Decline in biological soil crust N-fixing lichens linked to increasing summertime temperatures

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Biological soil crusts (biocrusts), comprised of mosses, lichens, and cyanobacteria, are key components to many dryland communities. Climate change and other anthropogenic disturbances are thought to cause a decline in mosses and lichens, yet few long-term studies exist to track potential shifts in these sensitive soil-surface communities. Using a unique long-term observational dataset from a temperate dryland with initial observations dating back to 1967, we examine the effects of 53 y of observed environmental variation and *Bromus tectorum* invasion on biocrust communities in a grassland never grazed by domestic livestock. Annual observations show a steep decline in N-fixing lichen cover (dominated by *Collema* species) from 1996 to 2002, coinciding with a period of extended drought, with *Collema* communities never able to recover. Declines in other lichen species were also observed, both in number of species present and by total cover, which were attributed to increasing summertime temperatures. Conversely, moss species gradually gained in cover over the survey years, especially following a large *Bromus tectorum* invasion at the study onset (ca. 1996 to 2001). These results support a growing body of studies that suggests climate change is a key driver in changes to certain components of late-successional biocrust communities. Results here suggest that warming may partially negate decades of protection from disturbance, with biocrust communities reaching a vital tipping point. The accelerated rate of ongoing warming observed in this study may have resulted in the loss of lichen cover and diversity, which could have long-term implications for global temperate dryland ecosystems.

biological soil crust | lichens | global change

Dryland ecosystems cover ~40% of the land surface and house more than 2.5 billion people, despite having sparse plant cover and limited water resources (1–3). Climate change, human land-use impacts, and the spread of invasive plants are commonly noted stressors that contribute to ongoing dryland degradation (3–6). Once degraded, drylands can undergo loss of vegetation, soil erosion, and reduction of soil water-holding capacity and fertility, which can ultimately result in the ecosystem moving toward an alternate steady state characterized by reduced ecosystem services (1, 3–5, 7–9). Ecological theory on alternative steady states suggest that either long-term environmental drivers (e.g., increase in temperature and change in precipitation) and/or short-term trigger disturbances (e.g., fire, population outbreak of nuisance species, and trampling from humans or livestock) can result in the restructuring of ecosystems, which can ultimately push a system across a critical tipping point (8–12). Such tipping points or nonlinear changes make it extremely difficult or even impossible for an ecosystem to return to its original state (8, 10–12). Thus, identifying critical ecosystem indicators and potential tipping points in globally important biomes, such as drylands, is essential for anticipating, and potentially mitigating, long-term changes.

Due to their important role in dryland ecosystems globally, biological soil crust (biocrust) cover is commonly used to distinguish between two alternative steady states: an intact state with stable soils and productive vegetated states or a degraded state with reduced productivity and accelerated erosion (1, 7, 9, 13). In high biocrust cover states, biocrusts can cover up to 70% of the ground surface and are known to be vital yet vulnerable members of the ecosystem (1, 13–16). Comprised of mosses, lichens, cyanobacteria, and soil heterotrophs, biocrusts contribute significantly to dryland ecosystems through primary production, water retention, biogeochemical cycling, soil stability, and seed capture (16). The lichen genus *Collema* is especially important for contributing fixed nitrogen (N) to the soil environment, especially in dryland systems that are often N-limited ecosystems (17, 18). However, these soil surface communities are also highly sensitive to physical disturbance and trampling (7), with limited ability to return to a predisturbance state (9, 13, 16) and cascading feedback to overall ecosystem structure and function (19). In addition to physical disturbance, experimental studies

Significance

Across many global drylands, biocrusts form a protective barrier on the soil surface and fill many critical roles in these harsh yet fragile environments. Previous short-term research suggests that climate change and invasive plant introduction can damage and alter biocrust communities, yet few long-term observations exist. Using a globally unique long-term record of continuous biocrust surveys from a rare never-grazed, protected grassland on the US Colorado Plateau, we found lichen species diversity and cover to be negatively correlated with increasing summer air temperatures, while moss species showed more sensitivity to variation in precipitation and invasive grass cover. These results suggest that dryland systems may be at a critical tipping point where ongoing warming could result in biological soil crust degradation.

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suggest that biocrusts are also sensitive to variations in climate and exhibit declines in late-successional community organisms (lichens and mosses) with increases in temperature or altered precipitation patterns (7, 20–23). Warming experiments in the drylands of Spain found that increasing temperatures can reduce lichen species cover and richness (20–22), while moss species have shown sensitivity to altered precipitation patterns on the Colorado Plateau of North America (7, 9, 23). Additionally, climate manipulations show similar community compositional shifts as physical disturbance (7, 9), as do global synthesis and modeling projects (14), thereby calling into question biocrust state stability in a warming world.

Despite numerous short-term experimental studies exploring how warming may impact biocrust communities in the future, there is a lack of long-term data describing how biocrusts respond to warming over longer timescales (10+ y). Across many global drylands, increasing temperatures and altered precipitation are increasing drought frequency and severity (3, 5), which have resulted in vegetation shifts (24). However, it is unclear whether biocrusts are also responding to climate change. In areas where grass cover and other vascular vegetation may be in decline, biocrusts could potentially expand as more of the soil surface is available for colonization, especially for moss species (25). Conversely, the same climatic mechanism leading to declines in vascular vegetation (e.g., increases in drought and greater temperature extremes) could also negatively impact biocrust primary producers, ultimately leading to biocrust decline (1).

Using a long-term observational study of late-successional biocrust community components (lichens and mosses), we explore variations in biocrust communities over 23+ y in a rare never-grazed, protected temperate grassland on the Colorado Plateau in Canyonlands National Park in southeast Utah. Starting with the migration of settlers of European descent into the western United States in the late 1800s, over 90% of the Colorado Plateau was heavily impacted by livestock grazing, which often resulted in massive soil depletion and erosion (26–28), leaving never-grazed grasslands like the one studied here exceedingly rare across the region. Additionally, the Colorado Plateau is one of North America's most rapidly warming hot spots, with rates of warming of up to 2 to 3 °C within the last 100 y (28). These warming trends have already been linked to increasing drought severity, leading to loss of grass cover, and increases in aeolian sediment flux (29, 30). Observations of vegetation and biocrust cover for our study site date back to 1967 (31), with long-term monitoring plots established from 1996 to 1998 after an observed increase in cover of the nonnative cheatgrass *Bromus tectorum* (32). *B. tectorum* is a highly invasive annual grass that is known to alter North American dryland systems by outcompeting native bunchgrasses (6), resulting in an accumulation of litter that can constrain photosynthetic activity in biocrust (33). By studying a rare, protected ecosystem, we were able to isolate the role of climate drivers from other anthropogenic disturbances (e.g., livestock grazing) and invasive grass expansion on biocrust cover and explore potential ecological thresholds using breakpoint analysis. Additionally, for the *B. tectorum*–invaded plots, we asked if invasion had longer-term effects on biocrust cover.

Results

Long-term climate records from 1967 to 2019 from the Canyonlands Needles Visitor Center recorded a mean annual temperature of 13.3 °C (±0.8 SD) and 214.7 mm (±50.5 SD) of mean annual precipitation. Analysis of long-term climate

indicated that mean annual temperatures have steadily increased from 1967 to 2019 at a rate of ~0.27 °C (±0.05 °C) per decade (Fig. 1; $\tau = 0.388$, $P < 0.001$). Notably, from 1996 to 2019, mean annual temperatures were above the 52-y mean temperature of 13.3 °C for 17 of the 23 y (Fig. 1). Despite clear warming trends, no systematic patterns or directional changes in annual precipitation were observed across the same period (Fig. 1; $\tau = -0.026$, $P = 0.79$). Additionally, the standardized precipitation-evapotranspiration index (SPEI) also oscillated throughout the observation period, without directional change across the long-term record (Fig. 1; $\tau = 0.02$, $P = 0.76$). From 1996 to 2019, there were least two significant droughts (multiyear water deficits, where SPEI < -1): from 2000 to 2004 and from 2017 to 2018 (Fig. 1).

Study plots were established using a factorial design within two dominant native perennial grass community associations: a warm-season C_4 rhizomatous grass, *Pleuraphis jamesii*, and codominant cool-season C_3 bunchgrasses, *Hesperostipa comata* and *Achnatherum hymenoides*, both with and without *B. tectorum* invasion ($n = 3$ for each cover type for a total of 12 plots). However, *B. tectorum* was not consistently present across the years, even within *Bromus*-designated plots, with several observed booms and crashes in the invasive grass's cover. The highest cover years occurred early in the study, spanning from 1998 to 2001, which was followed by several years of little to no observed *Bromus* cover (*SI Appendix*, Fig. S1).

Long-term trends show declines in lichen species richness and cover, for both N-fixing lichen (lichens with cyanobacterial photobionts) and other lichen (lichens with green algae photobionts) communities (Figs. 2 and 3 and *SI Appendix*, Tables S1 and S2). N-fixing lichen cover declined from ~19% mean cover in 1967 and 1996 to ~5% mean cover in 2019 (Fig. 2 and *SI Appendix*, Table S2). Output from fitted generalized additive mixed models (GAMMs) indicates that community plant cover type also influenced N-fixing lichen variation, with the greatest difference between warm-season C_4 grass–dominated
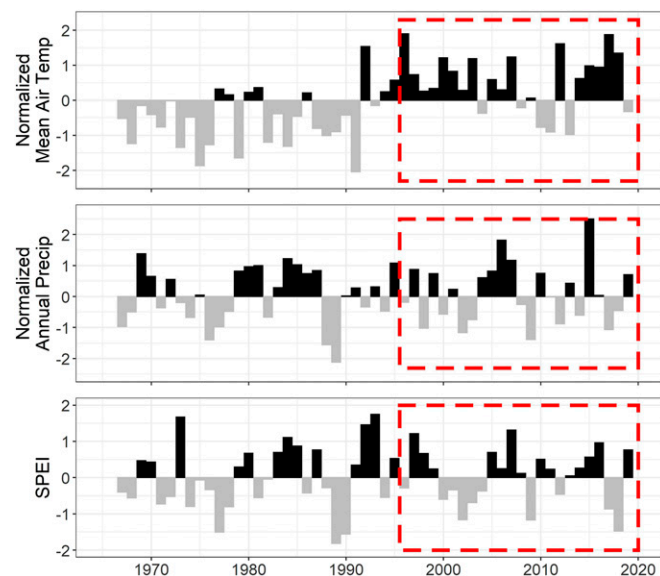
Fig. 1. Normalized and standardized climate analyses from 1966 to 2019 from the Canyonlands Needles Visitor Center, including normalized mean annual temperature (Air Temp) (*Top*), normalized annual precipitation (Precip) (*Middle*), and SPEI (*Bottom*). Normalized measurements were calculated as [(Observed − Mean)/SD]. For SPEI, positive numbers indicate water surplus compared to the mean, whereas negative numbers indicate water deficit compared to the mean. The red hashed box outlines the period of this study, from 1996 to 2019.
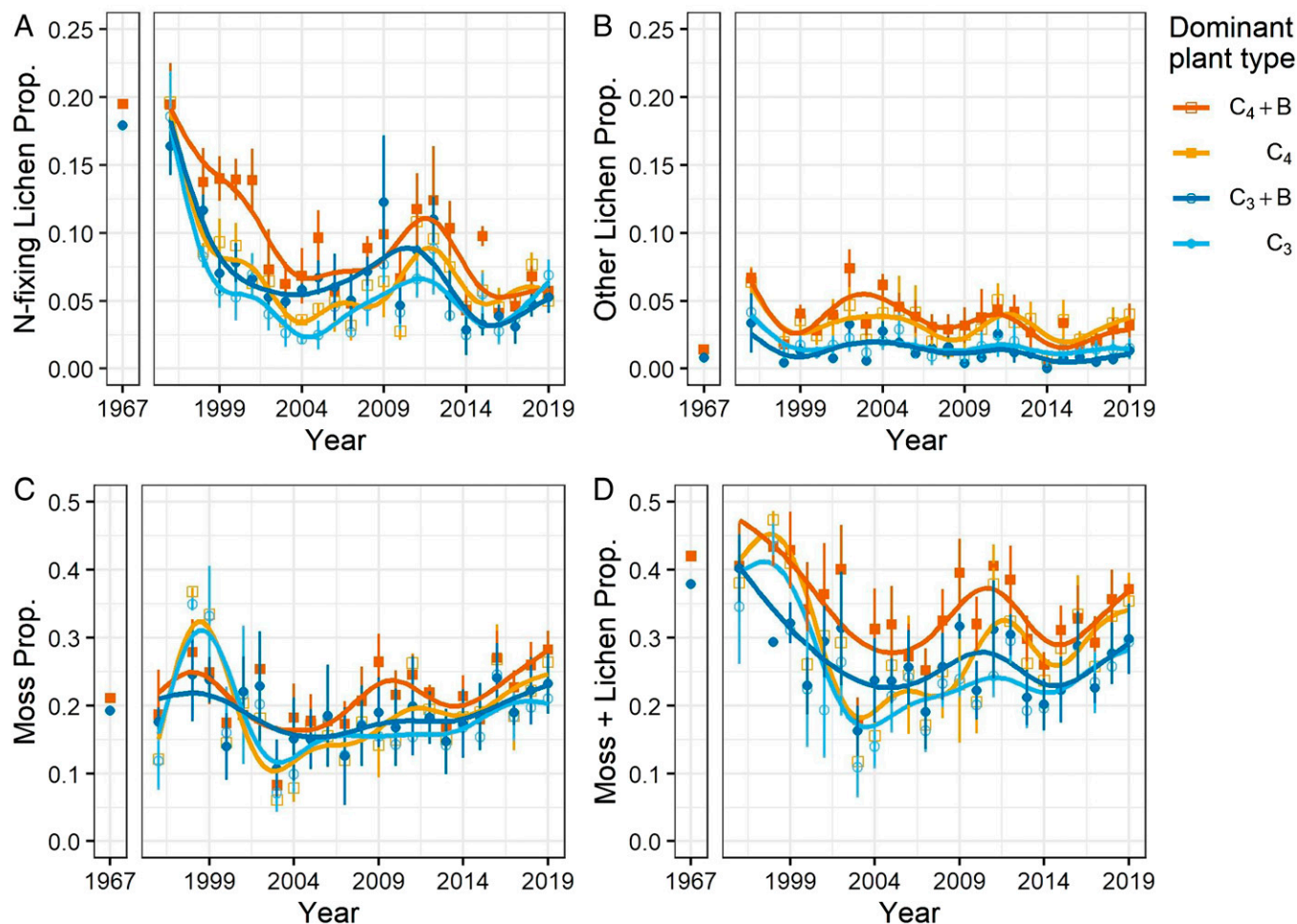
Fig. 2. GAMMs of long-term changes in proportional (Prop.) cover of late-successional biocrust components across different bunchgrass communities: C₃-dominated plots (C₃), C₃-dominated plots + *Bromus* (C₃ + B), C₄-dominated plots (C₄), and C₄-dominated plots + *Bromus* (C₄ + B) (*n* = 3 plots for each cover type for a total of 12 plots) for N-fixing lichens (*A*), other lichens (*B*), moss (*C*), and total biocrust cover (lichens + mosses) (*D*) from 1996 to 2019 and by dominant grass community cover type. Data points from 1967 were originally recorded by Kleiner and Harper (31). Summary statistics for GAMMs are presented in *SI Appendix*, Table S2. Error bars represent ±1 SE.

plots (which tended to have higher N-fixing lichen cover) and cool-season C₃ grass–dominated + *Bromus* plots (lowest N-fixing lichen cover) (Fig. 2 and *SI Appendix*, Table S2). Other lichens also experienced population declines over the 23-y study period, notably through both loss of species (*SI Appendix*, Table S1) and loss of total cover (*SI Appendix*, Fig. S2 and Table S2). Lichen cover was greater in C₄ grass–dominated plots than in C₃ grass–dominated plots across the time series (Fig. 2).

At the genus and species levels, we observed notable declines in cover of the other lichens, especially within the *Fulgensia* and *Psora* genera, with *Fulgensia* not observed since 2017 (*SI Appendix*, Table S1 and Fig. S1). Declines in the yellow lichen, *Fulgensia*, can also be readily observed in repeat photography (Fig. 3). *Aspicilia hispida* and *Placidium* species communities appeared to be more stable across the time series, with *Placidium* even appearing to increase in cover in the C₄ grass–dominated + *Bromus* plots (*SI Appendix*, Fig. S1 and Table S2).

Moss comprised the largest proportion of late-successional biocrusts and showed sensitivity to climate variation and episodic *Bromus* outbreaks (Fig. 2 and *SI Appendix*, Fig. S3). Moss cover was the highest in 1998 and 1999 in both C₄ grass–dominated plots and C₃ grass–dominated + *Bromus*-invaded plots (between 26 and 32%; Fig. 2), which coincided with a period of high *B. tectorum* cover (*SI Appendix*, Fig. S1).

However, the moss cover did not continue at similar levels during the start of the 21st century, and by 2003, there was no significant difference in moss cover across the different plant community cover types (Fig. 2). From 2003 to 2019, moss cover gradually increased in cover, as can be observed in the dominant moss, *Syntrichia caninervis*, especially in the C₄ grass–dominated plots, and largely regained losses in cover to pre-1998 levels (*SI Appendix*, Fig. S2).

Combined, late-successional biocrust cover components (lichens + mosses) slightly declined from the 1967 and 1996 values of ~40% across all surveyed plots to ~35% cover in C₄ grass–dominated plots and 28% cover for C₃ grass–dominated plots (Fig. 2). Declines in total biocrust cover corresponds with the steep decline of N-fixing lichens, driven largely by the loss of *Collema* species (comprising ~85% of the total N-fixing lichen community) (Fig. 2 and *SI Appendix*, Fig. S2), especially between 1996 and 2003. *Collema* species had a brief recovery from 2011 to 2012 but did not return to historically higher levels recorded in 1967 and 1996 (Fig. 2 and *SI Appendix*, Fig. S2). However, stability and even subtle increases in moss cover maintain >25% for late-successional biocrust communities throughout the duration of this study.

B. tectorum outbreak events, and the legacy of increased grass litter, impacted all components of late-successional biocrust communities (N-fixing lichens, other lichens, and moss) yet
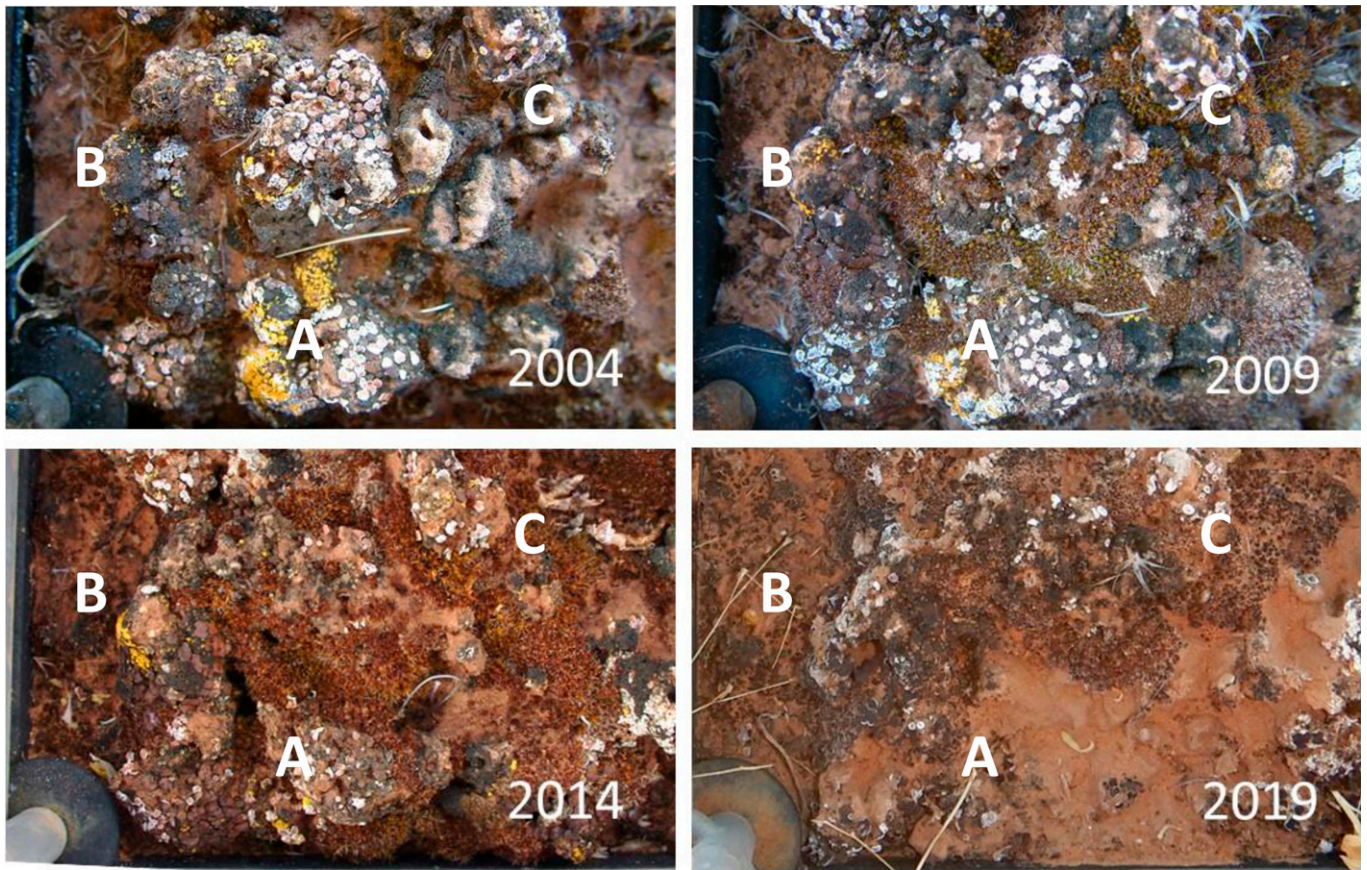
Fig. 3. Series of repeat photographs of biocrusts taken from the same area in 2004, 2009, 2014, and 2019. Letters on photographs indicate the same spot across the time series. Notable declines in the yellow lichen species of *Fulgensia* can readily be observed near letters A and C. Declines in the white edge lichen, *Psora decipiens*, can be observed throughout the photos.

explained very little of the overall observed variance (*SI Appendix,* Fig. S3). Spring *B. tectorum* cover correlated positively with moss cover ($z = 2.78$, $P < 0.001$) and marginally with N-fixing lichen cover ($z = 1.81$, $P = 0.07$) (Fig. 4). Grass litter correlated negatively with all biocrust components (Fig. 4). Additionally, at subplots that were heavily invaded from 1998 to 2000 (*B. tectorum* cover recorded as higher than 50%), we found that total biocrust cover remained lower, even years and decades following outbreaks (Fig. 4).
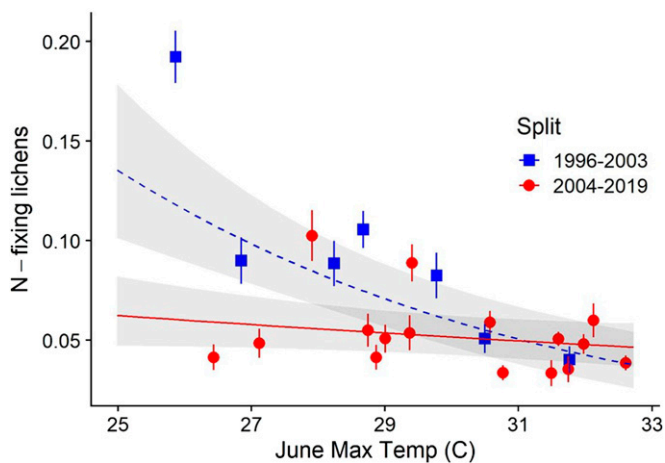
Fig. 4. GLMM predicting the proportion of N-fixing lichen proportional cover by June maximum temperatures (Max Temp, °C) both prior to 2003 (blue squares) and after 2003 (red circles). Error bars represent SE. R^2 conditional = 0.03, R^2 marginal = 0.41.

Mean maximum June temperatures were negatively correlated with lichen cover, both for N-fixing lichens and other lichens (*SI Appendix,* Table S3). June temperatures were of particular interest as this is a known period of lichen activity and sensitivity (32). Additionally, for N-fixing lichens, changepoint analysis identified an apparent tipping point around 2003, after which the population was unable to recover back to previously recorded levels from 1996 and 1967, despite cooler June temperatures (Fig. 4). Moss cover also showed negative correlation to mean maximum summertime temperatures and winter precipitation yet positive correlation with spring precipitation (*SI Appendix,* Table S3).

Discussion

Here, we show that ongoing climate change may be deleteriously impacting biocrust communities, even in a pristine dryland community that has avoided anthropogenic disturbances, such as livestock grazing and human trampling. It appears that increasing regional air temperatures over the previous 20 y are more negatively correlated with changes in biocrust community structure, via declines in biocrust lichens, than a notorious invasive grass, *B. tectorum*. We found that several lichen species have suffered a precipitous decline in total cover over the last 23+ y (Figs. 2–4). The lichen declines were negatively correlated with rising temperatures (Fig. 1), especially in the summer months of June and July (Fig. 4 and *SI Appendix,* Table S3), and to a lesser effect, *B. tectorum* invasion and the incidental accumulation of grass litter in nonoutbreak years (*SI Appendix,* Table S3) (32). This long-term study also captures a nonlinear

change for N-fixing lichen species populations which have declined rapidly, potentially caused by persistent increases in air temperatures and episodic drought conditions (Fig. 4). Similar declines in *Collema* lichen populations have also been observed in a neighboring experimental warming experiment on the Colorado Plateau, which demonstrated biocrust sensitivity to increasing temperatures (7). We hypothesize that persistent warming and drying trends across the Colorado Plateau over the last two decades (34) may be nearing a tipping point for N-fixing lichen recovery (Fig. 4) (7, 10, 11). The loss of N-fixing lichens is also likely to influence the greater ecosystem, as N cycling dynamics may shift due to declining atmospheric N inputs from biocrust lichens (18). Importantly, with average lichen cover now equaling only ∼5% of total ground cover in this protected site, biocrust community composition is similar to that of adjacent sites that have previously experienced extensive livestock trampling (13, 32), potentially marking a shift in the ecosystem that may persist after the current drought abates. This supports other long-term observational and experimental studies in the greater Colorado Plateau area that demonstrate that elevated temperatures can be as detrimental to biocrusts as physical disturbances (7, 9).

However, the question remains: what physiological mechanisms are driving the alleged climate-induced lichen species declines in a highly protected grassland on the Colorado Plateau? Here, we propose a few plausible explanations. First, experimental evidence suggests that at higher temperatures, the net carbon exchange of lichen species can be negative, which could lead to carbon loss or starvation (7, 35–37). Previous work by Lange et al. (35) showed experimentally that at 41 °C, *Collema tenax* had a negative net carbon flux, even during extremely dry conditions. In contrast, lichens under cooler treatment conditions had zero net carbon exchange until there was adequate moisture in the soil system (35). On the Colorado Plateau, soil surface temperatures in June and July are likely several degrees warmer than recorded air temperatures (37, 38) and frequently exceed 41 °C (37). Additionally, lichen species' metabolic processes may be primed and activated by small amounts of moisture in the form of relative humidity and dew points, thereby further exacerbating carbon losses in hot summer months (39).

Another potential explanation for declining lichen populations at our study site could be varying population-level and species-level tolerances to heat stress. Lichen populations within our study system, particularly *Collema* species, are potentially more sensitive to high temperatures than their more southernly, and thus potentially heat-adapted, relatives. Experimental research by Grote et al. (36) found that dark biocrusts from the Colorado Plateau had lower rates of net photosynthesis than dark biocrust collected from the hotter Chihuahuan Desert of New Mexico, especially when soil moisture was below 20%. Additionally, different lichen species are also known to have different tolerances to changes in temperatures, with *Psora* species exhibiting more sensitivity to warming than *Diploschistes* species and *C. tenax* (35). Finally, the observed negative correlations between lichen species and June maximum temperatures could simply be a spurious correlation with other regional climate signals, with hot Junes linked to another set of climate properties that the biocrusts are responding to, rather than a specific direct impact of, hot June temperatures. Due to the complex nature of environmental change and the relatively limited number of data points (even with the 23 y of observation), we cannot attribute true causality.

Interestingly, warming during the 23 y of observation likely did not cause a decline in biocrust moss cover (Fig. 3). Instead, mosses may have compensated for the loss of lichens by increasing proportional cover from 2003 to 2019 (Fig. 3). One possible explanation for moss increases in the last 10+ y of the study could be due to growth compensation following initial declines after a major *B. tectorum* outbreak and decrease in biocrust community competition due to lichen declines. We found that moss cover was positively correlated with spring precipitation (*SI Appendix*, Table S3), suggesting that growing-season precipitation events might also aid in moss growth (40). However, these environmental modeling results should be interpreted with caution, as warmer July temperatures were negatively correlated with moss cover, suggesting a delicate balance between increasing temperatures and variations in precipitation. Changes in the frequency and amount of water falling in a given precipitation event can adversely impact biocrust moss and lichen success (7, 40, 41). A nearby long-term field experiment showed that moss populations decline if the frequency of small (<2 mm) rainfall events increases during the hot summer months of June, July, and August (7, 41, 42). Such observed declines in late-successional biocrust populations are often attributed to carbon starvation, as small rainfall events do not provide enough moisture to compensate for the cost of repairing and priming metabolic and photosynthesis machinery (40, 43). If ongoing climate change on the Colorado Plateau leads to more small rainfall events and much hotter summers, then the observed trajectory of moss increase could be quickly reversed (7, 41, 42). Finally, it should also be noted that both dark and light cyanobacterial biocrusts are abundant across our study system, so even with declines in lichen cover and shifts in moss cover, observations suggest that biocrusts still cover much of this environment (44). Thus, despite declines in lichen species abundance and cover, biocrusts are still present and thus able to offer some level of stability and resistance to soil erosion (30).

Despite correlations between moss and lichen cover with environmental factors, edaphic and community interactions likely also partially regulate biocrust composition and temporal dynamics. First, we found that late-successional biocrust cover was generally highest in warm-season C_4 grass–dominated communities as compared to cool-season C_3 grass–dominated communities (Figs. 3 and 4), most likely due to differences in soil properties, with C_3 communities often consisting of higher proportions of sand than C_4 communities (31, 32, 45). Second, community interactions, both between *B. tectorum* outbreak events (32, 33) and between different biocrust components (46), likely influenced observed trends and variations in late-successional biocrust components. Moss cover notably decreased in both C_4 and C_3 grass–dominated plots during a widespread *B. tectorum* outbreak in the late 1990s (Fig. 2), potentially due to an increase in litter, blockage of light on photosynthetically active biocrust surfaces (33), and extended drought conditions (Fig. 1). However, observed declines in moss cover were reversible, especially as *Bromus* cover failed to reach previous levels in later years of this study (Fig. 2). Additionally, it is also possible that moss species were able to recover and expand following recorded low cover in the early 2000s due to dieback of lichens freeing up previously occupied soil surfaces. Abiotic stress, due to increasing summer temperatures and variations in precipitation, can also increase intra- and interspecific biocrust competition, as scarce resources like water and nutrients become more limiting (46). Therefore, like most ecological systems, biocrust communities are being shaped by direct climatic and competitive forces, as well as complex interactions of climate, soils, vegetation, and the rest of the biocrust community.

Conclusions

During the 23+ y of this study, we observed a potential climate-driven transition of a never-grazed temperate grassland biocrust system, with an equal proportion of lichen and moss at the study onset, to a community that is much more moss dominated. This study duration also coincided with a documented megadrought in southwestern North America, the likes of which have not been seen in over 500 y (34). The decline in lichen was mostly attributed to warming summer temperatures, with the dominant lichen genera (*Collema*) experiencing a stark decline correlated with warming June temperatures (post-2003; Fig. 4), where despite cooler subsequent June temperatures, populations were unable to recover to pre-1998 levels of cover. However, due to the limitations of this study, further experimentation and observations are needed to corroborate the temperature sensitivity of Colorado Plateau lichen species. Observed declines in *Collema* species could ultimately reduce the amount of atmospheric N entering the system, as these species are known to be important for N fixation (18), which could have long-lasting and important ecological implications with potential declines in primary production and biogeochemical cycling (20, 35). Additionally, the disappearance of numerous lichen species, including the yellow lichen species of the *Fulgensia* genus (Fig. 3 and *SI Appendix*, Figs. S1 and S2), suggests that lichen components of the biocrust community may be nearing a threshold due to ongoing regional warming. Only one genus of lichen, *Placidium*, appears to be stable (*SI Appendix*, Fig. S2), if not slightly increasing within our study area, suggesting that as a group, biocrust lichens might have lower resiliency to ongoing warming than once thought. Moss species cover also shows dynamism across the study period, notably by steadily increasing following a recorded low in *Bromus*-invaded plots in the late 1990s. Combined, our results suggest that ongoing climate change may have already impacted biocrust communities and that associated deleterious changes will likely continue, both within and outside this study system.

Potential climate-driven shifts and declines in late-successional biocrust communities could ultimately lead to an ecological state change in biocrust-dominated ecosystems (1, 7, 9). Nonnative plant invasion, namely in the form of *B. tectorum* outbreak events, have the potential to add further stress on these systems, potentially exacerbating precariously balanced systems. Such changes could drastically impact biogeochemical cycling, water retention, and soil stability across drylands (16, 19). Considering that many *Collema* species are known to play an important role in fixing atmospheric N (17, 35), continued declines in cover and abundance of these species could limit the amount of N that is accessible to dryland plant-soil systems. Additionally, shifts in biocrust communities and loss of protective lichen and moss cover might ultimately leave soils more susceptible to accelerated erosion and subsequent loss of soil fertility and water-holding capacity (1, 7, 9, 20). Suggested decreases in the resiliency of biocrusts to regional warming and drying trends indicate that these crucial living skins of drylands may be more susceptible to climate change than once thought, and continued monitoring and protection is warranted.

Materials and Methods

Site Description. To explore the impact of climate variation and cheatgrass (*B. tectorum*) invasion on biocrust stability through time, we studied a grassland known as Virginia Park (VP) within the Needles District of Canyonlands National Park, Utah, that was never grazed by domestic livestock despite widespread grazing in the area prior to park establishment. This grassland comprises two distinct and common perennial grassland community associations: one dominated by the predominately spring-active C$_3$ grasses, *H. comata* and *A. hymenoides,* and another community dominated by the warm-season active C$_4$ grass *P. jamesii* (32, 47). Soils at the study sites were predominantly fine sandy loams derived from aeolian sands, with some sandstone alluvium and residuum at depth and weak soil horizon development [dominantly Ustic Torripsamments and Ustic Haplocambids (31, 32, 45)]. Previous research in the area found differences in soil texture between the different plant cover types, with soils of C$_4$ grass–dominated sites having slightly finer textures (more silt and fine sand) than C$_3$ grass–dominated sites.

Ecological monitoring of VP occurred in the 1967, when Kleiner and Harper estimated vegetation and cryptogamic (biocrust) cover across several transects within the grassland (31).The Kleiner and Harper transect sites were revisited in 1994, at which time the invasive grass *B. tectorum* appeared to have advanced across numerous VP sites. Therefore, to track long-term vegetation change and to document the potential impacts of *Bromus* invasion, long-term monitoring plots were established (32).

Long-Term Vegetation and Biocrust Monitoring. Monitoring plots were established in 1996 to 1998, with yearly springtime sampling around mid-May occurring most years from 1996 to 2019. Twelve permanent 0.5-ha plots were established in both C$_3$ and C$_4$ grass–dominated plots, both with and without *Bromus* invasion, to create a factorial study design including four different vegetation cover types: C$_3$-dominated plots, C$_3$-dominated plots + *Bromus*, C$_4$-dominated plots, and C$_4$-dominated plots + *Bromus* (n = 3 plots for each cover type for a total of 12 plots). Within each plot, 20 replicates of 0.25-m^2 frames were marked for subplot-level replication for vascular vegetation and biocrust cover estimates. Daubenmire (48) cover classes were used to estimate cover of vascular vegetation and ground litter with 6 different canopy cover classes: 1) 0 to 5%, 2) 5 to 25%, 3) 25 to 50%, 4) 50 to 75%, 5) 75 to 95%, and 6) 95 to 100%. Additionally, at all 20 subplots within a vegetation cover type plot, biocrust and ground cover estimates were sampled using a point-hit method, with a 0.1-m^2 frame containing 20-point intercept hits. The point-hit method was applied to account for the minute size of the mosses and lichens, as well as the highly discontinuous coverage of biocrust community members. When possible, lichens and mosses were sampled when dry, as surface moisture can obscure differences among dark-colored species and significantly alter cover of mosses and lichens. Percentage of cover was then calculated as the number of hits of a given biocrust component divided by the total number of point intercept hits. In the earliest years of the study (1996 and 1998), biocrust surveys were split into defined functional types: *Collema* spp. (later further grouped into N-fixing lichens), other lichens, moss, bare, and cyanobacteria. Starting in 1999, lichens were identified to species, and mosses were identified to species starting in 2002. Cyanobacteria ground cover throughout the study was also identified, but lightly versus darkly pigmented soil cyanobacteria were not distinguished, thereby limiting our ability to detect changes in the cyanobacterial component; thus, these data were not included.

In addition to repeated measures study plots, repeat photography of biocrusts started in 2004. Five 15 × 11 cm permanent frames were installed along five different randomly selected plots which allowed for a camera-holding frame to be placed above the biocrust for consistency from year to year. Biocrusts were lightly moistened and shaded when photographed to accentuate moss and lichen components.

Weather Data and Climate Analysis. Climate data collection for the Canyonland National Park Needles District at the visitor center began in 1965 following national park designation, with temperature and precipitation measurements recorded hourly. We acquired daily maximum and minimum temperature and precipitation data (January 1966 to December 2019) from the Needles Visitor Center through the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information Global Historical Climatology Network database (49) (data downloaded through http://www.climateanalyzer. org) to analyze long-term climate trends. Long-term weather records for mean annual temperature and annual precipitation were analyzed from 1966 to 2019 using the nonparametric Kendall-Mann trend test following data normalization [(Observed − Mean)/SD]. Additionally, to examine periods of drought, we used SPEI (50). SPEI is a drought index based on precipitation and temperature data

that incorporates climate water balance through the calculation of potential evapotranspiration (PET). To calculate SPEI, we first calculated daily PET using local climate data using the Hargreaves equation within the SPEI package in R (51). Next, we calculated SPEI in R using a 12-mo timescale, with positive numbers indicating wetter-than-average conditions and negative numbers reflecting drier-than-average conditions.

Additionally, an hourly recording weather station was established in VP in 1998 as a part of the US Geological Survey (USGS) Southwest Climate Impact Meteorological Stations network (52). However, due to the remote location of the weather station, periodic interruptions of data collection occurred throughout the study period. Gaps in climate data collection were filled using temperature and precipitation data from the Needles Visitor Center. Because there was a slight difference in temperature between these sites, a regression model was used to adjust temperature data collected at the Needles Visitor Center.

Using the gap-filled weather data from VP, we next summarized weather conditions for the 12 mo prior to annual monitoring visits (June to May the preceding year) to explore relationships between environmental variation and biocrust components (N-fixing lichens, other lichens, and moss). These 12-mo composite summaries included mean annual temperature, mean annual precipitation, and SPEI. Additionally, for modeling potential environmental controls on biocrust cover, we also calculated previous June, July, and August mean maximum temperature and previous seasonal precipitation for winter (December to February), spring (March to May), summer (June to August), and fall (September to November), as these variables have previously been suggested to be important to biocrust cover (32).

Statistical Analysis. All statistical analyses were conducted in R version 4.03.

To track variations in biocrusts over the 23-y study period, we constructed GAMMs for N-fixing lichen, other lichens, moss, total moss + lichen, and dominant species or genera comprising the biocrusts, including *Fulgensia* species, *A. hispida*, *Psora* species, *Placidium* species, *Collema* species, and *S. caninervis* (SI Appendix, Fig. S2 and Table S2), across all four plant cover types: C_3, C_3 + *Bromus*, C_4, and C_4 + *Bromus*. GAMMs are nonparametric generalized regression models that fit smoothing curves using cubic regression splines and allow for random effects and autoregressive variance structures (for time series analysis) to be implemented (53). GAMMs were constructed with a smoothing function for year and plant cover type by year interactions so that four different smoothing curves were fit to the four different cover types for each biocrust component. GAMMs were fit using the mgcv package in R (54) using the restricted maximum likelihood method to stabilize smoothing parameters and a Gaussian family distribution with a logit link to meet model assumptions. Additionally, to account for temporal autocorrelation in the residuals, we included a first-order continuous autoregressive (CAR) process (1) in the model. A CAR (1) process is an exponentially decreasing function of temporal separation that allows for the uneven spacing in observation timing and missing years of data (55).

After GAMMs were developed to explore temporal trends in the observational data, we tested for potential breakpoints or thresholds across the time series.

First, we constructed threshold models (e.g., segmented, step, and stegmented regressions), to identify potential years when a threshold was met by identifying the point of maximum curvature within the GAMMs, and selected the most parsimonious model, both including and excluding thresholding, through Akaike information criterion (AIC) comparison (5). Next, we used the threshold years identified above to create a dummy variable to demark years before and after a given threshold and named this variable Split, to be used in the construction of generalized linear mixed-effects models (GLMM) exploring the influence of environmental variables on biocrust components. For quality assurance, breakpoints were checked against the original GAMMs to insure consistency in analysis.

To explore the potential influence of environmental variability on biocrust components, candidate GLMMs were constructed for N-fixing lichens, other lichens, and moss cover using a binomial distribution with plant community type/plot as random intercepts. Additionally, we used a first-order autoregressive covariate structure nested within each plant community type to account for the autocorrelation of biocrust cover by year of observation. Candidate GLMMs included the climate summaries from the gap-filled VP weather station (see above) as potential explanatory environmental predictors, and the most parsimonious models were selected through AIC comparison and pseudo-R^2 [as calculated through the MuMIn package (56)]. If Split was included in the final model, we also tested for interaction between Split and the other continuous variables.

We also explored the impact of *B. tectorum* peak cover events on biocrust components by constructing GLMMs for the C_3 + *Bromus* and C_4 + *Bromus* study plots from 1998 to 2019. GLMM for vegetative triggers included that year's *Bromus* cover and total grass litter cover estimates. Additionally, to consider the ongoing legacy effects of episodic *Bromus* outbreaks, we divided subplots into heavily invaded (greater than 50% *Bromus* cover in 1998) and low-level invaded plots (less than 50% *Bromus* cover in 1998) to see if this grouping aided in model performance. For these models, we also used a binomial distribution for GLMM construction, with year and plant cover type/plot/subplot as random effects to isolate the effect of *Bromus* and grass litter alone.

Data generated during this study are available from the USGS ScienceBase-Catalog (44).

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