

Review

Hydrologic variability in dryland regions: impacts on ecosystem dynamics and food security

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Research on ecosystem and societal response to global environmental change typically considers the effects of shifts in mean climate conditions. There is, however, some evidence of ongoing changes also in the variance of hydrologic and climate fluctuations. A relatively high interannual variability is a distinctive feature of the hydrologic regime of dryland regions, particularly at the desert margins. Hydrologic variability has an important impact on ecosystem dynamics, food security and societal reliance on ecosystem services in water-limited environments. Here, we investigate some of the current patterns of hydrologic variability in drylands around the world and review the major effects of hydrologic fluctuations on ecosystem resilience, maintenance of biodiversity and food security. We show that random hydrologic fluctuations may enhance the resilience of dryland ecosystems by obliterating bistable deterministic behaviours and threshold-like responses to external drivers. Moreover, by increasing biodiversity and the associated ecosystem redundancy, hydrologic variability can indirectly enhance post-disturbance recovery, i.e. ecosystem resilience.

Keywords: interannual rainfall fluctuations; dryland ecosystems; resilience

1. INTRODUCTION

Drylands are regions characterized by permanent or seasonal conditions of limited water availability. They are typically classified on the basis of their climate, hydrologic conditions, soil properties and vegetation composition, although mean annual precipitation remains the main indicator used to define their spatial extent and geographical distribution [1]. In these regions, however, water availability may also be determined by the presence of exogenic rivers, the source areas of which are located in wetter climates (e.g. the Nile, Okavango, Colorado, Rio Grande). It has been estimated that, altogether, arid, semiarid and dry sub-humid regions cover about 41 per cent of the Earth's land surface and that more than two billion people live in drylands [2]. Drylands are typically located in the tropics (regions of predominant air mass divergence), in the rain shadow of mountain chains, in the middle of continental landmasses or in subsidence zones close to cold ocean surfaces [3].

Most dryland regions exhibit a high interannual variability in their rainfall regime [4,5]. Figure 1 shows the global map of the coefficient of variation of precipitation (s.d.: mean). Strong interannual variability is found in arid and semiarid regions, while low variability exists in the middle of major deserts and hyperarid zones, which are areas of persistent high

atmospheric pressure conditions. There is some evidence of an ongoing global increase in the interannual variability of precipitation and intensification of extreme events [5,7–10]. However, it is still unclear how dryland ecosystems might respond to these variations in rainfall regime [11]. It has been argued that changes in the stochastic *seasonal* patterns of precipitation might have stronger effects on ecosystem productivity [12] and nutrient cycling [13] than changes in the mean. Similarly, *interannual* rainfall variability is likely to have an important impact on the composition, structure, diversity and productivity of dryland ecosystems [14–16]. How will ecosystem dynamics respond to changes in interannual rainfall variability? Most of the research on ecosystem response to climate change has considered the effect of shifts in the mean climate variables, while the impact of changes in the variance of precipitation has remained poorly investigated [15,17]. Although changes in mean climate conditions have important effects on ecosystem structure and function, here we show that changes in the variance of climate drivers may also play an important and counterintuitive role in ecosystem dynamics.

An increase in variability of environmental drivers is commonly expected to induce disorganized random fluctuations in the state of the system around its stable configuration(s). However, recent research in physics, chemistry and biology [18–20] has shown that, in addition to this trivial effect, an increase in the variance of environmental noise could have more counterintuitive impacts on system dynamics: it could generate new bifurcations, enhance ecosystem

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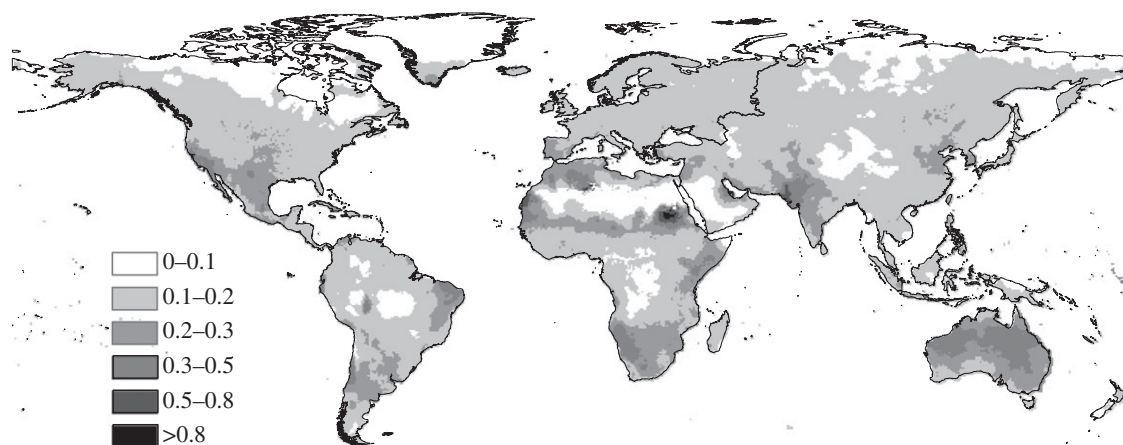


Figure 1. Coefficient of variation (s.d.: mean) of annual precipitation. Based on a gridded dataset (CRU TS 3.1) developed by the Tyndall Centre for Climate Change Research and the Climate Research Unit (CRU), the University of East Anglia [6] for the period 1901–2009.

stability or induce pattern formation [20]. In this paper, we will first evaluate changes in the interannual variability of precipitation around the world, and then discuss their possible impact on the stability and resilience of dryland ecosystems. We will focus in particular on the case of bistable ecosystems, which are known for having a limited ecological resilience, because of their susceptibility to abrupt shifts to qualitatively different states.

2. SOME GLOBAL PATTERNS OF CLIMATE VARIABILITY

To investigate the possible effect of climate variability on dryland ecosystems, we first analyse recent patterns of change in precipitation variability and identify regions that have been affected by variations in the precipitation regime in the last century. To this end, we have used the CRU TS 3.1 gridded rainfall dataset developed by the Tyndall Centre for Climate Change Research and the Climate Research Unit (CRU) of the University of East Anglia [6]. This dataset was obtained by interpolating station data with a resolution of $0.5 \times 0.5^\circ$ [21,22]. Because there is only a limited number of precipitation stations in most drylands [22], this analysis of change in variability of precipitation only includes grid cells that are within 200 km from precipitation stations that were in operation in 1901 (figure 2a); new stations that were in operation by 1928 (figure 2b) and 1955 (figure 2c) were also considered.

Zhang *et al.* [23] used observed and simulated precipitation anomalies between 40° S and 70° N from 1925 to 1999 and found that regional precipitation in the Northern Hemisphere mid-latitudes and Southern Hemisphere subtropics and deep tropics increased, and decreased in the Northern Hemisphere subtropics and tropics. Hence, the Sahel became drier while the deserts in Southern Hemisphere became wetter. Important changes in the precipitation regime have been observed not only in the mean annual precipitation, but also in the variance. A number of studies have documented an increase in interannual rainfall variability and an amplification of extreme events in

the twentieth century [8,9,24,25], a trend that is predicted to continue in the future [26]. However, our analysis shows that the global patterns of precipitation variability in the past 100 years have been more complex (figure 2). Some major dryland regions have experienced a decrease in the variability of precipitation including the Namib Desert, and the Tanami, Simpson and Stzelecki deserts in Australia. In these regions, variability increased in the first half of the twentieth century and decreased in the following decades. The precipitation variability in the Thar Desert in India has increased in the latter part of the century. The North American deserts and the Kalahari Desert in Botswana have alternated between high and low variability throughout the twentieth century, however, the variability has increased in the north-eastern Kalahari in the second-half of the twentieth century. Thus, not all dryland regions underwent a consistent increase in the interannual variability of precipitation. Nevertheless, because relatively strong interannual rainfall fluctuations are a recurrent feature of dryland ecosystems (figure 1, see also [27]), understanding the role played by rainfall fluctuations in the dynamics of these ecosystems remains an important task. To this end, in the following sections, we will examine ecosystem response to environmental change and discuss the effect of changes in the variability of climatic and hydrologic drivers.

3. ECOSYSTEM RESPONSE TO ENVIRONMENTAL CHANGE

Ecosystem dynamics are often investigated by looking at steady configuration(s)—or ‘equilibria’—and at the system’s response to displacements from equilibrium points. A steady state is said to be ‘stable’ (or an ‘attractor’) if, after a ‘small’ displacement, the system tends to converge back to that state. Conversely, it is unstable if the dynamics diverge. Ecological resilience is an attribute of stable states, which expresses the ability of an ecosystem to recover a stable configuration after a disturbance ([28]; figure 3).

Interestingly, some ecosystems may exhibit more than one stable state [29–31]. The emergence of

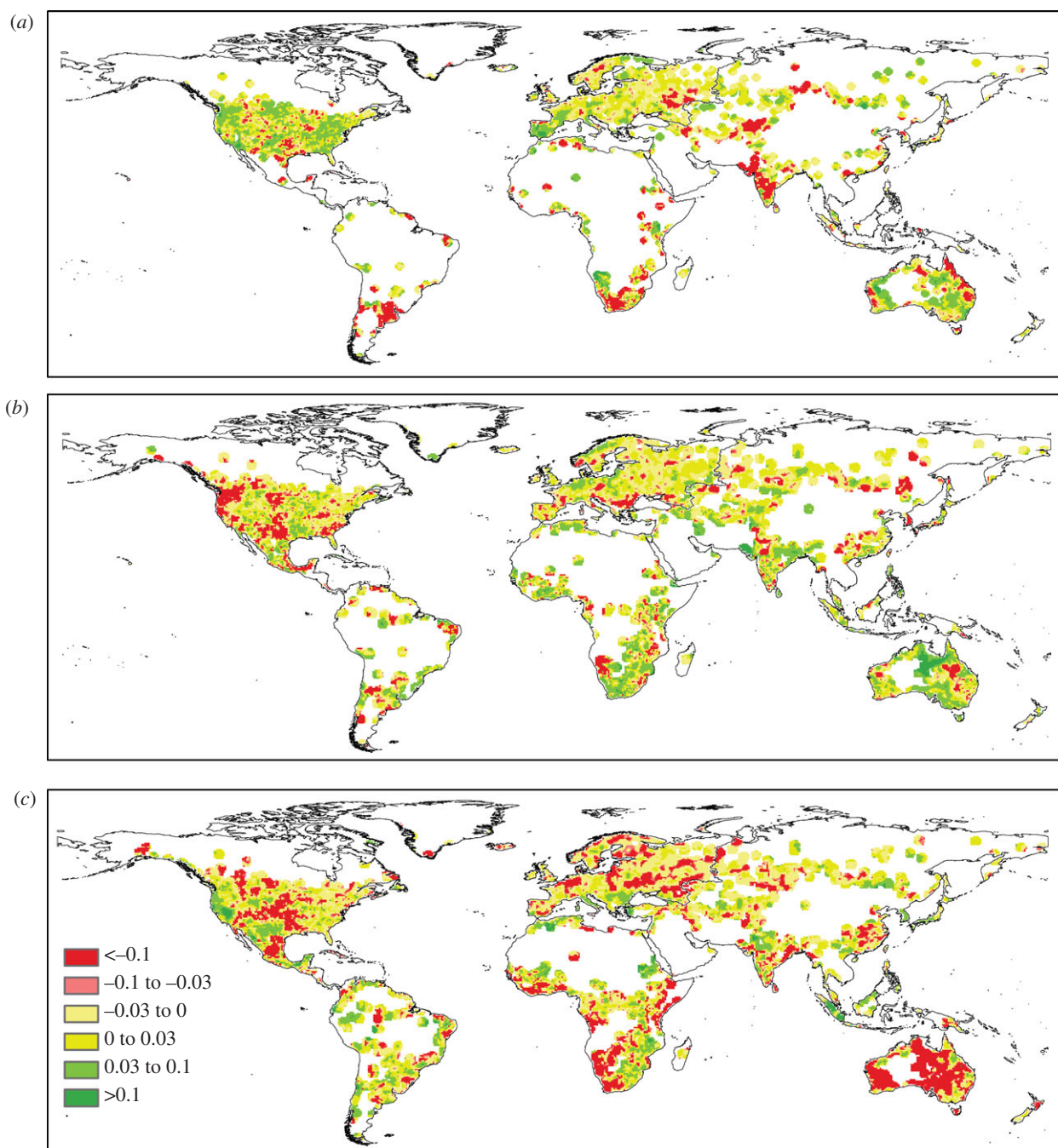


Figure 2. Differences in the coefficient of variation (CV) of annual precipitation between (a) 1928–1954 and 1901–1927; (b) 1955–1981 and 1928–1954; (c) 1982–2009 and 1955–1981. Only grid cells that are within 200 km of a weather station are used for this analysis.

bistability has profound effects on the way an ecosystem may respond to changes in environmental conditions or disturbance regime. In fact, unlike systems with only one stable state, bistable dynamics exhibit a threshold associated with the presence of a ‘divide’ (or ‘potential barrier’) between their two attractors. Thus, while each attractor is a stable state with respect to ‘small’ perturbations, when the magnitude of the perturbation exceeds a critical threshold, the system can cross a potential barrier (figure 3) and diverge towards its alternative stable state. The regime shift can be highly irreversible because the new configuration is also stable, which means that the system would not spontaneously return back to its initial state as it would in the case of dynamics

with only one stable state (figure 3a). Thus, the attractors of bistable dynamics have only a limited resilience: they can recover only from disturbances smaller than a critical magnitude, while if they cross a critical threshold, recovery is unlikely to occur. Because a variety of dryland ecosystems may exhibit bistable dynamics, some of the early ecological theories on alternative stable states in environmental dynamics were developed and applied to arid and semiarid landscapes [29,31].

Ecosystems may respond in different ways to shifts in climate and hydrologic conditions. In the case of linear response, the state of the system changes proportionally to the variations in the external drivers (figure 4a). In most cases the dependence on environmental drivers

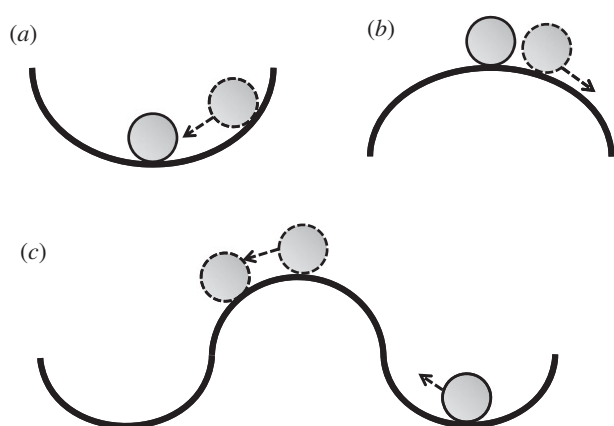


Figure 3. Schematic of (a) stable and (b) unstable states of a dynamical system; (c) in the case of bistable ecosystems the dynamics exhibit two alternative (meta-stable states separated by a potential barrier).

is not necessarily linear (figure 4c,d). Figure 4b shows the case of a system whose stable states are a continuous nonlinear function of the external driver; in other cases this dependence can be discontinuous: it can exhibit thresholds, abrupt transitions (figure 4c) and fold-type bifurcations (figure 4d). The ecological implications of these nonlinearities are that small changes in the environmental driver (e.g. rainfall regime) can induce big changes in the ecosystem's state. In particular, when a threshold response exists (figure 4c,d) almost no perceptible change may occur until the system crosses a critical threshold. While in the case of figure 4c the system returns back to its initial state as soon as the threshold is crossed in the opposite direction, if a fold-type bifurcation is present (figure 4d) there is a hysteresis, whereby a different threshold needs to be crossed for the system to recover its initial state. Because this behaviour is induced by the presence of a bistable regime, there is a direct association among the emergence of alternative stable states, the irreversibility of state transitions and the ability of the system to recover its initial configuration after a disturbance, i.e. the ecosystem's resilience. In the study of how changes in environmental drivers (e.g. precipitation) may affect the terrestrial biosphere it is important to understand what affects ecosystem resilience. To this end, in the following sections we will discuss a number of factors that can enhance or reduce ecological resilience. In particular, we focus on the effect of hydrologic fluctuations on ecosystem bistability, biodiversity and vegetation pattern formation.

The view emerging from the previous discussion on reversibility and resilience is that the existence of alternative stable states reduces ecological resilience because in bistable systems post-disturbance recovery is unlikely to occur after a critical threshold has been crossed. In fact, once the system transitions to the other state, it remains locked in that state's domain of attraction. For example, a temperate forest that recovers after logging is more resilient than a tropical forest that is prone to post-disturbance loss of most of its soil resources. In the first case, the forest is the only stable configuration of the system, while in the second case the forest is a (meta-) stable state of

bistable dynamics with two alternative stable states of forest and degraded land [32]. Thus, from this perspective, factors determining ecosystem resilience are the same factors that favour or inhibit metastability, i.e. the emergence of alternative stable states.

Ecosystem bistability is often associated with the presence of positive feedbacks with the limiting resources or disturbance regime [33]. For example, desertification is typically defined as a permanent change in vegetation, soil properties and climate sustained by a self-reinforced sequence of processes whereby an initial loss of vegetation could—for instance—reduce precipitation or cause loss of soil fertility, thereby further decreasing vegetation density (see [3] for a review). A number of feedback mechanisms may affect the dynamics of dryland ecosystems. In table 1, we provide a synthesis of the main mechanisms and of their supporting literature. We classify them depending on whether they involve limiting resources—as in the desertification example discussed above—or the disturbance regime (e.g. fires, flooding), though in some cases these feedbacks involve both disturbances and resources. It is interesting to observe that most of the feedback mechanisms affecting dryland ecosystems involve ecohydrological processes, i.e. interactions between water and the biota.

The existence of ecosystem bistability is often difficult to assess. When the processes involved in a feedback operate at relatively large scales (e.g. the study of the hydroclimatic impact of regional deforestation), direct experiments are not feasible and the possible emergence of bistable dynamics can only be investigated using model simulations. Only in some rare cases can manipulative experiments be used to purposely cause a transition to a possible alternative state [79]. More commonly, state shifts are investigated capitalizing on relatively permanent changes in ecosystem state resulting from land use, particularly, if they occur in landscapes with adjacent areas subjected to different land use histories. For example, in the case of shrub encroachment in desert grasslands—a typical example of state shift in bistable dryland ecosystems [3,74,80]—the high degree of irreversibility of the grass-to-shrub transition has been assessed in landscapes where decades of overgrazing and fire control caused an abrupt increase in woody plant cover. The failure of a number of shrub removal programmes aiming at maintaining rangeland productivity [81–84] is good evidence of the fact that this state shift is likely to be permanent and the underlying dynamics bistable.

In other cases, bistability can be inferred from the presence of spatial discontinuities (or 'switches') in ecosystem state, i.e. an abrupt transition in space [33]. In fact, the coexistence of the two states in a landscape with the same climate, soils and other environmental conditions is a good indicator of bistability. This bistability could be induced by positive feedbacks operating at the local scale, whereby two plant communities could—for example—coexist in the same landscapes because one of them (or both) modifies its physical environment to create its own habitat. Known as 'ecosystem engineering' [85], this phenomenon is ubiquitous in dryland ecosystems,

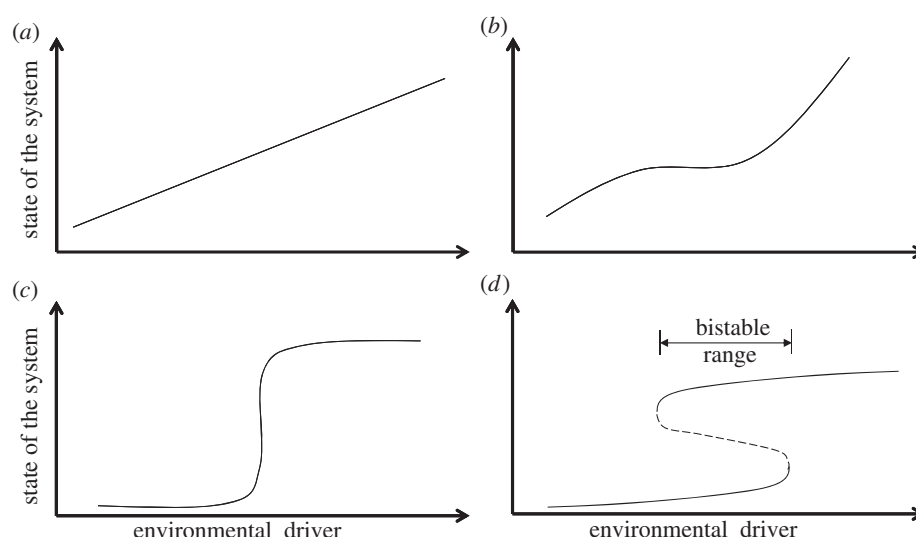


Figure 4. Examples of possible responses on an ecosystem to environmental drivers: (a) linear; (b) nonlinear; (c) threshold-like; (d) threshold-like with hysteresis and bistable dynamics within a range of environmental conditions (solid line, stable; dashed line, unstable).

Table 1. Summary of major feedback mechanisms in dryland ecosystems classified on the basis of whether they are resource feedbacks (R) or disturbance feedbacks (D), supported by experimental observations (E) or modelling studies (M).

feedback	mechanism	type	supporting studies
vegetation–precipitation	more vegetation → more precipitation → more vegetation	R, M	[34–40]
vegetation–soil moisture	higher soil moisture beneath vegetated soil patches → favourable conditions for plant establishment	R, E	[41–45]
		R, M	[31,45–48]
canopy–fog deposition	canopies trap fog droplets or favour condensation (dew) → enhanced water availability	R, E	[49–52]
canopy–atmospheric deposition	canopies trap nutrient-rich airborne particulate → increased nutrient availability	R, E	[43,53–59]
		R, M	[32]
vegetation–groundwater	evapotransp. and uptake drain the root zone from shallow water tables → soil aeration and no waterlogging → good conditions for plant growth	D, E	[60–66]
		D, M	[67]
vegetation–salinity	plants drain shallow ground water → less exfiltration → less soil evaporation and less salt accumulation → good conditions for plant growth	D, E	<i>Sensu</i> : [68,69]
		D, M	[70,71]
vegetation–fire	more grasses (fuel load) in savannahs → increased fire pressure → tree mortality → enhanced grass cover	D, E	[72,73]
		D, M	[74–76]
erosion–vegetation	if vegetation is removed, erosion reduces soil resources → prevents re-establishment.	D, R, E	[55]
		D, R, M	[77,78]

where organisms have been reported to enhance their access to resources, reduce disturbance intensity or create an exceedingly unfavourable habitat for their competitors [55,59,86,87].

In the absence of switches, one might design some experiments to assess the existence of a positive feedback. Feedback testing entails the search for evidence both of ecosystem response to a certain environmental driver, and of that driver's impact on the ecosystem. For example, to test the fire–vegetation feedback in savannahs (table 1), we need to show that (i) fires are more frequent and intense in the presence of higher amounts of grass fuel (figure 5a); and (ii) that grass cover increases with increasing fire pressure (figure 5b). The existence of a positive feedback is not the conclusive evidence of bistability, but remains

an important indicator (i.e. sufficient although not a necessary condition) of the possible emergence of alternative stable states and of the susceptibility of the system to irreversible states shifts.

4. EFFECT OF HYDROCLIMATIC FLUCTUATIONS ON ECOLOGICAL RESILIENCE

In the previous section, we have stressed how positive feedbacks may reduce ecosystem resilience because of their ability to generate alternative stable states. Thus, resilience is expected to decrease as the intensity of positive feedbacks increases [45]. It is interesting to investigate conditions that could enhance ecosystem resilience. Two major mechanisms are based on: (i) a stabilization effect of environmental fluctuations

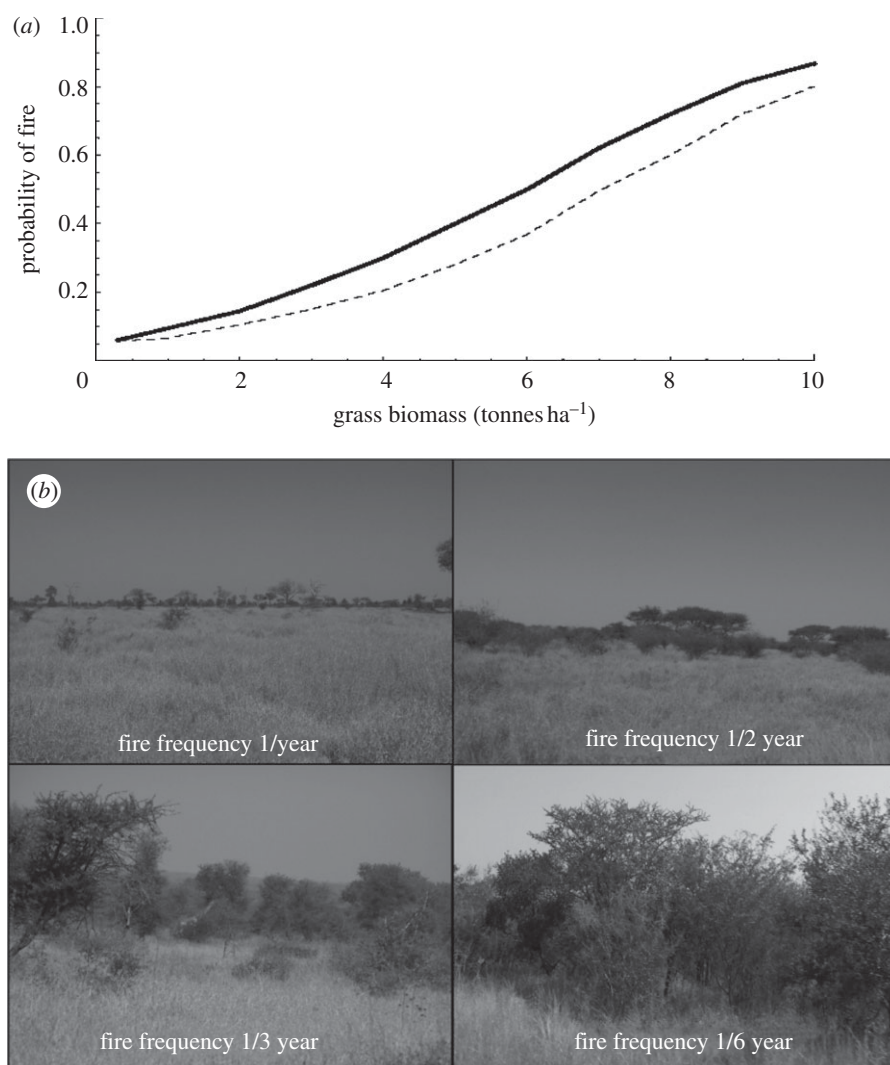


Figure 5. (a) Effect of grass biomass on the probability of fire occurrence at Kruger National Park, South Africa on two different years (redrawn from [88]) and (b) effect of fire frequency on grass biomass and plant community composition, based on pictures of burn control plots at Kruger National Park (2004).

[89]; and (ii) the redundancy of species' functional traits associated with higher levels of biodiversity [90].

(a) *The effect of climate fluctuations*

Environmental variability (e.g. interannual rainfall fluctuations) may play an important role in dryland ecosystems, particularly, if the underlying deterministic dynamics are bistable [20]. Random hydroclimatic fluctuations are typically expected to generate transitions of a bistable system from a domain of attraction to the other [91]. However, it has been argued that, besides this trivial effect, environmental noise may also play a more fundamental role [18]. For example, random fluctuations may induce the emergence of two preferential hydroclimatic states despite the underlying deterministic system having only one stable state [92]. Similarly, random fluctuations may turn a bistable deterministic system into one with only one preferential state. D'Odorico *et al.* [89] investigated the case of bistable deterministic ecosystems, which in the absence of random environmental drivers exhibit two alternative stable states: vegetated land and unvegetated ('desertified')

conditions. This bistable behaviour could be induced by a positive feedback, as discussed in the previous sections (see table 1). Random hydrologic fluctuations may entail a repeated switching between water stress conditions in which the system tends to the stable unvegetated attractor, and unstressed conditions in which the dynamics converge to a stable vegetated state. As a result of the switching between these two attractors, the dynamics are stabilized in an intermediate configuration, which would be unstable in the absence of the random hydrologic fluctuations. Thus, in this case, random environmental variability may turn bistable deterministic dynamics into a stochastic system with only one preferential state (see figure 6). As noted before, the stochastic system has a much higher resilience than its bistable deterministic counterpart [93].

A similar effect of random environmental variability has been discussed by other authors [38,94,95]. Using a coupled biosphere-regional climate model, Zeng & Neelin [38] showed that a positive feedback between rainfall and vegetation could induce bistable dynamics in two distinct regions of Africa, namely the Sahel and the Kalahari. Depending on the initial land cover conditions, these two regions could converge either to a

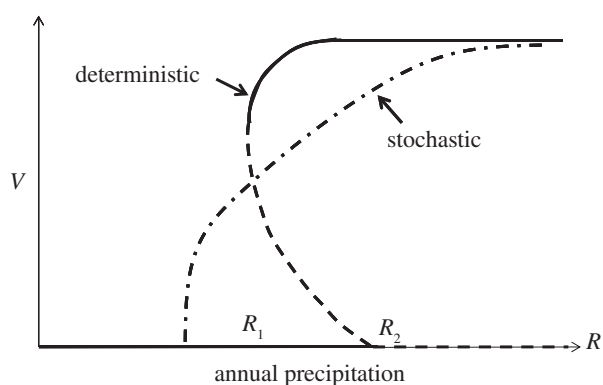


Figure 6. Effect of stochastic environmental fluctuations on the stability and resilience of a dryland ecosystem. In the absence of interannual rainfall fluctuations the system exhibits a 'fold-type' bifurcation with a bistable range for $R_1 < R < R_2$. Within this range the dynamics have two stable states (solid lines) separated by an unstable state or 'potential barrier' (dashed line). Random interannual fluctuations may turn these dynamics into a system with only one stable state (dash-dotted line). (Adapted after [89]).

stable vegetated state or to desert-like conditions. However, environmental variability associated with fluctuations in sea surface temperatures obliterates this bistable behaviour and stabilizes the system in an intermediate state. This effect becomes stronger as the amplitude of the fluctuations increases. Similarly, Bathiany *et al.* [95] used a coupled vegetation-climate model to investigate the abrupt change in vegetation cover during the mid-Holocene decline of the 'green-Sahara' [96] and found that environmental noise may stabilize the 'green' state of the system.

Overall, random hydrologic fluctuations may have a non-trivial effect on the dynamics of dryland ecosystems. It is commonly expected that, by inducing disorganized fluctuations about the stable state(s) of the system, hydroclimatic variability acts as a source of disturbance in ecosystem dynamics. Model simulations, however, indicate that environmental fluctuations may have a more 'constructive' role, in that they may lead to the emergence of new preferential states and enhance resilience by turning a bistable process into a system with only one preferential state (figure 6).

Environmental variability may have a similar effect on the spatial dynamics of vegetation. Recent research has related vegetation pattern formation to ecosystem processes [97–99] and ecological resilience [100,101]. It has been suggested that arid ecosystems can enhance their productivity and resilience by developing spatial interactions, which result in the emergence of organized plant distributions [101–103]. Environmental variability can be a major contributor to pattern formation [20]. D'Odorico *et al.* [104] considered the case of a spatially extended system that randomly switches between a water-stressed and an unstressed state. In stressed conditions the system tends to zero vegetation cover; conversely, unstressed vegetation dynamics tend to a homogeneous cover. The random switching between these two states may lead to the emergence of an organized patchy distribution of vegetation as shown in figure 7. Thus, a synergism between spatial interaction and hydroclimatic

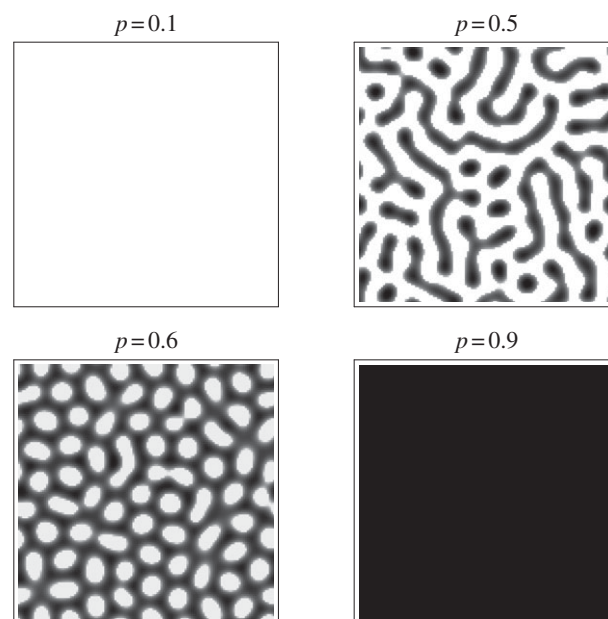


Figure 7. Noise-induced patterns generated by a spatially explicit model simulating the random occurrence of water stressed (with probability $1 - p$) and unstressed (with probability p) conditions as a dichotomous Markov process [104]. When the switching is weak (i.e. p close to 0 or 1) either state persists for long enough to allow the system to converge to bare soil or uniform vegetation cover conditions. With more intense switching (i.e. p close to 0.5) patterns emerge. Interannual rainfall fluctuations allow a (patterned) vegetated state to exist even when the mean annual precipitation would be too low for the persistence of a stable vegetated state under non-fluctuating rainfall conditions.

fluctuations may enhance the stability and resilience of vegetation in arid climates where, in the absence of fluctuations, no vegetation cover would persist.

(b) Resilience and biodiversity

Besides environmental fluctuations, there are other factors that can contribute to ecosystem resilience. It has been argued that biodiversity enhances resilience because more diverse systems are more likely to be redundant in that they have more than one species able to perform the same ecosystem function [90,105,106]. Thus, if one of them goes extinct or its population density decreases, there are other species with similar functional traits but different sensitivity to disturbance, which can ensure that function. Known as 'insurance hypothesis' [107,108], the idea that biodiverse systems are more redundant and therefore exhibit a higher resilience is supported by some experimental evidence [109,110]. In particular, post-disturbance recovery is enhanced by species redundancy associated with response diversity [111], which requires that taxa with different response traits exist within the same functional group [112,113].

Thus, the search for factors contributing to ecosystem resilience can be partly approached by investigating conditions that favour or reduce biodiversity [114]. What are the ecosystem attributes that enhance biodiversity? Interestingly, it has been observed that spatial heterogeneity and temporal variability can maintain higher levels of biodiversity [115–119].

Tree-grass coexistence in savannahs has been explained by some authors as an effect of temporal variability associated with disturbances and climate fluctuations [104,120–122]. The idea that temporal variability induced by disturbances may enhance species diversity [123] is consistent with the ‘intermediate disturbance hypothesis’, which postulates that disturbances of intermediate intensity favour biodiversity [124,125]. Thus, while species diversity enhances ecosystem ability to respond to environmental variability [108,126], fluctuations induced by disturbances of intermediate intensity maintain high levels of diversity [124,127]. D’Odorico *et al.* [17] developed a stochastic population dynamics model showing how environmental noise of moderate intensity may enhance biodiversity, consistently with the intermediate disturbance hypothesis. The higher levels of species diversity can in turn enhance ecosystem resilience (insurance hypothesis). Presently, there is no direct evidence of the ability of hydrologic fluctuations to enhance resilience. However, there is some experimental evidence of the ability of biodiversity to enhance ecosystem resilience in coral reefs [110], kelp forests [109] and boreal forests [128]. At the same time, the ability of moderate disturbances to sustain higher levels of diversity (intermediate disturbance hypothesis) has been documented in the case of tropical forests, coral reefs and a few other ecosystems [124,127]. The ability of environmental fluctuations to enhance biodiversity has been supported by experimental observations in the case of rock shore communities of algae and invertebrates exposed to the same mean conditions but with fluctuations of different intensity [129,130].

(c) *Resilience and food security*

Similar concepts are often applied to the study of *societal resilience* with respect to droughts or other stressors [131]. Redundancy of key resources and income diversification are crucial elements that maintain resilience while reducing societal vulnerability to climate change and environmental degradation [132]. Loss of redundancy in the life support system may cause major losses of societal resilience. An example is provided by the societal dependence on freshwater resources used—directly or indirectly—for food production. It has been observed [133] that some societies rely on the importation of food because the water resources locally available are not sufficient to meet the needs of their growing populations. Thus, food trade is associated with a virtual transfer of freshwater resources from areas of food production to importing regions. Virtual water transfers have allowed some societies to reduce famine and avoid water wars [133]. During major droughts, food aid programmes have virtually transferred water resources to areas of crisis. In some cases, agricultural land had to substantially increase in the food-producing country to meet the demand of drought regions. For instance, in 1974, during the early stages of the recent multidecadal drought in West Africa, the USA had to put under cultivation 10 million hectares [134]. If this increase in cultivated land is not just a temporary measure to face that particular emergency (at that point there were

only 28 days left in the global grain reserve), the system would lose part of its redundancy. Thus, when the next drought strikes a different part of the world, there would be fewer options available to implement a similar food (and water) solidarity programme. Therefore, it has been suggested that an effective water solidarity strategy aims at providing virtual water resources in areas affected by a major drought and crop failure only for the duration of the emergency and without enhancing the long-term dependency of the water-poor country on foreign regions of food production [3].

As a result of the ongoing intensification of virtual water trade [135], there are less freshwater resources in water-rich countries that are not used on a regular basis to support the population of water-limited societies. D’Odorico *et al.* [136] have shown that the ongoing globalization of water has the effect of reducing the worldwide redundancy of freshwater resources, thereby reducing societal resilience. A loss of redundancy limits the ability of societies to recover from drought-induced crop failure by increasing food imports. Similarly, the ongoing unsustainable depletion of groundwater resources [137] reduces the redundancy of freshwater availability, thereby depriving future generations of a pool of resources that can be tapped in conditions of crisis. At the same time, however, investments in the development of new technology and in infrastructures for agriculture (e.g. irrigation systems, dams, bioengineered crops) may alleviate the shortages of water during dry years and allow agriculture to sustain adequate production rates despite the occurrence of adverse hydrologic conditions [138]. Nevertheless, these technological improvements will not be sufficient to offset the effect of population growth and the associated need for an increase in human appropriation of freshwater resources [139].

Thus, while the persistence of hydrologic conditions suitable for adequate food production may become more uncertain because of a presumable increase in climate variability, the ongoing global demographic growth will increase the need for a global redistribution of virtual water, which limits redundancy, thereby causing a loss of societal resilience. Both effects are placing food security at risk [136].

5. CONCLUSIONS

Dryland ecosystems are particularly affected by relatively intense hydroclimatic fluctuations [4]. There is some concern that the interannual variability of precipitation in dryland regions might increase in the future thereby enhancing the occurrence of severe water stress conditions in ecosystems and societies. However, this paper has shown that climate variability and its impact on dryland ecosystems and food security might be more complex. First, despite the existence of some evidence of an ongoing and predicted increase in hydroclimatic variability, the results presented in §2 suggest the occurrence of a decrease in the interannual variability of precipitation between the first- and the second-half of the twentieth century in many drylands around the world. Second, rainfall variability is usually associated with an effect of disturbance on ecosystems

and societies. The intensification of climate fluctuations entails an increase in the frequency of extreme events and the enhancement of the perturbations exerted by hydrologic anomalies on the biota. However, besides this trivial effect of disturbance, interannual rainfall fluctuations may play a more fundamental, constructive and counterintuitive role in ecosystem dynamics: they may enhance resilience, favour the maintenance of biodiversity and induce pattern formation. While positive feedbacks may induce the emergence of bistable dynamics thereby making dryland ecosystems prone to abrupt and irreversible shifts to alternative stable states, random environmental variability can convert bistable dynamics into a system with only one preferential state, which is therefore more resilient than its bistable deterministic counterpart. Resilience is also enhanced by environmental variability through the maintenance of relatively high levels of biodiversity, which may allow dryland ecosystems to recover after severe disturbances, including those induced by extreme hydroclimatic events.

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