ECOLOGY

Biocrust as one of multiple stable states in global drylands

Ning Chen[1,2], Kailiang Yu[3*†], Rongliang Jia[4], Jialing Teng[4‡], Changming Zhao[1,2*]

Biocrusts cover ~30% of global drylands with a prominent role in the biogeochemical cycles. Theoretically, biocrusts, vascular plants, and bare soil can represent multiple stable states in drylands. However, no empirical evidence for the existence of a biocrust stable state has been reported. Here, using a global drylands dataset, we found that biocrusts form an alternative stable state (biocrust cover, ~80%; vascular cover, ≤10%) besides bare soil (both biocrust and vascular cover, ≤10%) and vascular plants (vascular cover, >50%; biocrust cover, ~5%). The pattern of multiple stable states associated with biocrusts differs from the classic fold bifurcation, and values of the aridity index in the range of 0 to 0.6 define a bistable region where multiple stable states coexist. This study empirically demonstrates the existence and thresholds of multiple stable states associated with biocrusts along climatic gradients and thus may greatly contribute to conservation and restoration of global drylands.

INTRODUCTION

Drylands cover around 45% of the terrestrial land surface, representing the largest terrestrial biome on Earth, and are home to more than 2.5 billion people (*1*). Around 10 to 20% of dryland ecosystems have already been degraded, a trend that is expected to increase in the future (*2*). The ongoing degradation associated with reduction or loss of vegetation cover makes it crucial to design management and restoration measures to conserve desirable ecosystem states and prevent undesirable states (*3*). Thus, developing an appropriate management strategy can be better informed by using a theoretical framework of multiple stable states (*4*–*6*).

Theoretically, multiple stable states of an ecosystem may exist along a range of environmental conditions. When exogenous drivers and endogenous positive feedbacks push an ecosystem across a critical threshold, the ecosystem can abruptly shift to another stable state, resulting in marked changes in ecosystem structure, function, and service (*5*, *7*). Similarly, different initial system states may lead to different final stable states (*8*). Once the ecosystem shifts to another stable state, it is extremely difficult or even impossible to return to its previous state, a typical characteristic of multiple stable state theory called hysteresis (*7*).

It has long been recognized that woody-grass, vegetation-bare, and uniform-patchy vegetation can form multiple stable states (*9*–*11*). However, another critical and integral component of drylands, biological soil crusts or biocrusts (relative to vascular plants mentioned above), has remained largely understudied from the perspective of multiple stable state theory. Biocrusts, consisting of communities of cyanobacteria, algae, bacteria, lichens, and mosses, occur on or within millimeters to centimeters of the soil surface. Biocrusts cover ~30% of the global dryland surface area (*12*) and serve as an organizing component for dryland ecosystems. Constituting a crucial atmosphere-soil interface, biocrusts act as a selective force to mediate the cycles of water (*13*), nutrients, and gases (*12*, *14*). For example, biocrusts can contribute as much as ~46% of total fixed nitrogen and ~7% of the net primary production by terrestrial organisms worldwide (*14*). Therefore, biocrusts may greatly alter dryland ecosystem states. Studies have suggested that biocrusts may tightly interact with environmental factors and vascular plants and, thus, exist as a stable state rather than just an influencing factor of dryland ecosystems (*15*, *16*). For example, once transformed to a degraded state, it may be difficult or impossible to effectively restore or rehabilitate biocrusts (*17*). Alternatively, with little or no vascular plant cover, biocrusts alone can play an essential role in the functioning of dryland ecosystems (*18*), a requirement in multiple stable state theory (i.e., divergence and irreversibility) (*5*, *6*). However, statistically robust empirical evidence of biocrusts coexisting with bare soil and/or vascular plants as multiple stable states has not yet been reported at broad spatial scales.

How could biocrusts be one of multiple stable states? Bare soil is a stable state, typically controlled by low annual precipitation, high wind-induced shear stress, and/or strong grazing pressure in many drylands (*19*). Biocrusts, however, can survive under similar harsh conditions and can expand spatially relative to vascular plants due to their low water requirement and high resistance to wind-induced shear stress (*15*). Moreover, biocrust can self-reinforce its survival and growth through positive feedback loops that reduce wind-induced shear stress and increase soil nutrients and water availability via rainfall interception in soils (*10*, *16*, *20*). Furthermore, biocrusts may impede seed entrapment and germination of vascular plants, thus avoiding competition and replacement by vascular plants, although the overall effects of biocrusts may be context dependent [(*21*), reviewed in (*22*)]. Therefore, a biocrust state (e.g., biocrust cover of ≥50% and vascular plant cover of <10%) may be one of multiple stable states (*16*, *23*, *24*). As water availability increases and/or wind-induced shear stress decreases, both biocrusts and vascular plants increase to cover a larger proportion of the land surface. Furthermore, horizontal water redistribution between biocrusts and vascular plants may lead to the formation of self-organized vegetation patterns (a mixed state) rather than solely biocrust plant– or vascular plant–dominated states (*10*, *13*). Thus, a mixed state of biocrusts and vascular plants may be maintained as one stable state (*15*). However, vascular plants

[1]State Key Laboratory of Grassland Agro-ecosystems, School of Life Sciences, Lanzhou University, No.222, Tianshui South Road, Lanzhou, Gansu 730000, China. [2]Yuzhong Mountain Ecosystem Observation and Research Station, Lanzhou University, No.222, Tianshui South Road, Lanzhou, Gansu 730000, China. [3]Department of Environmental Sciences, University of Virginia, Charlottesville, VA, USA. [4]Shapotou Desert Research and Environment Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, No.320, Donggang West Road, Lanzhou, Gansu 730000, China.
*Corresponding author. Email: zhaochm@lzu.edu.cn (C.Z.); kai86liang@gmail.com (K.Y.)
†Present address: Princeton Environmental Institute, Princeton University, Princeton, NJ 08544, USA.
‡Present address: University of Chinese Academy of Sciences, No.19(A), Yuquan Road, Shijingshan District, Beijing 100049, China.

generally obtain competitive advantages over biocrusts because of canopy and litterfall shading and/or higher water consumption. This leads to biocrust decay, although vascular plants may benefit biocrusts beneath plant canopies under harsh environments (*22*, *25*). The retreat of biocrusts further promotes dominance by vascular plants (*20*). Therefore, two or three of the bare-biocrust-vascular plant states could coexist under a range of environmental conditions and form multiple stable states (*9*). Given the accelerating rate of dryland degradation under global change (*2*), studies on multiple stable states associated with biocrusts are needed to inform conservation and restoration of dryland ecosystem functioning and services (*12*, *16*).

Here, we compiled a global dataset of biocrust and vascular plant cover in dryland ecosystems that were not disturbed or had experienced long-term restoration (>30 years). Four biocrust or vascular plant states were defined: biocrust (biocrust cover, >50%; vascular plant cover, <10%), bare soil (both biocrust and vascular plant cover, ≤10%), vascular plant (biocrust cover, <10%; vascular plant cover, >50%) and mixed states (other situations; see Fig. 1 and refer to Materials and Methods) (*26*–*28*). We used frequency distribution analyses to test the modes of vegetation cover along an aridity gradient quantified through aridity index (AI) and precipitation, which were used as drivers because they are the most important limiting factors for drylands at a global scale (*29*). On the basis of multiple stable state theory, a system can exhibit a multimodal frequency distribution because a system is more likely to spend more time and remain close to the stable states. Potential analysis, a method to estimate the number of system states, was used to characterize the stability landscape along the aridity and precipitation gradients (*30*). The existence of multiple stable states will result in a fold of stable states under a specific range of the driver variables. We hypothesized that biocrusts could exist as one of multiple stable states in addition to bare soil and vascular plants within a specific range of the driver variables.

RESULTS

Data compilation

A total of 584 data points reporting biocrust cover were compiled over global drylands. Data points were located in hyperarid (*n* = 4), arid (*n* = 257), semiarid (*n* = 297), and dry subhumid lands (*n* = 26), respectively. Across global drylands, there were five biocrust research hot spots—the Great Basin-Mojave-Sonoran Deserts in western United States (*n* = 167), the Loess Plateau–Gurbantungut Desert in northern China (n = 282), the Tabernas Desert in southeast Spain (*n* = 44), the Kalahari-Karoo-Namib Deserts in southern Africa (*n* = 50), and New South Wales in southeast Australia (*n* = 32; Fig. 2). In the dataset, vascular plant cover was also reported for 337 points.

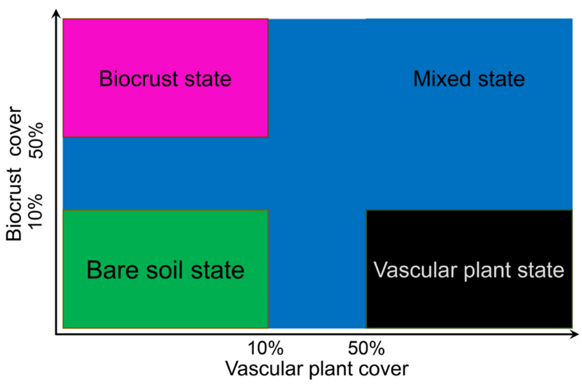

Fig. 1. Illustration of ecosystem states used in this study. Biocrust state (pink), high biocrust cover (>50%), and low vascular plant cover (<10%); bare soil state (green), both biocrust and vascular plant covers are low (<10%); vascular plant state (black), low in biocrust cover (<10%) and high in vascular plant cover (>50%). Other situations belong to the "mixed state" (blue).

Frequency distribution

The analysis of frequency distribution demonstrated three modes, namely, high biocrust cover of ~80%, low biocrust cover of ~5%, and middle biocrust cover of ~40%, with two frequency minima at ~20 and ~65% (grey regions in Fig. 3A; table S1). Along an aridity gradient, biocrust cover showed successively bifrequency (AI < 0.2), unifrequency (0.2 < AI < 0.5), and bifrequency (AI > 0.5) distributions (Fig. 3, B to G, and table S2). Thus, this pattern differed from the classic fold bifurcation, which would predict a pattern of uni-, multi-, and unimodality along the aridity gradient (*8*). Furthermore, the peaks in the frequency distributions under different ranges of aridity (Fig. 3, B to G) might not closely coincide with those for the entire range of aridity due to gradual changes between stable states in some cases (Figs. 3 and 4). These results were largely robust when the frequency distributions of biocrust cover were analyzed under different groupings (figs. S1 and S2 and tables S3 and S4), using the partial dataset with both biocrust cover and vascular plant cover reported (fig. S3 and tables S1 to S4), or using precipitation as the driver (fig. S3 and table S2).

There was a possibility that the multimodal distribution of biocrust cover might be induced by the multimodality in aridity, and other climate and soil factors (e.g., precipitation, wind velocity, temperature, and soil bulk density). However, we were unable to find such evidence, i.e., a similar sign of bi- or multimodal distribution in environmental drivers (figs. S4 and S5). Microenvironmental conditions (e.g., aspect effect) may also produce "multimodality" that was not induced by multiple stable states (*31*). However, we removed any microenvironmental influences when compiling the data (refer to the "Data compilation" section in Materials and Methods).

Stability landscape

We conducted stability landscape analysis to infer the stable and unstable states in driver space. If drylands contain multiple stable states, then we expected that system states would approximately stabilize to at least two minima in the stability landscape (*30*, *32*). Using this approach, we found that two minima (solid lines) of ~5 and ~80% folded over the aridity gradient at AI = 0 to 0.2 and 0.5 to 0.6 (Figs. 3 and 4). Only one stable state existed for the middle range (0.2 < AI < 0.5) and high end (AI > 0.6) of aridity gradient and was associated with a biocrust cover of ~40% and a biocrust cover of ~5%, respectively (Figs. 3 and 4). As aridity changed, biocrust cover along two branches shifted from 0–5% to ~80%, but in opposite directions (Fig. 4). That is, two branches in the system of stable states crossed, at an AI of 0.2 and a biocrust cover of 20% (Fig. 4). The critical thresholds of shifting to the other branch differed between two branches, i.e., AI values were ~0.6 and ~0 for the increasing and decreasing branches, respectively (Fig. 4). Therefore, biocrust cover exhibited hysteresis in response to changes along the aridity gradient.

We repeated this analysis using the partial dataset and found a similar stability landscape for biocrust cover (fig. S6), while vascular

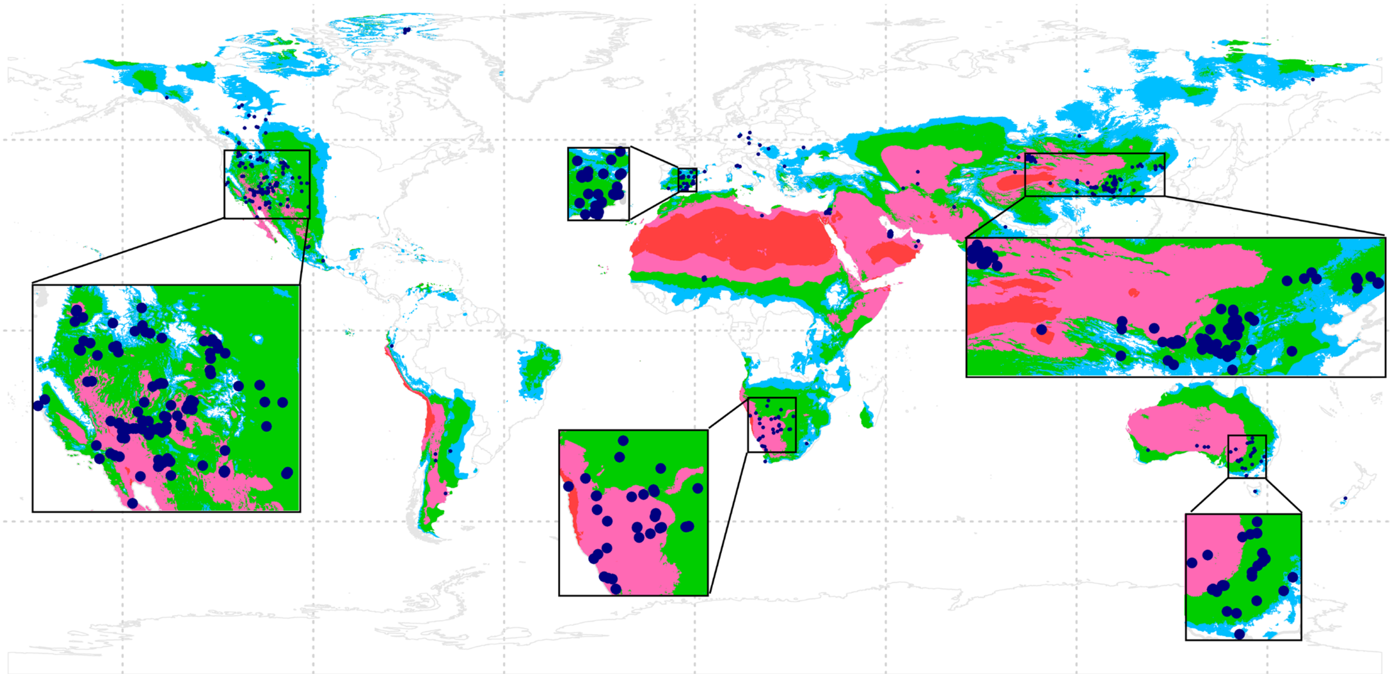

Fig. 2. The distribution of biological soil crust (biocrust) sites in global drylands. Different colors outline four subtypes of drylands (red, hyperarid land; pink, arid land; green, semiarid land; and light blue, dry subhumid land). Deep blue points show distributions of biocrust data compiled in this study.

plant cover tended to linearly increase with the aridity ($R^2 = 0.26$, $P < 0.001$) and exhibited a unimodal frequency distribution along the aridity gradient, i.e., there is no evidence of multiple stable states based on vascular plant cover alone (fig. S6 and tables S1 to S4). Therefore, at the low end of the aridity gradient (AI < 0.2), there were two coexisting stable states: biocrust (high biocrust cover and low vascular plant cover; pink line in Fig. 4) and bare soil states (both low biocrust and low vascular plant cover; green line in Fig. 4). Along the middle range of aridity (0.2 < AI < 0.5), only one stable state appeared: mixed state (low-high biocrust cover and intermediate vascular plant cover; blue line in Fig. 4). For the mid to high range of aridity (0.5 < AI < 0.6), two coexisting stable states also occurred: mixed (both high biocrust and vascular plant cover; blue line in Fig. 4) and vascular plant states (high vascular plant cover and low biocrust cover; black line in Fig. 4). Similar patterns were also found when using annual precipitation instead of aridity as the driver variable (fig. S6, C and D).

DISCUSSION

Despite the prominent importance of biocrusts in biogeochemical cycling, studies of biocrusts as one of multiple stable states have been scarce [but see (*16*, *23*, *24*)].Three primary factors may explain the relative lack of awareness of biocrust as a stable state in dryland ecosystems. First, research on biocrusts did not attract much attention until only the last two decades (*18*). Second, because of slow growth rates, it generally takes more than a decade for biocrusts to reach a stable state following disturbance (*17*). Frequent disturbances such as grazing, trampling, fires, and sand burial may maintain biocrusts in a transient phase (*33*). Last, the pattern of multiple stable states associated with biocrusts differs markedly from the classic pattern of fold bifurcation, as shown in the results and explained in detail below. The lack of applicable statistical methods makes it difficult to empirically validate biocrusts as one of multiple stable states and interpret their underlying drivers and mechanisms.

This study compiled a large field of dataset over global drylands and demonstrated that biocrusts displayed a "crossed" fold bifurcation. The crossed fold bifurcation has not been reported in previous studies, while a crossed fold bifurcation can be directly obtained from the swallowtail or butterfly catastrophes (*4*, *6*). We thus used crossed fold bifurcation here because the two branches of stable states cross over. Across the environmental (aridity or precipitation) gradient, ecosystems displayed bistable states (bare soil and biocrust), one stable mixed state (biocrust and vascular plants), bistable states (mixed state and vascular plants), and one stable state (vascular plants). A similar pattern has been reported previously in theoretical studies that involved biocrusts as a system state variable (*16*, *23*, *24*). The crossed fold bifurcation differs from the classic fold bifurcation, for which two detached branches of stable states are separated by one unstable transition state (Fig. 5). For instance, as water availability changes, the system state shifted from the biocrust state (high biocrust cover and low vascular plant cover; pink range) to the vascular plant state (low biocrust cover and high vascular plant cover; black range) for the decreasing branch. Or along the increasing branch, the system shifted from the bare soil state (low cover in both biocrust and vascular plants; green range) to the mixed state (other cases; blue range) (Fig. 4), rather than remaining in one stable state for each branch in the classic fold bifurcation (Fig. 5). As a result, the unstable state in this crossed fold bifurcation remained at a high value of biocrust cover of 80% and was generally higher than both branches of the stable states (Figs. 4 and 5A). However, both fold bifurcation patterns exhibit similar attributes of multiple stable state theory (*4*, *5*): (i) multiple stable states can coexist under similar environmental conditions (Fig. 5); (ii) the system state can abruptly

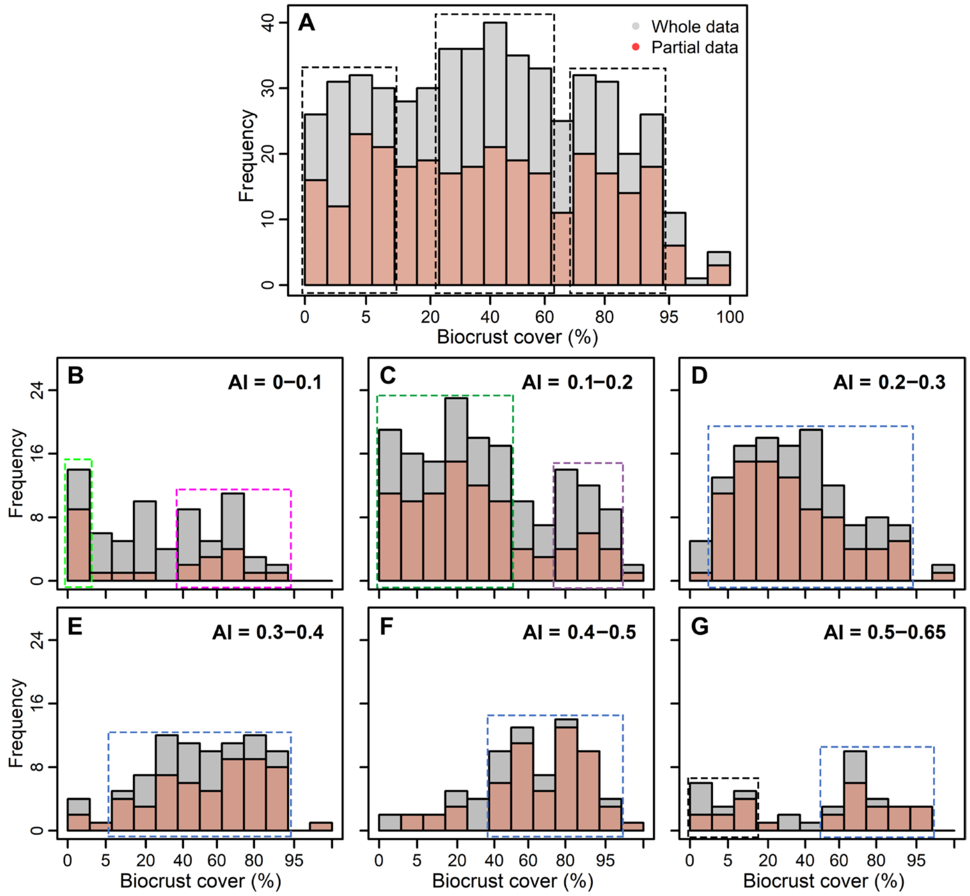

Fig. 3. Frequency distribution of biological soil crust (biocrust) cover. Frequency distribution of biological soil crust (biocrust) cover under the entire (**A**) or divided (**B** to **G**) range of the AI. (A) "Partial data" refer to the data points where vascular plant cover data were also available. Dashed squares show different modes of frequency distribution. (B to G) Different colors of squares indicate different states corresponding to Fig. 1 (green, bare soil state; red, biocrust state; blue, biocrust-vascular mixed state; and black, vascular plant state). Squares with other colors denote the intermediate states. Note that vegetation cover data have been arcsine–square root transformed.

shift to another stable state when crossing the bistable region, as shown by the vertical lines and arrows in Fig. 5; and (iii) the two paths that go forward and return backward (Fig. 5) do not coincide, resulting in hysteresis.

What is driving the crossed fold bifurcation? At the low end of water availability (e.g., AI < 0.1), the lack of water input may limit biocrust and particularly vascular plant growth, and in turn, the low cover of biocrusts and vascular plants may result in higher water loss (e.g., due to soil erosion and higher evaporation rate) (*13*, *20*). The positive feedback loop may lock the system into the bare soil state, given initial low cover of biocrusts (*6*, *16*, *28*). However, under higher initial cover of biocrusts (e.g., >50%), their lower water demand relative to vascular plants due to lower compensation points in physiological processes (e.g., photosynthesis) (*14*), the facilitation by shading that reduces evaporation rate and ultraviolet-induced impair (*22*), and reduced competition from vascular plants for soil water combine to maintain a relatively high biocrust cover (Fig. 6). Furthermore, biocrusts increase soil nutrients through carbon and nitrogen fixation, retain soil water, and/or reduce wind-induced shear stress, all of which can further promote biocrust growth (*12*, *15*, *16*). Therefore, as suggested by Bowker *et al.* (*26*), the biocrust-dominated state can persist (the semidesert sandy loam case therein), and biocrust and bare soil states coexist as bistable states under low water availability (Fig. 4). Additional evidence of biocrust-bare soil stable states can be found in the Biota Southern Africa project that reported coexisting contrasting states between Kleinberg (biocrust cover of <1%) and Wlotzkasbaken (biocrust cover of ~70%) in the Namib Desert under similar climate (e.g., AI = ~0.01) and soil conditions (https://biota-africa.org/).

Increasing water availability can result in even higher biocrust cover (a positive feedback loop) as biocrusts intercept more water for growth because of their large water absorbing capacity (*20*). Therefore, ecosystems have the potential to maintain high biocrust cover, although this state may be unstable in some circumstances (Figs. 4 and 5A). Extra water inputs may exceed the water demands of biocrusts and would favor the growth of vascular plants (*15*), thus potentially leading to the stable state of mixed biocrusts and vascular plants. Biocrusts may also stabilize the land surface and, thus, indirectly benefit vascular plants (*22*). Moreover, biocrust patches may increase runoff [but see review in (*13*)] and, thus, benefit water-receiving vascular plant patches. Horizontal water redistribution from biocrust to vascular plant patches may also favor a series of mixed states instead of solely biocrust– or vascular plant–dominated states (*10*). This process can perhaps explain the wide variety of system states within a single branch in the stability landscape (Fig. 4). On the other end, high vascular plant cover may affect biocrusts

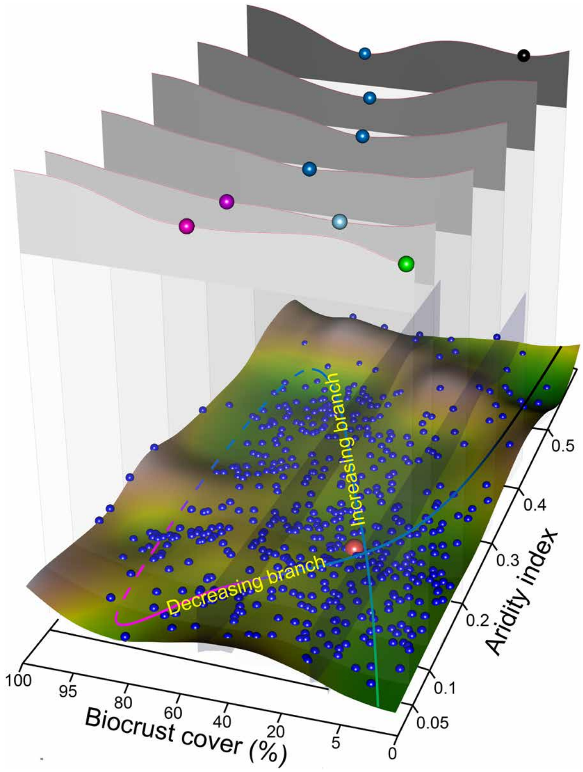

Fig. 4. Stability landscape of biological soil crust (biocrust) cover in driver (AI) space. Green and white in the bottom panel describe the local maxima and minima of the stability landscape, respectively. The solid and dashed lines outline the stable (i.e., local minima) and unstable (i.e., local maxima) states. Green, blue, pink, and black segments denote the bare soil, mixed, biocrust, and vascular plant states, respectively. The red ball in the bottom panel denotes the "cross" point where two branches of stable states cross. Two light blue shadow walls on the bottom panel indicate the values delimiting different states (refer to the "Data compilation" section in Materials and Methods). The gray-black walls and balls on the top show attraction basins and local minima of ecosystems as a function of aridity. Different colors of balls correspond to different states over the range of aridity (refer to Fig. 1). Biocrust cover data have been arcsine–square root transformed.

through litter deposition, canopy shading, and increased rainfall infiltration into deep soils, which benefits deep-rooted vascular plants relative to biocrusts (*25*). The relationship between biocrusts and vascular plants becomes competitive for light and soil water when both vascular plant and biocrust covers are high (Fig. 6). This process may form another positive feedback loop that maintains the vascular plant–dominated stable state (Fig. 6) (*22*). Therefore, there are bistable states under high water availability—mixed and vascular plant states. Evidence for the mixed-vascular plant bistable states occurs in semidesert on shallow sandy loam soils in (*26*), which found that a shrub-biocrust mixed state may shift to a shrub-dominated state.

Furthermore, some disturbances, such as grazing, trampling, fire, and sand burial, may interfere with or even completely halt the positive feedbacks maintaining the biocrust state [reviewed in (*34*)]. For instance, trampling may directly and markedly destroy biocrust communities (*35*) or break the positive feedback between biocrust and shallow soil water by increasing infiltration to deeper soil layers. This study does not explicitly investigate the effects of these disturbances, which have been excluded from the compiled dataset. Besides, other disturbances (e.g., wind-induced shear stress) may also tightly interact with biocrusts and vascular plants and form other positive feedbacks that shape dryland ecosystem states, which had been suggested to be (at least partially) responsible for multiple stable states associated with biocrusts (*24*). Future studies can further explore how integration of water availability and wind-induced shear stress affects the pattern of biocrusts as one of multiple stable states.

This study has the potential to advance our knowledge of dryland transition and resilience. First, our work leverages a large-scale field dataset to demonstrate the existence of a biocrust stable state, which previously has only been hypothesized in theoretical studies (*16*, *23*, *24*). The results suggest that biocrusts alone may cover a large proportion of drylands, especially in areas with low water availability (i.e., AI < 0.2, covering 17.2% of the global terrestrial land surface). With accelerating land degradation in these highly water-limited regions (*2*) where vascular plants struggle to survive, biocrusts are expected to play a prominent role in ecosystem functions and services, including carbon sequestration, nitrogen fixation, and land surface stabilization (*12*, *26*). Second, these dryland multiple stable states reflect a kind of crossed fold bifurcation that differs from the classic fold bifurcation (*4*, *6*). When approaching the aridity threshold (an AI of 0.2 and a system state of 20%), two options are available, namely, higher or lower biocrust cover (Fig. 4). The cross suggests that to avoid an undesirable system state under decreasing water availability, actively implementing management actions, such as inoculating biocrust constituents to increase biocrust cover, is recommended (*36*). Meanwhile, the shifts between multiple stable states are more likely to occur in drylands with low and high water availability (AI < 0.2 or >0.5) rather than in the middle range of water availability (e.g., 0.2 < AI < 0.5), as would be expected under the classic fold bifurcation (Fig. 4 and fig. S1). Third, for highly water-limited regions (e.g., AI < 0.2), biocrust may increase, and not necessarily decrease as predicted by the classic fold bifurcation. These results provide guidance for restoring degraded ecosystems in highly water-limited lands by increasing biocrust cover, especially where vascular plants cannot survive (*26*). Last, at the wet end of water availability (e.g., AI > 0.5), biocrusts and vascular plants can coexist as multiple stable states where competition between biocrusts and vascular plants occurs. Thus, the restoration and/or management options that are used to improve ecosystem functioning and services by promoting or conserving desired stable states (i.e., vascular plants) also need to account for the role of biotic interactions.

In this study, we compiled a large-scale field dataset to investigate the potential for biocrusts to be one of multiple stable states in global drylands. We empirically demonstrate the existence of bare soil, biocrust, and vascular plant stable states. The critical thresholds of 0 to 0.6 in the AI define a bistable region where multiple stable states can exist and cover a large proportion of global drylands. Meanwhile, the crossed fold bifurcation found here differs from the classic fold bifurcation. Shifts between these system states may occur under global change (e.g., long-lasting abnormal water availability) or strong disturbances (e.g., sandstorms), which disrupt the positive feedbacks maintaining one stable state over another under similar environmental conditions (*8*). These findings may inform restoration practices in the degraded dryland ecosystems and provide management options in undisturbed ecosystems, across spatial environmental gradients, and under the influence of climate and other anthropogenic changes.

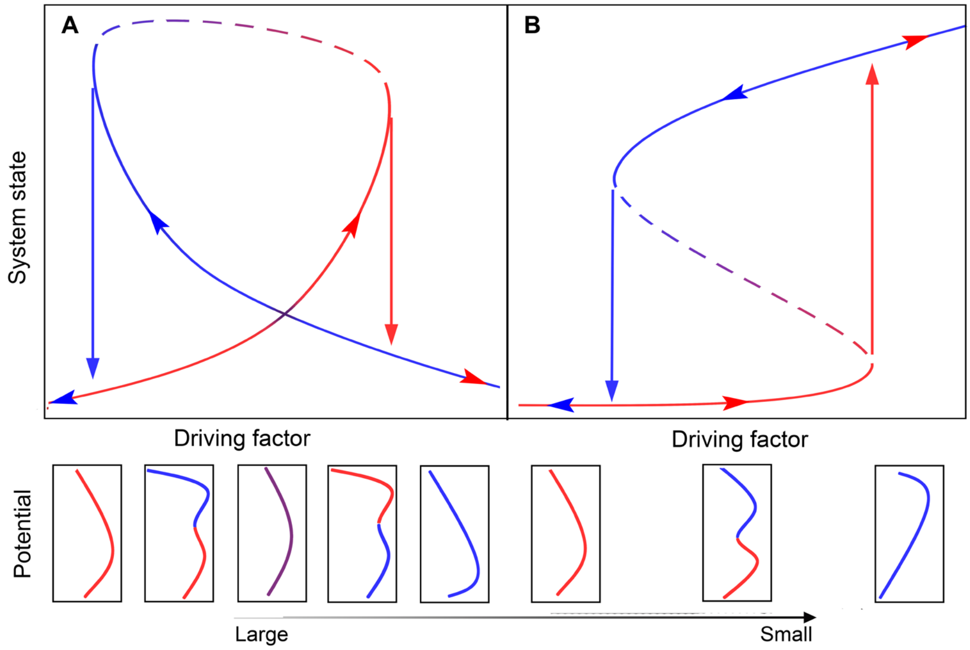

Fig. 5. Comparison of the "crossed" and "classic" fold bifurcations. (**A**) The "crossed" fold bifurcation. (**B**) The "classic" fold bifurcation. Solid and dashed lines signify the stable and unstable states, respectively. Lines and arrows in the same color demonstrate the changes of system state as the driver variable increases or decreases. The bottom panels demonstrate the potential of system state as a function of the driver variable. Lines with different colors indicate different stable states.

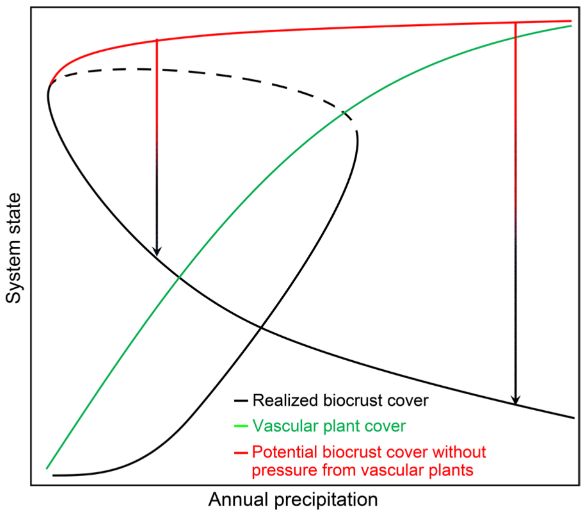

Fig. 6. Illustration of the effects of vascular plants on biocrusts.

MATERIALS AND METHODS

Data compilation

Biological soil crust (biocrust) consists of microscopic (cyanobacteria, algae, and bacteria) and macroscopic (lichens and mosses) organisms and occurs on or within millimeters or centimeters of the soil surface. Relative to vascular plants, biocrusts are generally pioneer species that occupy bare soils. The state of the system is quantified by cover of the constituents, i.e., the percentage of land surface covered by one specific life form (biocrust or vascular plant) at the ecosystem scale. When biocrust cover is greater than 50% and vascular plant cover is less than 10%, an ecosystem is classified as being in the biocrust state. A similar rule was used for the vascular plant state, which has a biocrust cover <10% and a vascular plant cover >50%. The bare soil state is defined as a state with low cover of biocrusts and vascular plants (both ≤10%). In other cases, the system state is in a mixed (e.g., biocrust-vascular plant) state (Fig. 1). Notably, these values were used for defining the potential ecosystem states, and they were not used in the analysis of multiple stable states. It should also be noted that one ecosystem is classified into a specific state because the corresponding life-form dominates over the other life-form, rather than totally excluding it. A value of 50% is used to characterize dominance because there are only two life-forms according to the FAO (Food and Agricultural Organization of the United Nations) hierarchical rule for classifying predominant land use (*27*). A value of 10% is used to define bare soil because below this level, one life-form may not be able to play a notable role in ecosystem functioning. For example, Thomas and Leason (*28*) reported that vascular plants were not able to effectively limit sand transport when their cover was lower than 14%. Bowker *et al.* (*26*) found that when biocrust cover was less than 10%, the probability of a state transition increased to nearly 100%.

We compiled data on biocrust cover in drylands from the published references in the Web of Science (English) and CNKI (China National Knowledge Infrastructure, Chinese) from January 1980 to July 2019 using the search criteria: ("biogenic crust*" OR "biological crust*" OR "microphytic crust*" OR "microbiotic crust*" OR "microbiotic soil crust*" OR "biocrust*" OR "soil crust*" OR "bryophyte" OR "cryptogam*" OR "lichen" OR "moss*" OR "biotic crust*") AND ("dryland" OR "hyper*arid*" OR "arid*" OR "semi*arid*" OR "dry subhumid*"). These searches resulted in a total of 2832 publications—2551 from the Web of Science and 281 from CNKI. Among the publications, biocrust cover (and/or vascular plant cover) was reported in 1867 publications. In addition, we combined unpublished materials and recent reviews and books. Multiple publications might have been conducted in the same site and reported only one value of biocrust cover, and one publication reported multiple values of biocrust cover for the same site. As a result, 1125 data points were obtained. We confined our research scope to drylands defined as regions with an AI (annual precipitation divided by potential annual evapotranspiration) <0.65 (*29*), thus leading to the total of 925 data points. However, we excluded cryptogams in dryland forest ecosystems because those forests differed from the more open bare soil-biocrust-vascular plant systems considered in this study. Data points without coordinate (latitude and longitude) were also removed because coordinate information was necessary to extract the climate and soil variables. Also, we eliminated studies from highly disturbed sites. However, studies reporting sites that had experienced long-term restoration (i.e., >30 years), which was generally longer than at least one life cycle for vascular plants, were retained because we assumed that the restored ecosystems had reached a steady state (*8*, *17*). Last, one study in Qatar reported a qualitative biocrust cover (three levels of 15, 45, and 75% biocrust cover) over ~11,000 km^2 with a resolution of 10 × 10 km, resulting in 91 data points (https://figshare.com/articles/Mete-data_of_biocrust_cover_in_global_drylands/9978812). Only 9 data points from that study spanning the entire AI range therein were retained to avoid any bias.

Biocrust cover was directly extracted from the references that reported vegetation cover at the ecosystem scale. Studies that averaged cover of biocrusts and vascular plants over multiple quadrats (in open areas or under vascular plants) were also included. For these data points, biocrust cover was scaled up to the ecosystem scale after weighing by the ratio of open areas and vascular plant–covered areas. Very large spatial heterogeneity may exist because of microtopography or aspect, both of which may affect the overall estimate of cover of system states at the ecosystem scale (*31*). If microhabitats (or microclimates) were reported, then only those data records on nonsunny slopes were used to estimate biocrust cover. Patterns at smaller scales (i.e., microhabitats, <1 m) are out of the research focus of this study. To avoid overrepresentation, data points for distances less than 5 km were integrated and were considered as a single ecosystem and were assigned an averaged value. Thus, we studied multiple stable states in these drylands at the ecosystem scale (≥5 km). A sensitivity test showed no significant differences in analyses without aggregated data. Ultimately, 584 data points were included in this study. In addition to biocrust cover, vascular plant cover data were also compiled when available (n = 337), using the same strategy for biocrust cover. More detailed information regarding the data points used in this study is available in a publicly accessible repository (https://figshare.com/articles/Mete-data_of_biocrust_cover_in_global_drylands/9978812).

AI was used as the driver because aridity is an important limiting factor for dryland ecosystems and directly reflects water availability. Another potential driver, annual precipitation (derived from the WorldClim database, version 2, with a resolution of ~1 km at the equator, averaged over a period of 1970–2000), was also used in all analyses and produced the similar results with aridity (see figs. S3 and S6 and table S2). AI values were obtained from the CGIAR-CSI database (version 2, with a resolution of ~1 km at the equator) according to site coordinates (i.e., longitude and latitude). CGIAR-CSI database calculated AI on the basis of mean monthly temperature, mean monthly temperature range, and mean monthly extraterrestrial radiation (radiation at the top of the atmosphere) from the WorldClim database (*37*).

Statistical analyses

Two types of datasets were used in the following analyses: (i) the whole dataset reporting only biocrust cover and (ii) the partial dataset reporting both biocrust and vascular plant cover. We used the partial dataset primarily because vascular plant cover could influence the biocrust stable state. Unless specifically stated, we refer to the whole dataset in this study.

Frequency distribution

System state may more frequently linger in the stable domains relative to the unstable domains, and thus, multiple stable sates may cause the frequency distributions of system variables to be bi- or multimodal (*30*, *32*, *38*). In this sense, bi- or multimodal frequency distributions are evidence of the existence of multiple stable states because the transitional states tend to be unstable with lower frequency. We investigated the frequency distributions of biocrust cover (and also vascular plant cover) using a latent class analysis realized in R (version 3.6.0) as the "flexmix" package (*32*). The method is a generic method that incorporates a more sophisticated algorithm called the expectation-maximization method to find the best fit for a certain number of normal distributions (*30*, *32*). We compared the model fits with one to five classes by using parsimony criteria [e.g., Bayesian information criterion (BIC)]. If multiple stable states associated with biocrusts existed, then the frequency distribution of biocrust cover should be bi- or multimodal rather than unimodal, that is, the fits of frequency distribution with the bi- or multimodes should have a lower BIC value than these with unimodal fits by at least a value of 2 (*39*). Before the analysis, we arcsine–square root transformed biocrust cover to meet the requirement of a normal distribution of residuals in model fits.

Stability landscape

The existence of multiple stable states will result in more than one stable state under a specific range of a driver variable, which can be captured in a stability landscape. Stability landscape has been widely used to test for the presence of multiple stable states (*30*, *32*). Potential analysis, an approach to estimate the number of system states along a gradient, was used to build the stability landscape as a function of AI for biocrust cover (and vascular plants) (*32*). Potential analysis was conducted using the "movpotential_ews" function in the "earlywarnings" package. We adopted the method from Scheffer *et al.* (*30*) and Hirota *et al.* (*32*). The basic procedure is as follows: 1)The dynamics of an ecosystem can be expressed as a potential stochastic differential equation with a potential function; 2)A corresponding Fokker-Planck equation connects the probability density to the potential of the data and reconstructs the data as a function of the probability density function; 3)We applied a Gaussian kernel-smoothing window (using a window size of 5% of driver range) to calculate the approximate potential for each driver value; 4)The equilibrium values were estimated by numerically determining the local minima and maxima, which are detected automatically, of the probability density function. Small local patterns (e.g., minima and maxima) that were smaller than a threshold value (0.005) were filtered out.

The minima and maxima of the potential correspond to the stable and unstable states, respectively. If there is more than one local minimum over a range of the driver variable (e.g., AI), then multiple stable states exist and the multistable region can be determined along the gradient of driver.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/39/eaay3763/DC1

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Ning Chen, Kailiang Yu, Rongliang Jia, Jialing Teng and Changming Zhao

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