DRYLAND ECOLOGY

Global ecosystem thresholds driven by aridity

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Aridity, which is increasing worldwide because of climate change, affects the structure and functioning of dryland ecosystems. Whether aridification leads to gradual (versus abrupt) and systemic (versus specific) ecosystem changes is largely unknown. We investigated how 20 structural and functional ecosystem attributes respond to aridity in global drylands. Aridification led to systemic and abrupt changes in multiple ecosystem attributes. These changes occurred sequentially in three phases characterized by abrupt decays in plant productivity, soil fertility, and plant cover and richness at aridity values of 0.54, 0.7, and 0.8, respectively. More than 20% of the terrestrial surface will cross one or several of these thresholds by 2100, which calls for immediate actions to minimize the negative impacts of aridification on essential ecosystem services for the more than 2 billion people living in drylands.

Drylands, areas where rainfall is <65% of evaporative demand (*1*), cover ~45% of emerged lands (*2*) and are especially vulnerable to climate change and land degradation (*3*, *4*). Increasing aridity [calculated as 1 – (precipitation/potential evapotranspiration)] is a major imprint of climate change in global drylands (*3*) and will affect multiple ecosystem structural and functional attributes [e.g., nutrient cycling, plant productivity, and microbial communities (*5*)]. However, it remains to be elucidated whether these impacts will be gradual or abrupt (*5*–*7*). Recent research (*1*, *8*) has shown abrupt losses of soil nutrient availability in the transition between semiarid and arid ecosystems (aridity levels ~0.7). Likewise, modeling studies have predicted the existence of single thresholds in particular structural attributes such as vegetation cover or spatial pattern along climatic gradients (*9*). Whether nonlinear responses of ecosystem attributes to increases in aridity are the norm rather than the exception and if these responses exhibit single or multiple thresholds remain largely unknown. Ecosystem attributes are highly interconnected (*5*, *10*, *11*); therefore, changes in a given attribute induced by increases in aridity may trigger sequential changes in others that depend on it but work at different spatial (*12*) or temporal (*10*) scales. If these interconnected changes are abrupt, then this could potentially result in a series of aridity thresholds affecting multiple ecosystem attributes. For instance, increasing aridity may cause a rapid shift in the composition of soil microbes, which in turn may trigger changes in plant–microbial interactions that later lead to changes in nutrient cycling and plant community composition (*13*). Therefore, understanding whether the interrelated responses of multiple ecosystem attributes to increasing aridity cancel each other out, buffering the negative impacts of climate change, or if they are characterized by one or multiple sequential ecosystemic thresholds that amplify them is crucial for improving forecasts of ecosystem responses to climate change. This information is also critical to depict vulnerabilities in global drylands and to forecast the provision of ecosystem services maintaining the >2 billion people that inhabit these areas worldwide, particularly in developing countries (*4*).

Herein, we evaluated whether multiple ecosystem structural and functional attributes exhibit linear or nonlinear responses to increases in aridity and if these responses are driven by the existence of single or multiple thresholds in global drylands. To do so, we compiled >50,000 data points that spanned multiple biological organization levels (from individuals to ecosystems) and global datasets, including standardized laboratory measurements, field surveys, map interpolations, and remote sensing information (table S1 and fig. S1). We evaluated 20 functional and structural ecosystem attributes, including physical (e.g., albedo, soil texture, precipitation variability), biological (e.g., plant cover, richness, functional traits, microbial communities), and chemical (e.g., soil organic carbon, leaf nitrogen) variables. These attributes are strongly related to the ability of drylands to provide essential ecosystem services such as climate regulation, nutrient cycling, and livestock production [the most extensive land use in global drylands (*6*)], and largely determine their responses to climate change and desertification drivers (*5*). We also studied variables related to plant–soil interactions [e.g., fertility islands associated with the presence of plant canopies (*14*)], plant–climate interactions (e.g., plant resistance to climatic variability), and plant–plant interactions (e.g., spatial networks), which underpin many ecosystem processes in terrestrial ecosystems [(*11*, *15*); see (*16*) for further rationale].

All of the ecosystem functional and structural attributes evaluated responded in a nonlinear manner to increases in aridity (table S2). In other words, once an aridity level was reached, small increases in aridity led to drastic changes in the value of the attribute (fig. S2) or modified its relationship with aridity (changing slope; fig. S3). Whereas all responses to aridity observed fit better to a nonlinear or abrupt change [i.e., discontinuous changes described in (*17*)] than to a linear monotonic model (table S2), for some variables, the variance explained was relatively low. This suggests that other environmental or human-related factors, such as topography or land use, may also interact with aridity to determine the observed nonlinear changes, which provides scope for actions aimed at minimizing these drastic shifts.

Contrary to what is commonly assumed by theoretical approaches (*9*), the observed responses of ecosystem attributes to increases in aridity followed a sequential series of thresholds. The presence of multiple thresholds has been conceptualized regarding ecosystem degradation (*18*), but this has not yet received empirical and quantitative support. Thus, our results suggest that the response of drylands to aridity can be organized into three phases characterized by concurring nonlinear or abrupt ecosystem shifts (Fig. 1). Observed ecosystem changes with increases in aridity start with a "vegetation decline phase" characterized by a sharp reduction in vegetation productivity [as measured using remote sensing; see (*16*)] at aridity levels > 0.54 (Fig. 2A). This reduction in vegetation productivity is consistent with observed decreases in light-saturated leaf

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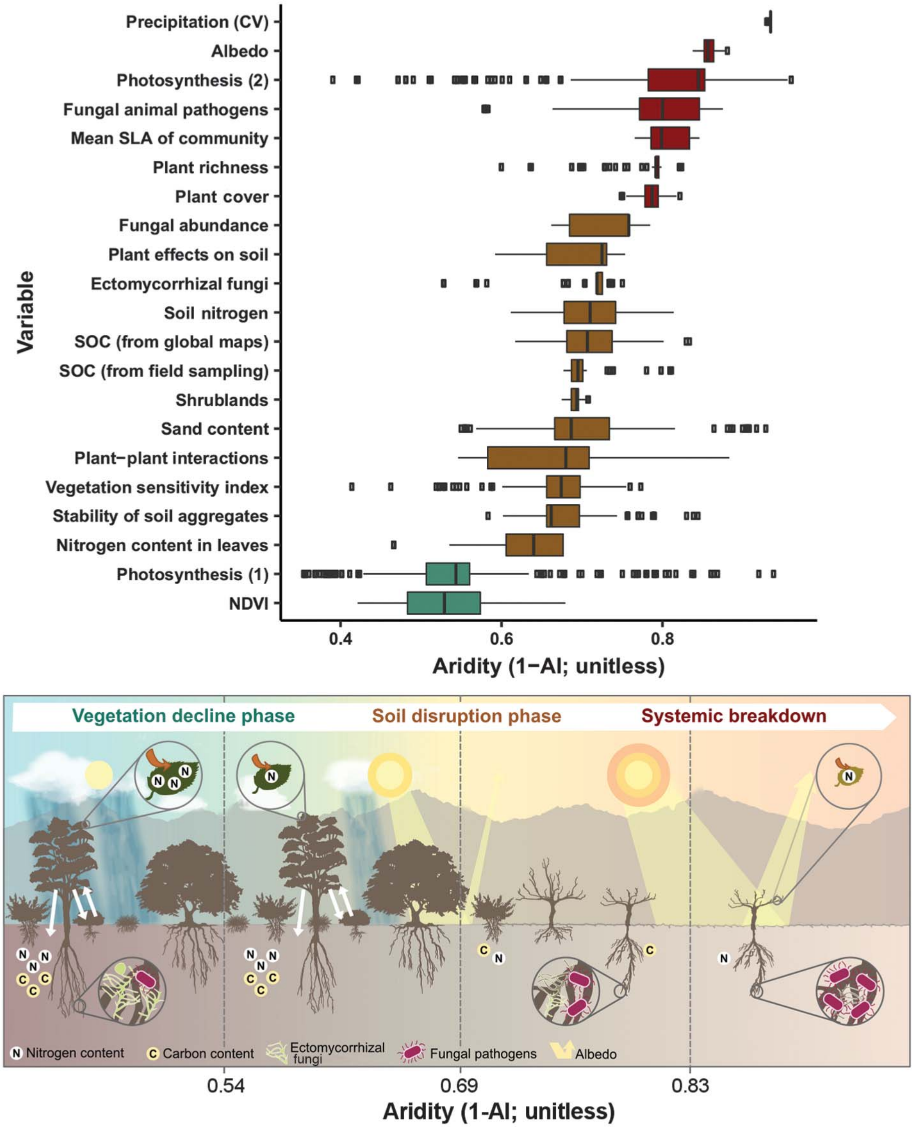
Fig. 1. Sequence of abrupt responses in global drylands as aridity increases. Top: values of the 21 aridity thresholds identified and their bootstrapped confidence intervals. Each color identifies a homogeneous set of variables that do not overlap others and defines phases of abrupt shifts. CV, coefficient of variation; SOC, soil organic carbon; NDVI, normalized difference vegetation index. Bottom: schematic representation of ecosystem changes associated with the crossing of the three phases identified in this study. The first threshold, related to a decay in vegetation productivity and photosynthetic activity, occurs when crossing an aridity level of ~0.54. At aridity levels of ~0.7, sharp declines in soil fertility, plant nitrogen content, and biotic (plant–soil, plant–plant) interactions, and drastic compositional changes in plant and soil microbial communities are observed. Finally, drastic reductions in plant cover, increases in soil albedo, and shifts in leaf traits toward stress avoidance were detected at an aridity level of ~0.8. Illustration by DharmaBeren Studio.



photosynthetic activity measured in situ on 809 plant species across the world (fig. S4). Plants typically reduce their leaf area to adapt to dry conditions (*19*), often increasing their leaf mass/area ratio, nitrogen content, and relative photosynthetic capacity per unit of leaf area (*20*). However, our results suggest that such leaf adaptation to drought may compromise raw plant photosynthesis and productivity, leading to a sharp decline in these key ecosystem attributes at aridity levels of ~0.54.

As aridity continues to increase, we identified a "soil disruption" phase characterized by changes in multiple ecosystem structural and functional attributes under aridity levels >0.7. These changes include abrupt declines in soil variables such as organic carbon (a key determinant of soil fertility), total nitrogen and clay contents, stability of aggregates, and relative abundance of fungal functional groups (Fig. 2C and fig. S5). Observed reductions in soil nutrients could be associated with decreased plant-derived organic inputs into the soil, which are driven by reductions in plant productivity observed during the vegetation decline phase and by drastic reductions in leaf nitrogen content occurring at aridity ~0.65 (Fig. 2B). This notion is further supported by the sharp decline in the positive effect of plant canopies (regarding bare soil areas) on soil organic carbon (Fig. 2D) and by the reduction in the relative abundance of saprotrophic fungi (fig. S5G), which are key drivers of the formation of "fertility islands" in drylands (*14*). We speculate that this net reduction in the quantity and quality of plant carbon inputs into the soil may occur as a consequence of the excessive costs needed for extracting water and nutrients to keep a positive carbon gain under increasingly arid conditions (*21*). Our results further show abrupt declines in the relative abundance of ectomycorrhizal fungi at this aridity level (fig. S5H), which have also been linked with abrupt changes in plant community composition and soil biogeochemical cycles (*13*). Other changes observed beyond the 0.7 aridity threshold include a decline in the frequency of positive plant–plant interactions [fig. S5I (*22*)], for which soil amelioration is a fundamental component (*9*, *23*). During this soil disruption phase, vegetation shifts from grasslands and savannahs to shrublands (fig. S5D), which are better adapted to nutrient-poor and sandy soils (*23*, *24*). We also found a steep decrease in the overall sensitivity of vegetation to climatic fluctuations (*25*) (fig. S5A), which

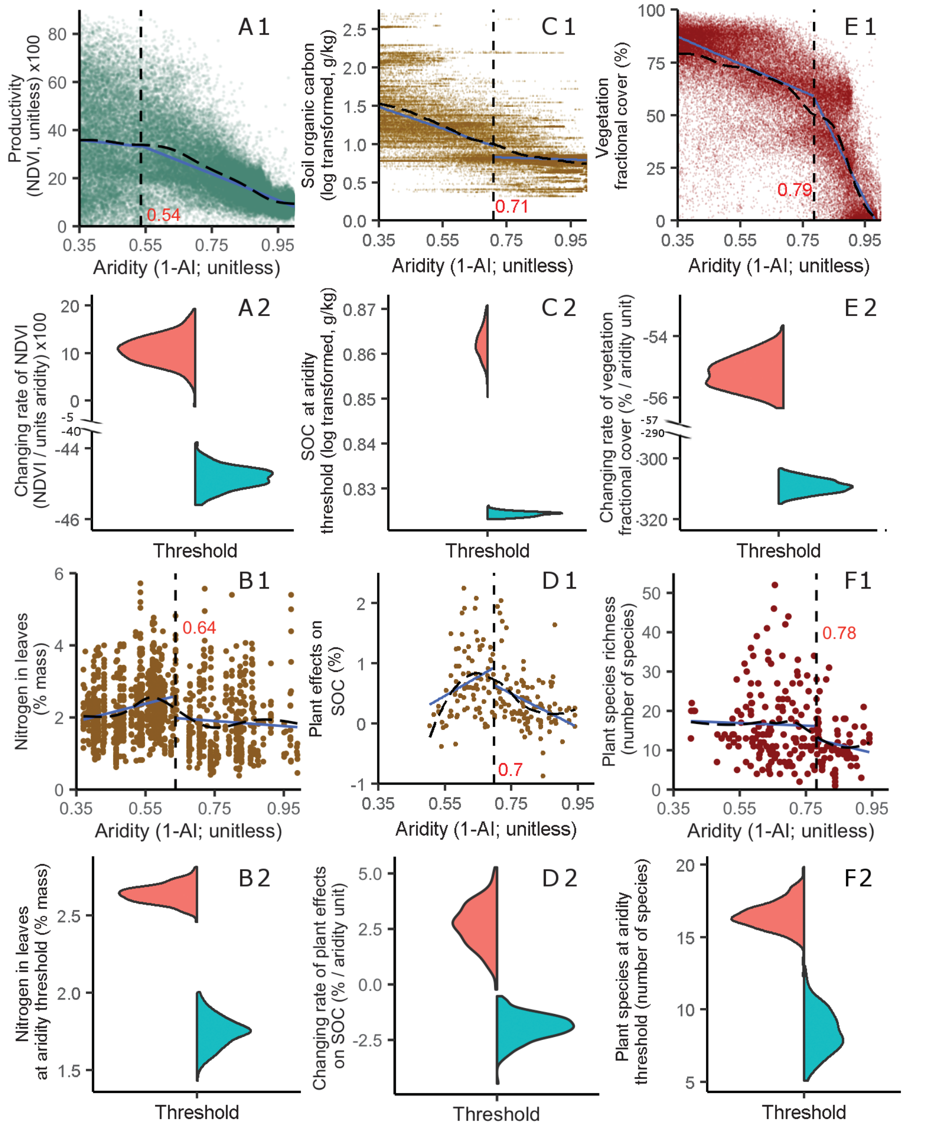


Fig. 2. Nonlinear responses of multiple ecosystem attributes to aridity. Examples of aridity thresholds observed for NDVI (**A**), leaf nitrogen content (**B**), soil organic carbon (**C**), plant effects on soil organic carbon (**D**), vegetation cover (**E**), and plant species richness (**F**). In (A.1) to (F.1), black dashed lines and blue solid lines represent the smoothed trend fitted by a generalized additive model (GAM) and the linear fits at both sides of each threshold, respectively. Inset numbers in red and the vertical dashed lines describe the aridity threshold identified. In (A.2) to (F.2), violin diagrams show bootstrapped slopes [(A.2), (D.2), (E.2)] or values of the predicted fitted trend at the threshold [(B.2), (C.2), (F.2)] of the two regressions existing at each side of the threshold (red: before the threshold; blue, after the threshold).

might be associated with the deeper root systems commonly found in shrubs that make them less sensitive to seasonal droughts (*24*). The shift to shrub-dominated vegetation observed adds to other transitions identified under wetter climates, such as those occurring between forests and savannas (*26*) or C3- and C4-dominant grasslands (*27*), and provides new and relevant information to explain how climate change may affect dominant vegetation and associated soil properties in large areas of our planet.

Finally, we detected an "ecosystem breakdown" phase, characterized by extreme reductions in plant cover and exponential increases in albedo beyond aridity values of 0.8 (Fig. 2E and fig. S6C). Once this aridity level is crossed, most plant species no longer survive shortages in water and nutrient availability. Accordingly, we observed a strong decline in plant species richness at this stage (Fig. 2F) consistent with a major turnover in species reported in other studies (*28*). These changes are associated with drastic increases in specific leaf area, a trait linked to plant resource use and litter decomposition (fig. S6B), and leaf photosynthetic rates (fig. S4). The observed changes could be related to a physiological limit for the existence of stress-tolerant strategies and evergreen vegetation at aridity levels >0.8 as this vegetation is replaced by stress-avoidant summer deciduous shrub species that may benefit most from the sparse and unpredictable rain events characterizing these environments (*21*, *29*) (fig. S6D). We also found a sudden increase in the relative abundance of fungal animal pathogens in the soil (fig. S6A), which adds to the negative effects of reducing plant cover and biomass by potentially increasing the incidence of important fungal diseases.

According to current climatic forecasts by the Intergovernmental Panel on Climate Change's (IPCC's) Representative Concentration Pathways (RCP) 8.5 scenario (*3*), up to 22% of the terrestrial surface (28.6% of current dryland area) will cross one or more of the three phases identified by 2100 (Fig. 3 and fig. S7). Therefore, according to our space-for-time substitution approach, these regions (Fig. 3) are at high risk of rapid declines in ecosystem functional and structural attributes, key to maintaining their capacity to provide essential ecosystem services. Areas expected to cross the 0.8 aridity threshold are particularly sensitive and may undergo massive vegetation collapse and species loss. Increases in albedo associated with these vegetation changes, however, may affect the energy balance of Earth's surface and partially buffer global warming (*30*). Nevertheless, we must

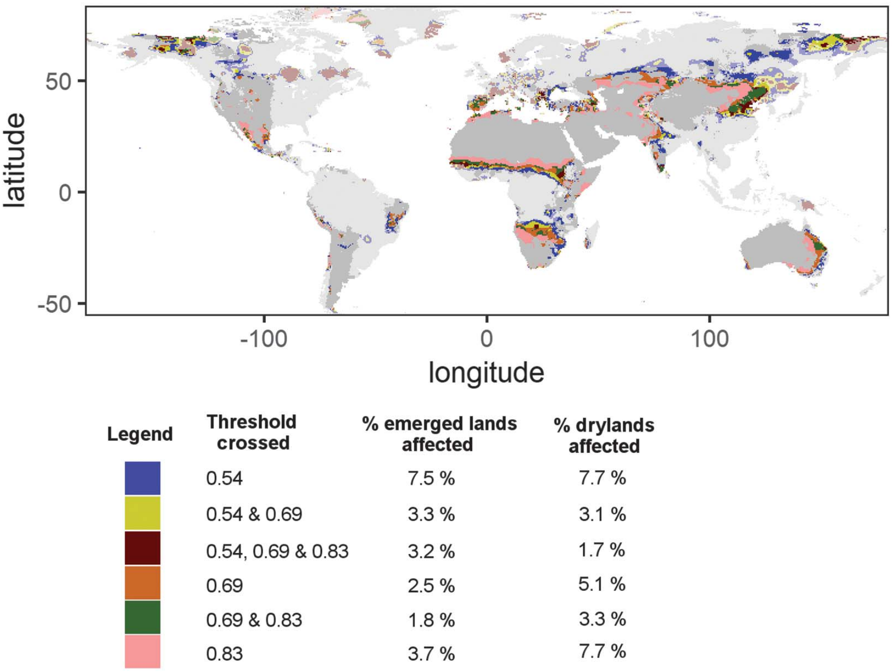


Fig. 3. Map of climate change vulnerability in global drylands. This map includes areas that will cross each (or several) of the thresholds described according to the aridity predicted for 2100 by the IPCC RCP8.5 scenario (i.e., under the assumption of sustained increase in CO_2 emissions). Transparent areas are outside of the range used for the data in this study [i.e., areas that are not drylands today; see (*16*) for further details].

remember that such changes would render these areas unable to sustain current animal and human populations, with fundamental and negative consequences for human well-being globally.

Our results, which are based on analyzing the most comprehensive empirical evidence available so far, show that the responses of multiple functional and structural ecosystem attributes to increases in aridity follow a series of sequential thresholds. Our work goes beyond current knowledge by identifying, for the first time, three phases of abrupt ecosystem changes characterized by consecutive aridity thresholds. Along with recent studies dealing with multiscale regime shifts (*12*), our study provides a well-defined framework for sequential shifts that can inspire a new generation of multiscale models to explore ecosystem responses to climate change. Our findings also set the stage for future studies exploring temporal changes in the ecosystem variables investigated, particularly in areas likely to cross the aridity thresholds identified in the future, and put the focus on identifying potential catastrophic shifts and early warning indicators for them. Finally, the framework introduced here can be used to identify those attributes for which the responses to aridity are more sensitive to buffering, and for establishing effective adaptation and mitigation actions aimed at preserving the capacity of drylands to supply essential ecosystem services needed to sustain a growing human population.

REFERENCES AND NOTES

1. M. Delgado-Baquerizo *et al*., *Nature* **502**, 672–676 (2013).
2. R. Prăvălie, *Earth Sci. Rev.* **161**, 259–278 (2016).
3. J. Huang, H. Yu, X. Guan, G. Wang, R. Guo, *Nat. Clim. Chang.* **6**, 166–171 (2015).
4. N. J. Middleton, T. Sternberg, *Earth Sci. Rev.* **126**, 48–57 (2013).
5. F. T. F. T. Maestre *et al*., *Annu. Rev. Ecol. Evol. Syst.* **47**, 215–237 (2016).
6. M. Cherlet, C. Hutchinson, J. Reynolds, J. Hill, S. Sommer, G. von Maltitz, *World Atlas of Desertification* (Publication Office of the European Union, ed. 3, 2018).
7. United Nations Department of Economic and Social Affairs, *The Sustainable Development Goals Report 2017* (United Nations, 2017); https://doi.org/10.18356/4d038e1en.
8. M. Berdugo, S. Kéfi, S. Soliveres, F. T. F. T. Maestre, *Nat. Ecol. Evol.* **1**, 0003 (2017).
9. S. Kéfi, M. Rietkerk, M. van Baalen, M. Loreau, *Theor. Popul. Biol.* **71**, 367–379 (2007).
10. J. F. Reynolds *et al*., *Science* **316**, 847–851 (2007).
11. W. H. Schlesinger *et al*., *Science* **247**, 1043–1048 (1990).
12. J. C. Rocha, G. Peterson, Ö. Bodin, S. Levin, *Science* **362**, 1379–1383 (2018).
13. M. Lu, L. O. Hedin, *Nat. Ecol. Evol.* **3**, 239–250 (2019).
14. R. Ochoa-Hueso *et al*., *J. Ecol.* **106**, 242–253 (2018).
15. L. Turnbull *et al*., *Ecohydrology* **5**, 174–183 (2012).
16. Materials and methods are available as supplementary materials.
17. P. M. Groffman *et al*., *Ecosystems (N. Y.)* **9**, 1–13 (2006).
18. S. Whisenant, *Repairing Damaged Wildlands: A Process-Orientated, Landscape-Scale Approach* (Cambridge Univ. Press, 1999).
19. P. B. Reich, *J. Ecol.* **102**, 275–301 (2014).
20. V. Maire *et al*., *Glob. Ecol. Biogeogr.* **24**, 706–717 (2015).
21. D. E. Carvajal, A. P. Loayza, R. S. Rios, C. A. Delpiano, F. A. Squeo, *J. Ecol.* **107**, 1079–1092 (2019).
22. M. Berdugo *et al*., *J. Ecol.* **107**, 190–202 (2018).
23. P. D'Odorico, G. S. Okin, B. T. Bestelmeyer, *Ecohydrology* **5**, 520–530 (2012).
24. M. L. Phillips, B. E. McNellis, M. F. Allen, E. B. Allen, *Am. J. Bot.* **106**, 1210–1218 (2019).
25. A. W. R. Seddon, M. Macias-Fauria, P. R. Long, D. Benz, K. J. Willis, *Nature* **531**, 229–232 (2016).
26. A. C. Staver, S. Archibald, S. A. Levin, *Science* **334**, 230–232 (2011).
27. S. I. Higgins, S. Scheiter, *Nature* **488**, 209–212 (2012).
28. W. Ulrich *et al*., *J. Biogeogr.* **41**, 2307–2319 (2014).
29. Y. Le Bagousse-Pinguet *et al*., *J. Ecol.* **105**, 1058–1069 (2017).
30. W. A. Rutherford *et al*., *Sci. Rep.* **7**, 44188 (2017).

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/367/6479/787/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S14
Tables S1 to S3
References (*31*–*124*)

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Thresholds of aridity

Increasing aridity due to climate change is expected to affect multiple ecosystem structural and functional attributes in global drylands, which cover ~45% of the terrestrial globe. Berdugo *et al.* show that increasing aridity promotes thresholds on the structure and functioning of drylands (see the Perspective by Hirota and Oliveira). Their database includes 20 variables summarizing multiple aspects and levels of ecological organization. They found evidence for a series of abrupt ecological events occurring sequentially in three phases, culminating with a shift to low-cover ecosystems that are nutrient- and species-poor at high aridity values. They estimate that more than 20% of land surface will cross at least one of the thresholds by 2100, which can potentially lead to widespread land degradation and desertification worldwide.

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