drylands (hyperarid, arid, semiarid and dry subhumid ecosystems) are a vast and vital part of the Earth system[1,2]. Multiple lines of evidence suggest drylands are degrading and expanding[3], with unknown consequences for the functions of these ecosystems and the livelihoods of those who depend on them[1,2]. Further, understanding the resistance[4,5], that is, the ability to remain unchanged following disturbance, and resilience[4], or the ability to recover following disturbance, of fundamental dryland organisms has important implications for land degradation. Although often overlooked, biological soil crusts (biocrusts) are a consortium of photosynthetic soil organisms, including mosses, lichens and cyanobacteria, that are found on every continent and have the potential to accelerate or slow land degradation, ultimately increasing or decreasing desertification rates[6,7]. However, both the direction and magnitude of feedbacks on land degradation driven by changes to biocrust communities remain unquantified. In part, this lack of quantification stems from large gaps in our understanding of how biocrusts respond to and recover from disturbance under current and future climates.

Biocrusts are common features of drylands worldwide[8] that are composed of keystone organisms[9,10] and occupy places plants do not. They play outsized roles in ecosystem functions, including the regulation of erosion control, carbon sequestration, soil water and soil fertility[11-15]. For example, biocrusts increase global dryland soil moisture storage by 14%[13] and make a sizeable contribution to Earth's terrestrial nitrogen (N) fixation[8]. Taken together these functions make biocrusts critical for combatting land degradation[6,7]. Importantly, biocrust contributions to ecosystem function vary greatly by species and depend on development stage and successional state[16-19], with late successional (for example, mosses and lichens) and intermediate successional (dark-pigmented cyanobacteria) states contributing more strongly to processes such as soil stabilization and N_2 fixation than early successional (light-pigmented cyanobacteria) counterparts[11,12]. At the same time, biocrust community structure is vulnerable to disturbance-induced state changes[8]. Accordingly, knowledge of how biocrust communities recover following disturbance is integral to forecasting future dryland function

and informing policy and land management efforts in the face of increased desertification and warming[20].

Global change is increasing instances of novel disturbance interactions that perturb ecosystems, heightening the risk of ecological state changes at abrupt thresholds[21,22]. Disturbances may create either an alternative, persistant[23] stable state[24] with no potential for recovery or a more temporary transient state[25] that suggests the system may recover to predisturbance conditions. In drylands, regime shifts are of critical concern because they can drive desertification[23]. Both climate and mechanical disturbance can drive state shifts—for example, warming and mechanical disturbance have decreased late successional (moss and lichen) cover[16]. This loss of late successional biocrusts could reduce soil fertility, stability, carbon storage and moisture retention[8,17], with substantial consequences for dust production[26], plant growth[14] and thus desertification. However, while we know biocrusts are sensitive to alterations in precipitation patterns and land-use change, very few studies assess how communities respond over time after disturbance ceases, or how an altered climate may affect recovery trajectories. Biocrust recovery following disturbance was thought to be on the order of centuries[27], yet rates of recovery are likely to be dependent on the frequency, severity and type of disturbance, as well as on underlying site characteristics such as soil texture and climate[18,28]. Further, the studies that do examine recovery of biocrusts following disturbance focus solely on recovery following mechanical disturbance (that is, not climate disturbance)[18,27]. Nevertheless, our ability to predict state transitions and their downstream consequences of land degradation depends on understanding biocrust community responses to multiple altered disturbance regimes[29] and determining whether disturbance-induced state changes create persistent regime shifts[30] or transient[25] states.

In this study, we examined how warming affects biocrust communities and how biocrusts recover from both mechanical and climate-induced disturbance. Two unique long-term experiments allowed us to investigate: (1) the recovery of biocrust constituents following the cessation of chronic mechanical disturbance under ambient temperatures and (2) after climate disturbance
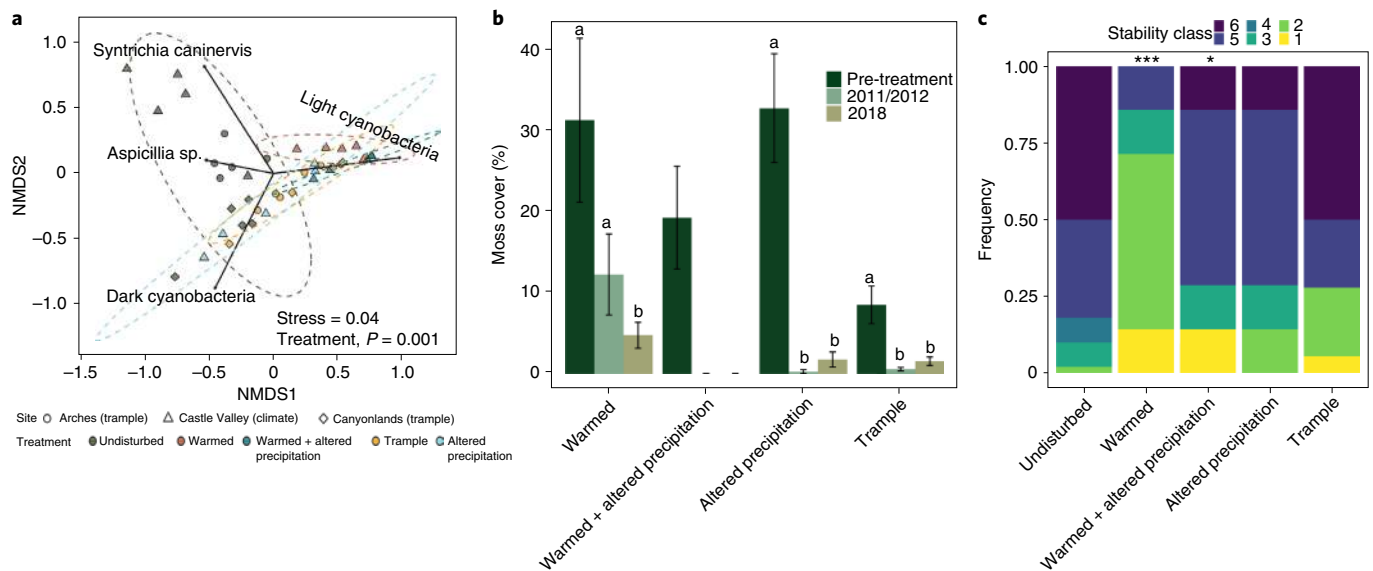
Fig. 1 | Biocrust community composition, abundance and effects on soil aggregate stability. a, Non-metric multidimensional scaling (NMDS) of biocrust photoautotroph communities using a Bray–Curtis distance matrix. Warming and the legacy of both mechanical and climate disturbance are affecting biocrust community composition ($R^2 = 0.5$, $P = 0.001$). Site was not affecting community composition ($R^2 = 0.1$, $P = 0.17$). Undisturbed control plots group together because of an abundance of late successional biocrusts, such as the moss species *Syntrichia caninervis*. The legacy of altered precipitation (alt. ppt.) and mechanical trampling is causing unwarmed disturbed plots to group together, driven by the abundance of dark-pigmented cyanobacteria (Dark Cyanobacteria). Ongoing warming causes plots to cluster because the early successional light-pigmented cyanobacteria (Light Cyanobacteria) dominate. **b**, Mean (± standard error) moss surface cover through time for each treatment. Pretreatment measurements were collected before treatments started (1996 for Trample, 2005 for all other treatments). The 2011/2012 measurements were collected after altered precipitation (2012) and physical trampling (2011) ceased, but warming was ongoing. This timing captures the effects of treatments on the moss community. Measurements taken in 2018 were six years after the altered precipitation disturbance ceased and seven years after mechanical disturbance ceased. This timing captures the recovery of the moss from the mechanical disturbance and the altered precipitation disturbance with and without the warming treatment, which was always ongoing. Letters indicate significant differences at $P < 0.05$. Warmed + alt. ppt. data were excluded from statistical analyses because in 2011/2012 and in 2018 there was no moss present. **c**, Frequency of scaled soil stability class values (with a stability class of 1 being the least stable and a score of 6 being the most stable) by treatment. Soil stability under warming and under warming with the legacy of altered precipitation differed from the undisturbed controls. *** indicates significant difference at $P < 0.001$. * indicates significant difference at $P < 0.05$. These data show that the warming-induced transition of biocrust communities to early successional states resulted in significant soil destabilization via reductions in soil aggregate stability.

(altered precipitation) under both ambient and warmed (+4 °C above ambient) conditions. To do this, we leveraged two long-term experiments (occurring at three sites) on the Colorado Plateau of North America: the first was a mechanical disturbance experiment where annual human-trampling occurred for 15 years at two sites (1996–2011) and the second was a 13-year (2005–2018) full-factorial in situ climate manipulation experiment (undisturbed control, warming, altered precipitation, warming + altered precipitation; Supplementary Fig. 1, Supplementary Tables 1 and 2). The altered precipitation disturbance consisted of small frequent rain events (1.2 mm), applied via hand sprayer that increased the long-term average frequency of small summer rains and that resulted in massive late successional biocrust mortality due to the negative effects of short hydration times[17] (Supplementary Fig. 2). High-frequency small rain events are a feature of dryland systems worldwide[31], including the Colorado Plateau (Supplementary Fig. 2), with predictions that summer rainfall regimes will change in numerous dryland ecosystems[32,33]. After six years (2005–2012) we ended the altered precipitation treatments and explored biocrust recovery with and without warming by resurveying plots in 2018 (six years post-climate disturbance; Supplementary Fig. 1). Both the mechanical and climate disturbances resulted in the mortality of late successional biocrusts, and the legacy of disturbance created communities that were structurally distinct from both undisturbed controls and pretreatment communities. Surprisingly, under the legacy of both disturbance types without warming, there were

relatively rapid increases in dark-pigmented cyanobacterial cover and mosses were returning, indicating a resilient system undergoing secondary succession. However, in the second experiment, warming alone decimated intermediate and late successional biocrusts, with even stronger effects when warming was combined with the legacy of altered precipitation.

Experimental warming

Experimental warming (+4 °C above ambient) decreased the cover of intermediate and late successional state biocrusts, resulting in the community's stagnation in an early successional state, predominately consisting of light-pigmented cyanobacteria (for example, *Microcoleus* spp.; Fig. 1a). These results agree with the results from our Bayesian multilevel model showing that light-pigmented cyanobacteria cover increased to 47% ± 9, while moss cover was drastically reduced by 15% compared to the undisturbed control communities (Fig. 2b). Warming also decreased moss cover relative to pretreatment levels (Figs. 1b, 3e and Supplementary Fig. 3; Supplementary Table 3). Under warming, community dissimilarities had been relatively stable since 2012, indicating that most of the community change happened before that year (Fig. 3b). However, there is still a significant relationship between community dissimilarity and interval (Fig. 3b and Supplementary Table 4), indicating that the community is still changing, which is due to increases in early successional light-pigmented cyanobacteria (Supplementary Fig. 4) and decreases in moss cover (Fig. 3e and Supplementary
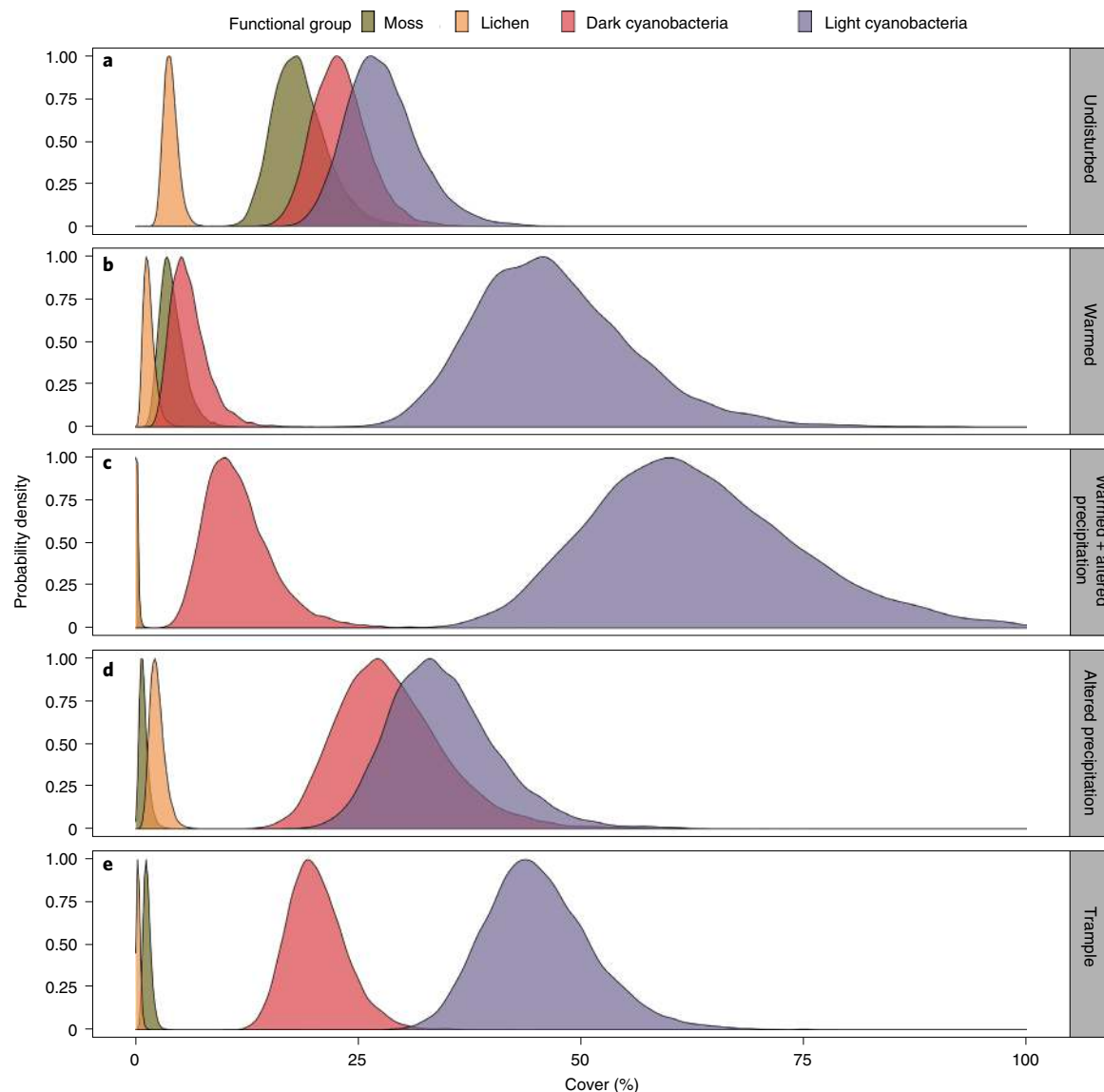
Fig. 2 | Biocrust recovery varies by disturbance type and functional group. a–e, Predicted posterior distributions from the Bayesian multilevel model showing treatment effects on biocrust functional groups under (**a**) undisturbed control, (**b**) ongoing warming, (**c**) ongoing warming and the legacy of altered precipitation, (**d**) legacy of altered precipitation and (**e**) legacy of physical trampling. **a,** Undisturbed controls have more lichens (4% ± 0.8 cover, mean cover ± s.d.) and mosses (19% ± 3 cover) than any of the disturbance or warming treatments. Active warming (**b,c**) decreases late successional lichen cover (warmed cover: 2% ± 0.7; warmed + alt. ppt. cover: 0.1% ± 0.7) and moss cover (warmed cover: 4% ± 1; warmed + alt. ppt. cover: 0), and shows replacement by light-pigmented cyanobacteria (warmed cover: 47% ± 9; warmed + alt. ppt. cover: 63% ± 12). Under the legacy of disturbance, dark-pigmented cyanobacteria (**d**, alt. ppt. cover: 29% ± 6; **e**, trample cover: 20% ± 3) have recovered to or surpassed the control levels (**a**, undisturbed cover: 23% ± 3). Under the legacy of disturbance, lichen (**d**, alt. ppt. cover: 2% ± 0.8; **e**, trample cover: 0.3% ± 0.3) and moss (**d**, alt. ppt. cover: 1% ± 0.5; **e**, trample cover: 1.3 % ± 1) have not recovered to undisturbed control levels, but are higher than under the combination of warming and altered precipitation.

Fig. 3; Supplementary Table 3). In addition to cover, we measured soil aggregate stability[34] in 2018 to explore soil erodibility, a major factor in desertification, and observed decreased soil stability in response to warming ($P < 0.001$; Supplementary Table 5; Fig. 1c). Soil aggregate stability is linked to biocrust type (light-pigmented cyanobacteria, dark-pigmented cyanobacteria, lichen and moss), with light-pigmented cyanobacteria conferring the most variable soil stability. Therefore, losses of moss, lichen and dark-pigmented cyanobacteria (Figs. 1a, 3e and 2c) are driving lower soil aggregate stability under warming. These results underscore that warming reduces late successional biocrusts (Fig. 1b and Supplementary Fig. 2b) and support previous observations of decreased biocrust health and diversity in response to warming[16,35].

The legacy of altered precipitation with and without warming

Ongoing warming under the legacy of altered precipitation halted biocrust recovery. Lichens and mosses remained completely absent seven years after the altered precipitation treatment ended with warming (Fig. 1a,b and Supplementary Table 6) yet showed signs of recovery in the unwarmed plots across that same time. The combination of warming and altered precipitation led to 19% and 4% decreases in mosses and lichens, respectively, when compared to the undisturbed control (Fig. 2c). Similar to the warming treatment alone, community dissimilarity of the warmed + altered precipitation treatment was relatively stable yet significantly related to interval (Fig. 3c and Supplementary Table 7) because of decreases in mosses
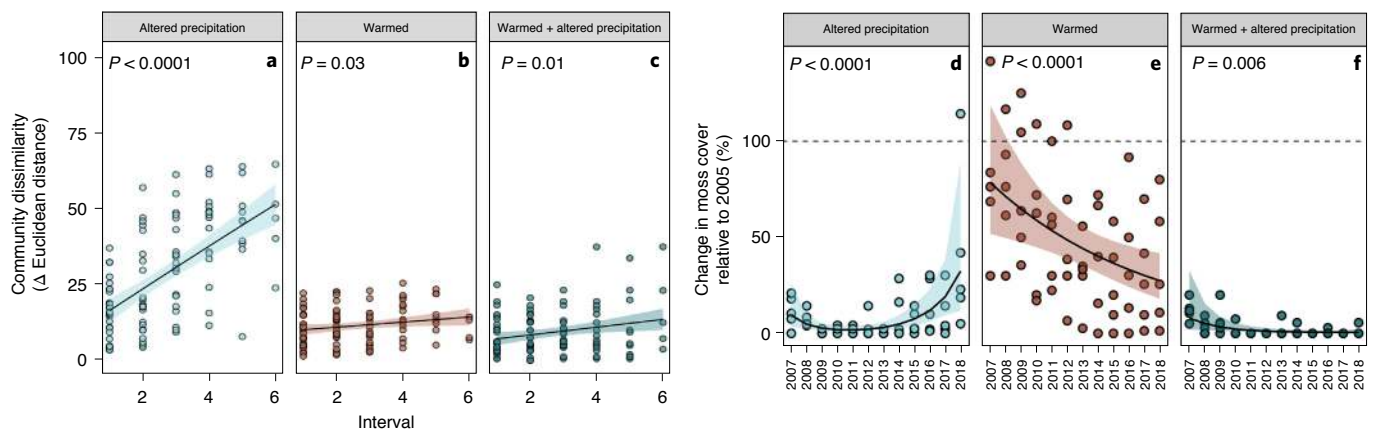
Fig. 3 | Moss shows no signs of recovery under warming. a–c, Interannual community dissimilarity calculated as the difference in Euclidean distance among years starting in 2012 (when the altered precipitation treatment ceased) with generalized additive models fitted. Standard error around the model fit is shown in coloured shading. The *x*-axis interval indicates increasing time lags: for example, 1 year time lag versus 6 year time lag. **a**, Altered precipitation has a strongly significant positive slope, indicating biocrust succession is ongoing. Treatments with ongoing warming (**b**, Warmed and **c**, Warmed + alt. ppt.) have relatively flat slopes, although there is a significant relationship between community dissimilarity and interval, indicating that the biocrust community is changing a small amount at a slow pace, which may be due to increases in early successional light-pigmented cyanobacteria. **d–f**, Change in moss cover relative to pretreatment moss cover from 2005. Horizontal dashed lines indicate where cover would be equal to pretreatment levels (that is, 100%). Points above the horizontal line indicate that moss cover is higher than mean pretreatment levels, whereas points below indicate that cover is lower than pretreatment levels. Generalized additive models show change in moss cover as the response and year as the predictor. Standard error around the model fit is shown in coloured shading. **d**, Altered precipitation drove decreases in moss cover until the treatment ceased in 2012, when the slope becomes positive indicating that moss declined and then remained low during the altered precipitation treatment but that, when that climate stressor ended in 2012, moss recovery began and is ongoing. **e**, Warming had a strongly significant negative slope, indicating that moss abundance is negatively impacted by warming. Points above the horizontal line in early years indicate that moss cover in some individual plots was higher than the mean pretreatment levels across all plots. **f**, Under Warmed + alt. ppt. there is a negative slope from 2007–2010 due to massive moss mortality; then the slope flattens, as there is no change in moss cover because mosses are absent and are not recovering.

(Figs. 2c, 3f and Supplementary Fig. 3; Supplementary Table 8), as well as increases in light-pigmented cyanobacteria (Fig. 2c and Supplementary Fig. 4). Further, we observed the largest increases in cover of light-pigmented cyanobacteria (35% higher than in the undisturbed control) under the legacy of altered precipitation with ongoing warming (Fig. 2c). In addition to shifts in community composition and abundance, we observed decreases in soil stability under the legacy of altered precipitation when coupled with ongoing warming ($P = 0.02$; Supplementary Table 5 and Fig. 1c). Destabilization of soils with a warmer climate was linked to the absence of late successional mosses and dominance of light-pigmented cyanobacteria (Figs. 1a,b and 2c). Decreases in both moss cover and soil stability in response to warming and the legacy of altered precipitation in concert, compared to the effects of each driver alone, support the idea that climatic drivers will strongly interact to create more intense ecological impacts than those caused by single drivers[36].

Recovery in the absence of warming

Contrary to the hypothesis that biocrusts recover on incredibly slow timescales[27], we found evidence that biocrust composition was recovering just six to seven years after disturbance in the absence of warming. The presence of late successional mosses and lichens drew the undisturbed control plots and plots under the legacies of disturbances (altered precipitation and trampling) together in ordination space on NMDS2 (Fig. 1a and Supplementary Fig. 5a). However, the mechanical and climate-disturbed biocrust communities remained distinct from undisturbed controls (Fig. 1a; $P = 0.001$). Late successional biocrust cover—particularly moss—remained lower than both pretreatment and undisturbed control levels for both disturbance types (Fig. 1b, Supplementary Fig. 5b and Supplementary Table 6). Moss cover was reduced by ~18% under the legacies of altered precipitation and trampling when compared to the undisturbed controls (Fig. 2a,d,e). However, community dissimilarity of the

control communities and under the legacy of altered precipitation increased through time (Fig. 3a and Supplementary Fig. 4a; Supplementary Table 9), indicating these communities were undergoing directional change[37]. Further, while moss cover remained low six years after the altered precipitation treatment ceased (as assessed in 2018), all plots showed some increase in moss cover (Supplementary Fig. 5), highlighting that secondary succession was ongoing (Figs. 1b, 3d, Supplementary Figs. 6a,c and 5; Supplementary Table 10). These small increases in moss under the legacy of altered precipitation suggest dominance by intermediate successional cyanobacteria with no late successional members may be a transient state[25], rather than a stable state[24].

Dark-pigmented cyanobacteria (intermediate successional biocrusts) were recovering under the legacies of both disturbances (Fig. 1a) with a 16% increase in cover under altered precipitation and a 3% increase under trampling compared to the undisturbed controls (Fig. 2a,d,e in pink and Supplementary Fig. 7; Supplementary Tables 11 and 12). This increase may be a result of a decrease in competition for physical space stemming from disturbance-induced moss and lichen mortality coupled with a release from disturbance. Additionally, soil aggregate stability did not differ from undisturbed control plots under the legacies of altered precipitation and trampling ($P = 0.14$ and $P = 0.08$, respectively; Supplementary Table 5 and Fig. 1c), suggesting soils regained their stability as later successional biocrust constituents recovered. Increases in moss cover (Fig. 1b) coupled with cover of dark-pigmented cyanobacteria rising to near undisturbed control levels (Figs. 1a, 2d,e and Supplementary Fig. 5a) drove higher soil aggregate stability (Fig. 1c).

Discussion

Overall, a reduction of moss cover in the warming-only plots and a complete lack of recovery in those with warming plus the legacy of altered precipitation, coupled with significant decreases in soil

stability under both treatments, support the idea that warming is driving a regime shift[30] in the biocrust community to an alternative stable state[24]. Taken together, these data point to the potential for warming to accelerate land degradation through losses of mosses and the strong soil stabilization they provide. The implications of this regime shift are large. Biocrusts may make up nearly half of the cover in drylands around the world[8], occupying the large interspaces among plants and promoting plant growth. It is important to note that our results come from three sites on the Colorado Plateau, yet they are representative systems in that they contain the main biocrust types and even the same species (for example, *Syntrichia caninervis*) found across drylands worldwide. This work highlights a need for more climate manipulation experiments in our global drylands and underscores the importance of studies that assess multiple global change drivers in tandem[38]. Nonetheless, a community dominated by early successional biocrusts has considerable implications for reduced ecosystem function, through decreases in soil stability, fertility and moisture retention[8,17], under a warming climate. However, some results suggested hope for biocrusts to continue their role in forestalling land degradation. In the absence of experimental warming, there were signs of biocrust recovery following both chronic altered precipitation and mechanical disturbance, suggesting that biocrust recovery is more dynamic than previously thought[27] and that dryland ecosystem resilience varies with disturbance type.

Climate forecasts for most drylands suggest increased severity and frequency of drought, greater variability in precipitation and, unswervingly, increased temperatures[32,39]. The Intergovernmental Panel on Climate Change (IPCC) highlights desertification and climate change as critical concerns, both individually and concomitantly, because they drive reductions in ecosystem functions and health in drylands[40]. Drylands cover over 40% of Earth's terrestrial surface[12], support the livelihoods of billions of people[2] and may increase dramatically in spatial extent in the coming decades[3,20]. Yet understanding of how climate change will drive regime shifts in dryland systems remains exceedingly poor[23], particularly for ecologically important biocrusts. Our results reveal how biocrusts respond and recover from multiple types of disturbance and under a changing climate. High vulnerability of late successional biocrusts to warming, coupled with our observation that warming halts recovery following disturbance, further underscores the potential of rising temperatures to result in increased desertification through losses of soil stability and fertility. In many dryland systems, biocrusts are the dominant cover type[8,41], suggesting they are potential bellwethers for predicting the fate of dryland ecosystem function in response to climate change. Therefore, a loss of these critical organisms under warming temperatures may accelerate land degradation (for example, soil erosion) in cold deserts.

Online content

References

1. *Science Plan and Implementation Strategy* IGBP Report No. 53/IHDP Report No. 19 (Global Land Project, 2005).
2. *Millennium Ecosystem Assessment—Ecosystems and Human Well-Being: Desertification Synthesis Encyclopedia of the Anthropocene* vols 1–5 (MEA, 2017).
3. Huang, J., Yu, H., Guan, X., Wang, G. & Guo, R. Accelerated dryland expansion under climate change. *Nat. Clim. Change* **6**, 166–171 (2015).
4. Pimm, S. L. The complexity and stability of ecosystems. *Nature* **307**, 321–326 (1984).
5. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).
6. Belnap, J. Surface disturbances: their role in acceleration desertification. *Environ. Monit. Assess.* **37**, 38–57 (1995).
7. Zhao, Y., Jia, R. L. & Wang, J. Towards stopping land degradation in drylands: water-saving techniques for cultivating biocrusts in situ. *Land Degrad. Dev.* **30**, 2336–2346 (2019).
8. Rodriguez-Caballero, E. et al. Dryland photoautotrophic soil surface communities endangered by global change. *Nat. Geosci.* **11**, 185–189 (2018).
9. Coe, K. K. & Sparks, J. P. Physiology-based prognostic modeling of the influence of changes in precipitation on a keystone dryland plant species. *Oecologia* **176**, 933–942 (2014).
10. Ferrenberg, S., Tucker, C. L. & Reed, S. C. Biological soil crusts: diminutive communities of potential global importance. *Front. Ecol. Environ.* **15**, 160–167 (2017).
11. Belnap, J. & Gillette, D. A. Soil surface disturbance: impacts on potential wind erodibility of sand desert soils in SE Utah, USA. *Land Degrad. Dev.* **8**, 355–362 (1997).
12. Rutherford, W. A. et al. Albedo feedbacks to future climate via climate change impacts on dryland biocrusts. *Sci. Rep.* **7**, 44188 (2017).
13. Duniway, M. C. et al. Wind erosion and dust from US drylands: a review of causes, consequences, and solutions in a changing world. *Ecosphere* **10**, e02650 (2019).
14. Ferrenberg, S., Faist, A. M., Howell, A. & Reed, S. C. Biocrusts enhance soil fertility and *Bromus tectorum* growth, and interact with warming to influence germination. *Plant Soil* **429**, 77–90 (2018).
15. Eldridge, D. J. et al. The pervasive and multifaceted influence of biocrusts on water in the world's drylands. *Glob. Change Biol.* **26**, 6003–6014 (2020).
16. Ferrenberg, S., Reed, S. C. & Belnap, J. Climate change and physical disturbance cause similar community shifts in biological soil crusts. *Proc. Natl Acad. Sci. USA* **112**, 12116–12121 (2015).
17. Reed, S. C. et al. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nat. Clim. Change* **2**, 752–755 (2012).
18. Concostrina-Zubiri, L. et al. Biological soil crusts across disturbance-recovery scenarios: effect of grazing regime on community dynamics. *Ecol. Appl.* **24**, 1863–1877 (2014).
19. Weber, B., Bowker, M., Zhang, Y. & Belnap, J. in *Biological Soil Crusts: An Organizing Principle in Drylands* (eds Weber, B., Büdel, B. & Belnap, J.) 479–498 (Springer, 2016).
20. Reynolds, J. F. et al. Global desertification: building a science for dryland development. *Science* **316**, 847–851 (2007).
21. Berdugo, M. et al. Global ecosystem thresholds driven by aridity. *Science* **367**, 787–790 (2020).
22. Bestelmeyer, B. T. et al. Analysis of abrupt transitions in ecological systems. *Ecosphere* **2**, e03360 (2011).
23. Bestelmeyer, B. T. et al. Desertification, land use, and the transformation of global drylands. *Front. Ecol. Environ.* **13**, 28–36 (2015).
24. Beisner, B., Haydon, D. & Cuddington, K. Alternative stable states in ecology. *Front. Ecol. Environ.* **1**, 376–382 (2003).
25. Fukami, T. & Nakajima, M. Community assembly: alternative stable states or alternative transient states? *Ecol. Lett.* **14**, 973–984 (2011).
26. Belnap, J. & Büdel, B. in *Biological Soil Crusts: An Organizing Principle in Drylands* (eds Weber, B., Büdel, B. & Belnap, J.) 305–320 (Springer, 2016).
27. Belnap, J. & Warren, S. D. Measuring restoration success: a lesson from Patton's tank tracks. *Ecol. Bull.* **79**, 33 (1998).
28. Belnap, J. & Elderidge, D. in *Biological Soil Crusts: Structure, Function and Management* (eds Belnap, J. & Lange, O. L.) 363–383 (Springer, 2001).
29. Turner, M. G. Disturbance and landscape dynamics in a changing world. *Ecology* **91**, 2833–2849 (2010).
30. Scheffer, M. & Carpenter, S. R. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18**, 648–656 (2003).
31. Sala, O. E. & Lauenroth, W. K. Small rainfall events: an ecological role in semiarid regions. *Oecologia* **53**, 301–304 (1982).
32. Cayan, D. R. et al. Future dryness in the Southwest US and the hydrology of the early 21st century drought. *Proc. Natl Acad. Sci. USA* **107**, 21271–21276 (2010).
33. Christensen, N. S., Wood, A. W., Nathalie, V., Lettenmaier, D. P. & Palmer, R. N. The effects of climate change on the hydrology and water resources of the Colorado river basin. *Clim. Change* **62**, 337 (2004).
34. Herrick, J. et al. Field soil aggregate stability kit for soil quality and rangeland health evaluations. *Catena* **44**, 27–35 (2001).
35. Escolar, C., Martínez, I., Bowker, M. A. & Maestre, F. T. Warming reduces the growth and diversity of biological soil crusts in a semi-arid environment: implications for ecosystem structure and functioning. *Phil. Trans. R. Soc. B* **367**, 3087–3099 (2012).

36. Scheffer, M. et al. Creating a safe operating space for iconic ecosystems: manage local stressors to promote resilience to global change. *Science* **347**, 1317–1319 (2015).

37. Collins, S. L., Micheli, F. & Hartt, L. A method to determine rates and patterns of variability in ecological communities. *Oikos* **91**, 285–293 (2000).

38. Rillig, M. C. et al. The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science* **366**, 886–890 (2019).

39. IPCC. *Climate Change 2014: Impacts, Adaptations, and Vulnerability* (eds Field, C. B. et al.) (Cambridge Univ. Press, 2014).

40. Mirzabaev, A. et al. in *IPCC Special Report on Global Warming of 1.5 °C* (eds Masson-Delmotte, V. et al.) Ch. 3 (WMO, 2018).

41. Torres-Cruz, T. J. et al. Species-specific nitrogenase activity in lichen-dominated biological soil crusts from the Colorado Plateau, USA. *Plant Soil* **429**, 113–125 (2018).

Methods

Site description. We surveyed biocrust response to climate manipulation and mechanical disturbance experiments at three sites located on the Colorado Plateau of southeastern Utah (Supplementary Table 1). This region is classified as a cool desert[42] with an annual temperature range of 4–13 °C and annual precipitation range of 205–510 mm. All three sites had similar biocrust community composition and structure before the experiments started, including light-pigmented cyanobacteria (*Microcoleus vaginatus*), dark-pigmented cyanobacteria (*Nostoc* spp., *Scytonema* spp. and *Tolypothrix* spp.), mosses (*Syntrichia caninervis* and *S. ruralis*) and lichens (*Collema tenax* and *C. coccophorum*)[16,43]. All sites had similar precipitation and temperature patterns throughout the study (Supplementary Figs. 8 and 9).

The climate manipulation began in October 2005 at a site located near Castle Valley, Utah (38.67° N, 109.42° W) containing $20 \times 5\,\text{m}^2$ plots in a randomized block design with four treatment types ($n = 5$): undisturbed control, warmed, altered precipitation and warmed + altered precipitation. This site is dominated by the shrub species *Atriplex confertifolia*, the perennial grass species *Achnatherum hymenoides* and *Pleuraphis jamesii* and the exotic annual grass *Bromus tectorum*. Infrared lamps, installed 1.5 m above the soil surface, heated the topsoil 2 °C above ambient for the first three years of the experiment and temperatures were increased to 4 °C above ambient starting on 30 June 2008 until present to account for modifications in temperature predictions. The altered precipitation treatments were designed to mimic 1.2 mm summer rainfall events and took place between 15 June and 15 September each year from 2005 to 2012. These treatments were applied with hand sprayers. During these years, plots received on average 35 events (roughly four times the average natural frequency)[12,17,43,44]. This treatment is similar to annual frequencies of rain events in the hotter North American deserts, which range from ~32–86 events annually[45]. Several studies near the time the experiments were initiated suggested that the Colorado Plateau will shift towards a rainfall regime with more frequent small rain events during the summertime[46–50]. The altered precipitation treatment drove rapid moss mortality, as mosses expended energy to activate when becoming wet, but were dry before they could regain that energy through photosynthesis. Increases in the frequency of these common events can kill a very common moss, but the driving factor was the time the mosses were wet[17].

The two mechanical disturbance sites were established in the spring of 1996 and are located in Arches (38.73° N, 109.54° W) and Canyonlands (38.46° N, 109.54° W) National Parks. At each site ten 2 m x 5 m plots were installed, where half were trampled by human footsteps and half were left undisturbed ($n = 5$)[43]. Treated plots were trampled by human steps once a year every May for 15 years until May 2011. Trampling entailed two gentle flat footsteps over the entire plot, with effort to minimize soil compaction and mixing. In May and June of 2018 the biocrust community was assessed following seven years of warming treatments and recovery from climate and mechanical disturbances (Supplementary Fig. 1). We examined ambient precipitation and temperature patterns at each of the sites using PRISM[51], and found the patterns were consistent across sites (Supplementary Figs. 9 and 10).

Biological soil crust assessment. Biological soil crust communities were assessed in two ways, both of which used 25×25 cm frames and a point intercept method with 20 points in each frame[52]. First, in May and June 2018, to assess recovery following mechanical and climate disturbance, biocrust community composition was determined using comparable within-plot locations at all three sites (under shrubs and in the interspace among vascular plants; Supplementary Tables 1 and 2). For the trampling sites in Arches and Canyonlands National Parks, a total of 240 frames were read (4,800 points), with 12 frames per plot and ten plots at each site (five control, five treatment; Supplementary Table 2). Frames were assessed under shrubs and in interspaces among plants away from plot edges to avoid edge affects. For the climate manipulation sites in Castle Valley, a total of 120 frames were read (2,400 points), six frames per plot, for each of the four treatments (five replicate plots per treatment; Supplementary Table 2). These frames were also assessed under shrubs and in interspaces among plants and away from the edges of the plots. Second, in addition to these cross-experiment assessments, biological soil crust community composition in the climate manipulation experiments was assessed annually using four frames per plot (80 frames and 1,600 points). To estimate plot level biocrust cover, we divided the number of species or biocrust type readings per plot by the total readings per plot. We included shrubs and interspaces together in our plot level calculations because we were interested in overall biocrust community responses to treatments. Further details on the experimental design and experimental treatments can be found in refs. [16] and [17].

Soil stability. We measured soil aggregate stability (a measure of erodibility) using the method outlined by Herrick et al.[34]. In this method, soil aggregates are ranked ('slake scores') on an ordinal scale of 1 (least stable) to 6 (most stable). We measured nine slake samples per plot for a total of 360 measurements. For each slake measurement the surface biocrust functional group (that is, Light-pigmented cyanobacteria, Dark-pigmented cyanobacteria, Lichen and Moss) was recorded. We scaled the slake scores for each plot using the relative abundance of each of the biocrust cover categories in the plot by multiplying the slake score for each group by the relative abundance of each group. We used the sum of the scaled slake scores to calculate a plot level soil aggregate stability value.

Data analyses. All analyses outlined below were conducted in R v.4.0.3 (ref. [53]). Undisturbed control plots were modelled at the site level in all analyses but are presented pooled in some figures for ease of interpretation. To understand overall differences in biocrust community composition among treatments and sites we used non-metric multidimensional scaling (NMDS) based on Bray–Curtis similarity. We visualized the NMDS using the 'ggplot2' package[54] and the 'stat_ellipse' function with 95% confidence intervals. We tested for homogeneity of variance using the 'betadisper' function from the 'vegan' package[55]. We tested for significant differences among biocrust communities, treatments and sites by performing permutational multivariate analysis of variance (PERMANOVA[56]) using the 'adonis' function (999 permutations[55]). We used a negative binomial generalized linear model to test for differences in moss cover among pretreatment, post-treatment and recovery for each treatment using the 'glm.nb' function in the 'MASS' package[57]. We calculated least-square means to make pairwise comparisons among pretreatment, post-treatment and recovery for each treatment using the 'emmeans' function from the 'emmeans' package[58]. We did not include Warmed + altered precipitation in the pairwise comparison because moss cover values were 0 in all plots for post-treatment (2012) and recovery (2018) time points (Fig. 1b). To uncover differences between the undisturbed control and each treatment in scaled slake score (soil stability), we used a maximum likelihood statistical significance test (G-test) using the 'GTest' function in the 'DescTools' package[59]. Summaries of maximum likelihood significance tests can be found in Supplementary Table 5.

To understand the pace at which communities are changing after the altered precipitation treatment ended, we assessed biocrust community dissimilarity from 2012 to 2018. We used the 'rate_change_interval' function from the 'codyn' package[60] to calculate Euclidean distances at each time interval. We fitted generalized additive models to these data, with Euclidean distance as the response and interval as the predictor using the 'gam' function in the 'mgcv' package[61]. Model summaries can be found in Supplementary Tables 3, 7 and 9. We visualized the community dissimilarity data using the 'ggplot2' and the 'stat_smooth' argument with the 'gam' method[54]. We calculated relative abundance of the biocrust functional groups using the 'decostand' function from the 'vegan' package[55]. To understand how quickly mosses and lichens were recovering, we looked at the change in cover of each group from predisturbance cover levels (2005) by subtracting the cover in each year from the cover in 2005 and then dividing by the cover in 2005. We were only able to do this for the climate manipulation experiment and not the mechanical disturbance experiment because we did not have annual measurements of biocrust composition and cover for the latter. We fitted generalized additive models to these data, with relative abundance as the response and time as the predictor using the 'gam' function in the 'mgcv' package[61]. Model summaries can be found in Supplementary Tables 4, 8 and 10. We visualized the moss and lichen relative abundance as well as the change in moss and lichen cover using the 'ggplot2' package and the 'stat_smooth' argument with the 'gam' method[54].

We examined the legacy effects of altered precipitation, as well as the ongoing effect of warming, on biocrust functional groups using a Bayesian multilevel model with default (non-informative) priors. This approach allowed a holistic look at how each functional group fares under warming and the legacy of disturbance, while also allowing us to directly compare treatments occurring at different sites. Biocrust cover was the response variable and functional group as population-level (fixed) effect and treatments within sites for each functional group as a group-level effect. This allowed varying slopes for each site:treatment combination. We chose this approach to account for the fact that all treatments did not occur at all of the sites. We also included a group-level effect for plot (sampling unit) that allowed for the intercept to vary. The response variable (biocrust cover) was heavily tailed and had many zeros; because of this we used a zero inflated negative binomial data distribution with a log link and link shape function. Models were fitted using the R package 'brms'[62]. We fitted four candidate models: two included a group-level effect for plot and two included functional group as an additional zero inflation parameter (zi). Each candidate model was run using two chains and 12,000 iterations using Hamiltonian Monte Carlo (HMC) sampling. We visually checked chains for mixing and used the potential scale reduction factor ($\hat{R}$) to assess model convergence[63]. The $\hat{R}$ value was 1 for all our models—this index is roughly equivalent to the F-ratio in ANOVA. It compares the between-chains variability to the within-chains variability to ensure that chains-specific characteristics (for example, starting value of the algorithm) do not have a strong effect on the overall result[63]. We used k-fold cross-validation for model selection to calculate leave-one-out (LOO) values for our models and compared them using expected log pointwise predictive density (elpd). Cross-validation splits the data into training and validation and rotates them until we evaluate how well we predict our entire dataset. It helps to avoid overoptimistic predictions and can be used to obtain an approximation of the model's predictive capabilities[64]. The elpd quantity indicates the predictive accuracy of the model for a single observation. We selected the model with the lowest LOO value and lowest elpd difference[64]. Additionally, we conducted graphical posterior predictive checks using the 'pp_check' and the 'ppc_stat' functions from the 'bayesplot' package[65]. The final model is detailed in Appendix S1. Summaries of population-level and group-level effects can be found in Supplementary Tables 13 and 14.

We calculated 90% and 95% credible intervals for posterior distributions of each functional group under each treatment at each site using the 'ci' function from the 'bayestestR'[66] package. A summary of posterior distributions can be found in Supplementary Table 15. We then used the 'posterior_epred' function in the 'brms'[62] package to calculate predicted posterior distributions for each of the functional groups for each of the treatments at each of the sites. For visualization we averaged the predicted posterior distributions of the undisturbed control treatment and trample treatments across sites because posterior distributions did not differ strongly among sites. We visualized these distributions using the 'geom_density' function in the 'ggplot2'[54] package. A summary of predicted posterior distributions and credible intervals can be found in Supplementary Table 11. We used the 'conditional_effects' function from the 'brms'[62] package to calculate the effects of each of the treatments at each of the sites. A summary of conditional effects can be found in Supplementary Table 12. Data and code are available from the USGS ScienceBase-Catalog[67].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
Data generated during this study is available from the USGS ScienceBase-Catalog[67].

Code availability
Code created for this study is available from the USGS ScienceBase-Catalog[67].

References
42. Omernik, J. M. & Griffith, G. E. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environ. Manag.* **54**, 1249–1266 (2014).
43. Kuske, C. R., Yeager, C. M., Johnson, S., Ticknor, L. O. & Belnap, J. Response and resilience of soil biocrust bacterial communities to chronic physical disturbance in arid shrublands. *ISME J.* **6**, 886–897 (2011).
44. Tucker, C. L., Ferrenberg, S. & Reed, S. C. Climatic sensitivity of dryland soil CO_2 fluxes differs dramatically with biological soil crust successional state. *Ecosystems* **22**, 15–32 (2018). https://doi.org/10.1007/s10021-018-0250-4
45. Cable, J. M. & Huxman, T. E. Precipitation pulse size effects on Sonoran Desert soil microbial crusts. *Oecologia* **141**, 317–324 (2004).
46. Karl, T. R., Knight, R. W. & Plummer, N. Trends in high-frequency climate variability in the twentieth century. *Nature* **377**, 217–220 (1995).
47. Kunkel, K. E., Easterling, D. R., Redmond, K. & Hubbard, K. Temporal variations of extreme precipitation events in the United States: 1895–2000. *Geophys. Res. Lett.* **30**, 1895–2000 (2003).
48. Kim, J. A projection of the effects of the climate change induced by increased CO_2 on extreme hydrologic events in the Western US. *Clim. Change* **68**, 153–168 (2005).
49. Smith, S. J. et al. Climate change impacts for the conterminous USA: an integrated assessment part 1. Scenarios and context. *Clim. Change* **69**, 7–25 (2005). https://doi.org/10.1007/1-4020-3876-3_2
50. Schwinning, S., Belnap, J., Bowling, D. R. & Ehleringer, J. R. Sensitivity of the Colorado Plateau to change: climate, ecosystems, and society. *Ecol. Soc.* **13**, 28 (2008).
51. Daly, C. et al. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* **28**, 2031–2064 (2008).
52. Jonasson, S. The point intercept method for non-destructive estimation of biomass. *Phytocoenologia* **11**, 385–388 (1983).
53. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2019).
54. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis* (Springer-Verlag, 2016).
55. Oksanen, A. J. et al. *Vegan: Community Ecology Package*. R package version 2.5-7 https://CRAN.R-project.org/package=vegan (2020).
56. Anderson, M. J. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* **26**, 32–46 (2008).
57. Venables, W. & Ripley, B. *Modern Applied Statistics with S.* (Springer, 2002).
58. Lenth, R., Singmann, H., Love, J., Buerkner, P. & Herve, M. *Package 'emmeans'* https://github.com/rvlenth/emmeans (2018).
59. Signorell, A. *DescTools: Tools for Descriptive Statistics* (2021).
60. Hallett, L. M. et al. codyn: an R package of community dynamics metrics. *Methods Ecol. Evol.* **7**, 1146–1151 (2016).
61. Wood, S. N. *Generalized Additive Models: An Introduction with R* 2nd edn 1–476 (CRC/Taylor & Francis, 2017).
62. Bürkner, P. C. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).
63. Gelman, A. & Rubin, D. B. Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 547–511 (1992).
64. Vehtari, A., Gelman, A. & Gabry, J. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432 (2017).
65. Modrák, M., Barrett, M., Weber, F. & Coronado, E. *bayesplot: Plotting for Bayesian Models*. R package version 1.8.0 https://mc-stan.org/bayesplot/ (2021).
66. Makowski, D., Ben-Shachar, M. & Lüdecke, D. bayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. *J. Open Source Softw.* **4**, 1541 (2019).
67. Phillips, M. L., Howell, A., Lauria, C. M., Belnap, J. & Reed, S. C. Data and software code from two long-term experiments (1996–2011 and 2005–2018) at three sites on the Colorado Plateau of North America (US Geological Survey, 2021); https://doi.org/10.5066/P9RUN1TP

Author contributions
J.B. acquired financial support and established the field projects. S.C.R. acquired financial support and provided overall direction of the field operation. A.H. and C.M.L. collected biocrust community data in the field and maintained the climate manipulation experiment. M.L.P. and B.E.M. analysed the data. M.L.P acquired financial support and wrote the initial draft of the manuscript. All authors contributed to the synthesis of data and the final manuscript.

Competing interests
The authors declare no competing interests.

Additional information
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Reporting Summary

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

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☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We did not use any software or code for our data collection.
Data analysis	We used the statistical program R (v 3.6.1), and the program Stan accessed through the R package 'brms' (v 2.14.4) as well as the 'codyn (v 2.0.5), 'MASS' (v 7.3.5),'vegan' (v 2.5.7), 'bayesplot' (v 1.8.0) ,'mgcv' (v 1.8.33) and 'BayestestR' (v 0.9.0) packages to run all statistical analyses. All analysis code is available: https://doi.org/10.5066/P9RUN1TP .

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Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data and code generated and creadted during this study are available as a USGS data release. Phillips, M.L., 2021, Data and software code from two long-term experiments (1996-2011 and 2005-2018) at three sites on the Colorado Plateau of North America: U.S. Geological Survey data release, https://doi.org/10.5066/P9RUN1TP. Figures 1a, 1c, 2, 3, and Supplementary Figures 7 of this manuscript have associated raw data.

Field-specific reporting

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Ecological, evolutionary & environmental sciences study design

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Study description	This study synthesized biological soil crust (biocrust) responses to climate manipulation and physical disturbance experiments at three sites located on the Colorado Plateau of southeastern Utah (Supplementary Table 1). All three sites had similar biocrust community composition and structure before the experiments started, including lightly-pigmented cyanobacteria (Microcoleus vaginatus), darkly-pigmented cyanobacteria (Nostoc spp., Scytonema spp., and Tolypothrix spp.), mosses (Syntrichia caninervis and S. ruralis), and lichens (Collema tenax and C. coccophorum).
	The climate manipulation began in October 2005 at a site located near Castle Valley, Utah (38.67° N, 109.42° W). This site is dominated by the shrub species Atriplex confertifolia, the perennial grass species Achnatherum hymenoides and Pleuraphis jamesii, and the exotic annual grass Bromus tectorum. Infrared lamps, installed 1.5 m above the soil surface, heated the topsoil 2 ºC above ambient for the first three years of the experiment and temperatures were increased to 4 ºC above ambient starting in June 30, 2008 until present. The altered precipitation treatments were designed to mimic 1.2 mm monsoonal rainfall events and took place between June 15 to September 15 each year from 2005-2012. These treatments were applied with hand sprayers. During these years, plots received on average 35 events (roughly four times the average natural frequency; 6, 7, 43, 44). The two physical disturbance sites were established in the Spring of 1996 and are located in Arches (38.73° N, 109.54° W) and Canyonlands (38.46° N, 109.54° W) National Parks. See Kuske et al. 2011for experimental design details. Treated plots were trampled by human steps once a year every May for fifteen years until May of 2011. In May and June of 2018 biocrust community was assessed following seven years of the warming treatments and recovery from climate and physical disturbances recovery (Supplementary Fig. 1). We examined ambient precipitation and temperature patterns at each of the sites using PRISM, and found the patterns were consistent across sites (Supplementary Figs. 9 and 10). We measured biological soil crust cover twice a year as well as soil aggregate stability. We assessed overall differences in biocrust community composition among treatments and sites using Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis similarity. We tested for significant differences among biocrust communities, treatments, and sites by performing permutational multivariate analysis of variance (PERMANOVA) using the 'adonis' function (999 permutations). We use a negative binomial generalized linear model to test for differences in moss cover between pre-treatment, post-treatment and recovery for each treatment using the 'glm.nb' function in the 'MASS' package. We calculated least-square means to make pairwise comparisons between pre-treatment, post-treatment and recovery for each treatment using the 'emmeans' function from the 'emmeans' package. We did not include Warmed + Altered Precipitation in the pairwise comparison because moss cover values were 0 in all plots for post-treatment (2012) and recovery (2018) timepoints (Figure 1b). To test for differences in scaled slake scores between the undisturbed control and each treatment, we used a maximum likelihood statistical significance tests (G-test) using the 'GTest' function in the 'DescTools' package. Summaries of maximum likelihood significance tests can be found in Supplementary Table 4. To assess biocrust community dissimilarity over time, we used the 'rate_change_interval' function from the 'codyn' package to calculate Euclidean distances at each time interval. We fit generalized additive models to these data, with Euclidean distance as the response and interval as the predictor using the 'gam' function in the 'mgcv' package. We examined the legacy effects of altered precipitation, as well as the ongoing effect of warming on biocrust functional groups, using a Bayesian multilevel model with default (non-informative) priors. Biocrust cover was the response variable and functional group as population-level (fixed) effects and treatments within sites for each functional group as a group-level effect. This allowed varying slopes for each site:treatment combination. We chose this approach to account for the fact that all the treatments did not occur at all of the sites. We also included a group-level effect for plot (sampling unit) that allowed for the intercept to vary. The response variable (biocrust cover) was heavily tailed and had many zeros, because of this we used a zero inflated negative binomial data distribution with a log link and link shape function. Models were fit using the R package 'brms'. The final model is detailed in Appendix S1.
Research sample	Research samples were biological soil crust composition and abundance from point intercept frames and slake scores derived from soil pedon samples using the method outlined in Herrick et al. 2001. Biological soil crust communities were assessed in two ways, both of which used 25 cm x 25 cm frames and a point intercept method with 20 points in each frame. We measured soil aggregate stability (a measure of erodibility) using the method outlined in Herrick et al. 2001. In this method, soil aggregates are ranked ('slake scores') on an ordinal scale of 1 (least stable) and to 6 (most stable).
Sampling strategy	Frames were assessed under shrubs and in interspaces among plants away from plot edges to avoid edge affects. First, in May and June 2018, to assess recovery following physical and climate disturbance, biocrust composition was determined using comparable within-plot locations at all three sites (under shrubs and in the interspace among vascular plants; Supplementary Tables 1 and 2). For the trampling sites in Arches and Canyonlands National Parks, a total of 240 frames were read (4800 points), with 12 frames per plot and ten plots at each site (five control, five treatment; Supplementary Table 2). For the climate manipulation sites in Castle Valley, a total of 120 frames were read (2400 points), 6 frames per plot, for each of the four treatments (five replicate plots per treatment; Supplementary Table 2). These frames were also assessed under shrubs and in interspaces among plants and away from the edges of the plots. Second, in addition to these cross-experiment assessments, biological soil crust community composition in the climate manipulation experiments is assessed annually using four frames per plot (80 frames and 1600 points), To estimate plot level biocrust cover, we divided the number of species or biocrust type readings per plot by the total readings per plot. We included shrub and interspace together in our plot level calculations because we were interested in overall biocrust community responses to treatments.

Data collection	PIs, Post-docs and technicians collected the data using point intercept frames within the plots twice a year. Soil samples were collected for soil stability. Measurements were recorded in the field data sheets and entered into excel spreadsheets.
Timing and spatial scale	Biocrust point intercept frames were measures in the fall and spring at the climate manipulation plots every year from 2005-2018. All frames at the experiment were measured within a two week period. In May and June of 2018 biocrust community was assessed following seven years of the warming treatments and recovery from climate and physical disturbances recovery.
Data exclusions	No data were excluded from the analysis.
Reproducibility	This is a data synthesis, with field monitoring data collected over time, so we can not reproduce the experiments exactly. However all all data and code for analyses from this synthesis are publicly available so that others may use our analytical approach with their own community composition data.
Randomization	The locations of control and experimentally manipulated plots were fully randomized within each study site.
Blinding	Blinding was not possible in this study due to requirements of field researchers to visually identify biocrust species.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	This region is classified as a cool desert with an annual temperature range of 4-13 C and annual precipitation range of 205-510 mm. Biocrust cover data was recorded in fall and spring.
Location	Location and site characteristics can be found in Supplemental table 1.
Access & import/export	Biocrust observations were taken by site PIs, Postdocs, and field technicians and were recorded on field data sheets and then sent to the lead author electronically, so no export of samples was necessary. The appropriate permits to access research sites were obtained whenever necessary and the permits/permissions necessary.
Disturbance	Data collectors only observed biocrust composition in plots, and did not disturb or step in the plots. Established walkways are used to minimize disturbance in the area. The warming treatments are provided using infared lamps that are placed in all plots, but only provide warming in the warmed treatments.

Reporting for specific materials, systems and methods

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Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging