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Understanding the role of ecohydrological feedbacks in ecosystem state change in drylands

L. Turnbull,[1]* B. P. Wilcox,[2] J. Belnap,[3] S. Ravi,[4] P. D'Odorico,[5] D. Childers,[6] W. Gwenzi,[7]
G. Okin,[8] J. Wainwright,[9,†] K. K. Caylor[10] and T. Sankey[11]

[1] *Arizona State University Global Institute of Sustainability Tempe, AZ 85287, USA*
[2] *Texas A&M University Department of Ecosystem Science and Management College Station, TX 77843, USA*
[3] *US Geological Survey Southwest Biological Science Center Canyonlands Research Station, 2290 S. West Resource Blvd., Moab, UT 84532, USA*
[4] *University of Arizona B2 Earthscience and UA Biosphere 2 Tucson, AZ 85721, USA*
[5] *University of Virginia Department of Environmental Sciences Charlottesville, VA 22904, USA*
[6] *Arizona State University School of Sustainability Tempe, AZ 85287, USA*
[7] *University of Western Australia School of Plant Biology 35 Stirling Highway, Crawley, WA 6009, Australia*
[8] *University of California Department of Geography Los Angeles, CA 90095, USA*
[9] *University of Sheffield Sheffield Centre for International Drylands Research, Department of Geography Sheffield S10 2TN, UK*
[10] *Princeton University Department of Civil and Environmental Engineering Princeton, NJ 08544, USA*
[11] *Idaho State University Boise Center Aerospace Laboratory 322 E. Front Street Suite 240, Boise, ID 83702, USA*

ABSTRACT

Ecohydrological feedbacks are likely to be critical for understanding the mechanisms by which changes in exogenous forces result in ecosystem state change. We propose that in drylands, the dynamics of ecosystem state change are determined by changes in the type (stabilizing vs amplifying) and strength of ecohydrological feedbacks following a change in exogenous forces. Using a selection of five case studies from drylands, we explore the characteristics of ecohydrological feedbacks and resulting dynamics of ecosystem state change. We surmise that stabilizing feedbacks are critical for the provision of plant-essential resources in drylands. Exogenous forces that break these stabilizing feedbacks can alter the state of the system, although such changes are potentially reversible if strong amplifying ecohydrological feedbacks do not develop. The case studies indicate that if amplifying ecohydrological feedbacks do develop, they are typically associated with abiotic processes such as runoff, erosion (by wind and water), and fire. These amplifying ecohydrological feedbacks progressively modify the system in ways that are long-lasting and possibly irreversible on human timescales. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS ecohydrology; state change; drylands; feedbacks; state change; resilience

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INTRODUCTION

In this paper, we explore how ecohydrological feedbacks control ecosystem states in drylands. *Ecosystem state change*, which refers to a change in the structure and function of an ecosystem (Beisner *et al*., 2003), is typically induced by exogenous forces (environmental drivers and disturbances) that either cause a direct change in system state or trigger changes in the internal system feedbacks that control the dynamics of an ecosystem, including its resilience. *Ecological resilience* is the capacity of a system to respond to exogenous forces and reorganize while undergoing change, so as to retain the same function, structure, and identity – i.e. the same state (Walker *et al*., 2004).

Until recently, the discourse regarding ecosystem state change has focused on ecological components of the system; consideration of *ecohydrological feedbacks* (among ecological, hydrological, and geomorphological processes) has been largely missing, even though they exert a profound influence on the structure and function of ecosystems (Huxman *et al*., 2005; Newman *et al*., 2006; Ravi *et al*., 2008; Turnbull *et al*., 2008; Wilcox *et al*., 2008; Turnbull *et al.,* 2010a, b; Wilcox, 2010). It is imperative that future work in ecosystem state change adopt this more comprehensive, ecohydrological focus – which we argue will be critical for understanding the mechanisms by which exogenous forces cause ecosystem state change, and how they affect the dynamics of change, in particular, the crossing of critical thresholds. Such an understanding is critical to successful environmental management – either to reduce the likelihood that a system will transition to a less desirable state or to restore a system to a more desirable state.

Thus, we explore how ecohydrological feedbacks control ecosystem state change in drylands by reviewing the current understanding of ecosystem state change in accordance with different types of exogenous forces, internal system feedbacks, and resulting dynamics of change. We then evaluate the significance of ecohydrological feedbacks by drawing upon five case studies, each of which addresses how exogenous forces affect ecosystem state, either directly or by altering the strength and/or type of ecohydrological feedback. Drawing upon these case studies, we explore different types of ecohydrological

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*Correspondence to: Correspondence to: L. Turnbull, Arizona State University, Global Institute of Sustainability, Tempe, AZ 85287, USA. E-mail: Laura.Turnbull@asu.edu

[†] Current Address: Durham University, Department of Geography, Durham, DH1 3LE, UK

feedbacks that are critical in terms of maintaining a stable state or propagating a transition to a new state in drylands, and if breaking stabilizing feedbacks alone is sufficient to cause a change in system state.

EXOGENOUS FORCES, ECOHYDROLOGICAL FEEDBACKS, AND ECOSYSTEM RESILIENCE

Exogenous forces affect ecosystems across a continuum of spatial and temporal scales. For example, climate change affects ecosystems across broad spatial scales and exhibits variation across multiple temporal scales, ranging from daily variations in light, temperature, and precipitation to multi-annual periodicities (such as El Niño Southern Oscillation and the North American Monsoon). These forces drive variations in ecological processes such as photosynthesis and respiration and hydrological and geomorphic processes such as runoff and erosion. Changes in climate that affect the state of a system may be directional, for example a decrease in precipitation, or they may have no overall directional effect, for example a shift in rainfall seasonality. Other exogenous forces may be abrupt and intense events that exhibit spatial and temporal variation, such as hurricanes, flood events, or sudden changes in land use (Scheffer *et al*., 2001).

Ecosystems respond to exogenous forces in two main ways (Holling, 1973; Wilson and Agnew, 1992; Beisner *et al*., 2003; Scheffer and Carpenter, 2003; Lawrence *et al*., 2007):

1. A direct change in ecosystem state occurs when a sufficiently large perturbation is applied (most often a short-duration disturbance).
2. Internal system feedbacks are altered, and in turn, the resilience of the ecosystem is modified. In some cases, the system may eventually be forced into a new state.

In drylands, where abiotic processes such as wind and water erosion exert a great influence on surface processes (Maestre and Cortina, 2004; Wainwright, 2009), exogenous forces are more likely to alter the type and/or strength of ecohydrological feedbacks through their influence on abiotic processes. Ecohydrological feedbacks are best understood as either *stabilizing* (or *negative*) agencies, which increase the resilience of an ecosystem state, or *amplifying* (or *positive*) agencies, which reduce the resilience of that state (Van Nes and Scheffer, 2007). When feedbacks decrease the resilience of the system – i.e. driving the system towards a critical threshold (Scheffer, 2009) – the system is more susceptible to being tipped into an alternative state by a small change in environmental conditions or by an abrupt disturbance. The alternative ecosystem state may then be irreversible (Noy-Meir, 1975; May, 1977; Walker *et al*., 1981; Scheffer *et al*., 2001; Suding and Hobbs, 2009). Because of this dynamic, ecosystems do not necessarily track environmental forcings in a linear way (King *et al*., 2011; Thrush *et al*., 2009).

The dynamics of ecosystem state change vary with the type of exogenous force(s) and the resulting changes in the strength and/or type of ecohydrological feedback(s). Ecosystems typically respond to exogenous forces in accordance with one of the following three models of ecosystem state change (Suding and Hobbs, 2009):

1. *The continuous change model*: An exogenous force causes ecosystem structure and function to change back and forth along the same trajectory as the strength of the exogenous force increases or decreases.
2. *The discontinuous change model without hysteresis*: An exogenous force causes a sudden change in ecosystem structure and function owing to the crossing of a critical threshold. A return of the exogenous force to its former condition, or its suppression, abruptly returns ecosystem structure and function to the prior state. Discontinuous change without hysteresis, then, is reversible.
3. *The discontinuous change model with hysteresis*: An exogenous force causes a sudden change in ecosystem structure and function owing to the crossing of a critical threshold, but because of hysteresis, the transition is not easy to reverse (Scheffer, 2009). A return of the exogenous force to its former condition does not restore the ecosystem to its former state.

We use the cusp-catastrophe manifold (Thom, 1975) as a basis for conceptualizing how the type of ecohydrological feedbacks (stabilizing vs amplifying) and the strength of these feedbacks affect the dynamics of ecosystem state change in accordance with the three models outlined above (Figure 1). In this conceptualization, amplifying ecohydrological feedbacks are weak or absent in the continuous change model of ecosystem state change, enabling continuous change between states (model 1). However, where amplifying feedbacks occur, the dynamics of ecosystem state change become discontinuous (model 2), and where amplifying ecohydrological feedbacks are strong, the dynamics of ecosystem state change are discontinuous and hysteretic (model 3).

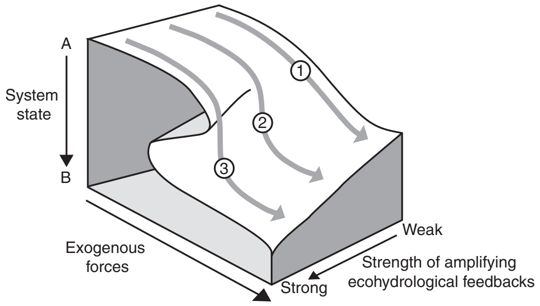

Figure 1. Cusp-catastrophe model showing the potential response of an ecosystem to a change in the strength of one or more exogenous forces such that the trajectory of ecosystem state change is determined by the strength of ecohydrological feedbacks. The three arrows represent ecosystem responses to exogenous forces in accordance with the continuous change model (arrow 1), the discontinuous change model without hysteresis (arrow 2), and the discontinuous change model with hysteresis (arrow 3).

THE ROLE OF ECOHYDROLOGICAL FEEDBACKS IN ECOSYSTEM STATE CHANGE

We use five case studies to investigate the role of ecohydrological feedbacks in ecosystem state change in drylands. These case studies represent ecosystems that have experienced different types (and combinations) of exogenous forcings, including those that cause a direct change in ecosystem state and those that affect internal system feedbacks (Figure 2). For each of these case studies, we evaluate (1) how exogenous forces affect ecohydrological feedbacks; (2) the mechanisms by which the feedbacks then lead to a change in ecosystem state; and (3) the dynamics of state change (i.e. continuous, discontinuous without hysteresis, discontinuous with hysteresis).

Case Study 1: Ecohydrological feedbacks in savannas

Savannas are mixed-plant communities in which grasses and woody plants coexist in a patchy landscape (e.g. Scholes and Archer, 1997). This coexistence has puzzled generations of ecologists, who have variously interpreted it as an effect of niche separation (in space or time), spatial interactions, or nonequilibrium conditions sustained by climate fluctuations and other disturbances (e.g. Walter, 1971; Sarmiento, 1984; Walker and Noy-Meir, 1992; Scholes and Walker, 1993; Rodriguez-Iturbe *et al*., 1999; Higgins *et al*., 2000; Sankaran *et al*., 2004; D'Odorico and Porporato, 2006). Another possible explanation for this apparently stable coexistence of tree and grass patches is based on the notion that, at the patch scale, vegetation dynamics exhibit two alternative stable states: tree dominance or grass dominance (Walker and Noy-Meir, 1992). The existence of these patch-scale, bi-stable states is typically attributed to difference types of feedback mechanisms between ecosystem state and either limiting resources or disturbance regimes. For example, important stabilizing ecohydrological feedbacks appear to exist between vegetation and soil moisture: Trees facilitate the infiltration of rainwater into deeper soil layers, thereby maintaining the higher levels of soil moisture that are crucial for their own establishment and survival (Greene, 1992; Bhark and Small, 2003; D'Odorico *et al*., 2007); grasses, on the other hand, shelter the ground surface from the erosive action of wind and water, thereby preventing the loss of shallow soil resources (Schlesinger *et al*., 1990; Okin *et al*., 2009). Grasses also trap sediment, whereas trees and shrubs enhance the trapping of airborne dust-size particles, thereby facilitating the deposition of phosphorus and nitrogen (Schlesinger and Pilmanis, 1998; Lawrence *et al*., 2007). These stabilizing feedbacks at the patch scale may explain the stable coexistence of trees and grasses.

At the landscape scale in savanna ecosystems, fire is a key disturbance influencing ecosystem state. Feedbacks between savanna vegetation and fire dynamics have been recognized as important contributors to the emergence of alternative tree–grass states (Scholes and Archer, 1997; Van Langevelde *et al*., 2003). These feedbacks are driven by the dependence of fire on grass fuel and by the sensitivity of woody plants to fires. Areas with higher grass cover are prone to more frequent fires (e.g. Van Wilgen, 2003), which tend to kill trees and to maintain a grass-dominated vegetation cover. Conversely, areas dominated by trees and other woody vegetation typically do not have sufficient grass fuel to maintain an active fire regime. Thus, where ecohydrological feedbacks favour trees, lack of fire disturbance can lead to a full cover of woody vegetation. Stabilizing ecohydrological feedbacks maintain the concentration of plant-essential resources, thus increasing the resilience of this state. In this way, fire–vegetation feedbacks in savanna ecosystems can lead to the emergence of two

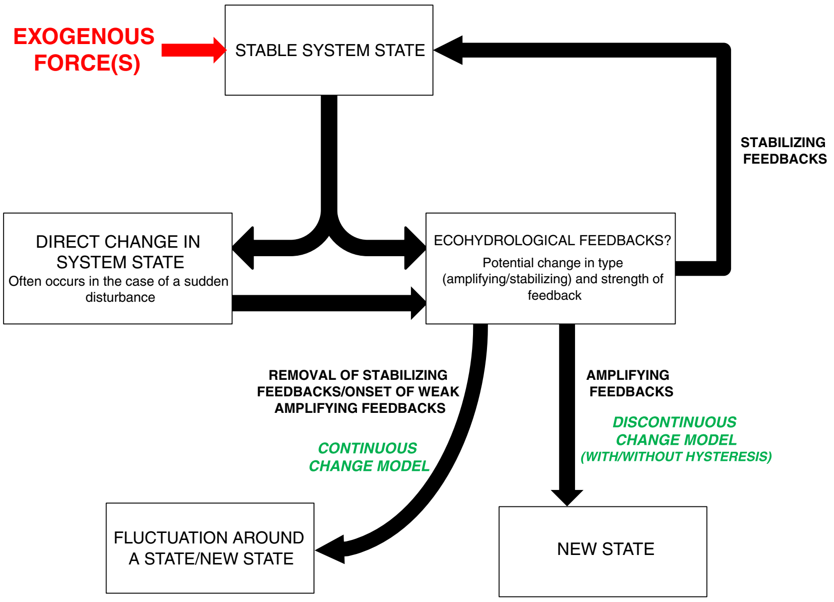

Figure 2. How ecosystems respond to exogenous forces, which either cause a direct change in ecosystem state or modify ecohydrological feedbacks. The type and strength of ecohydrological feedbacks influence the dynamics of ecosystem state change.

alternative states: (i) a grass-dominated landscape with frequent fires and low tree density and (ii) a woody plant-dominated landscape with low grass fuel and infrequent fires. Because of the amplifying effect of fire–vegetation feedbacks at the landscape scale, the shift from one state to the other is not gradual but abrupt (D'Odorico and Porporato, 2006).

Case Study 2: Ecohydrological feedbacks associated with conversion of native forest to cropland

In western Australia, the deep-rooted perennial vegetation has been replaced with irrigated, shallow-rooted crops and pasture. This disturbance has led to an increase in groundwater recharge, causing the water table to rise (Figure 3; Cramer and Hobbs, 2005). As it rises, the water table mobilizes salts stored within the soil; when it comes to within 2 m of the surface, the pronounced effect of capillary action draws salt through fine pores into the surface soil horizons [i.e. a threshold is reached at which surface soils become water-logged and more saline (Gordon *et al*., 2008)]. This amplifying feedback decreases the resilience of the agricultural state, rendering the soil inhospitable to vegetation and bringing about a shift to yet another state, this time degraded – either bare soil or soil dominated by halophytic weeds – which is difficult or impossible to reverse (Cramer and Hobbs, 2005).

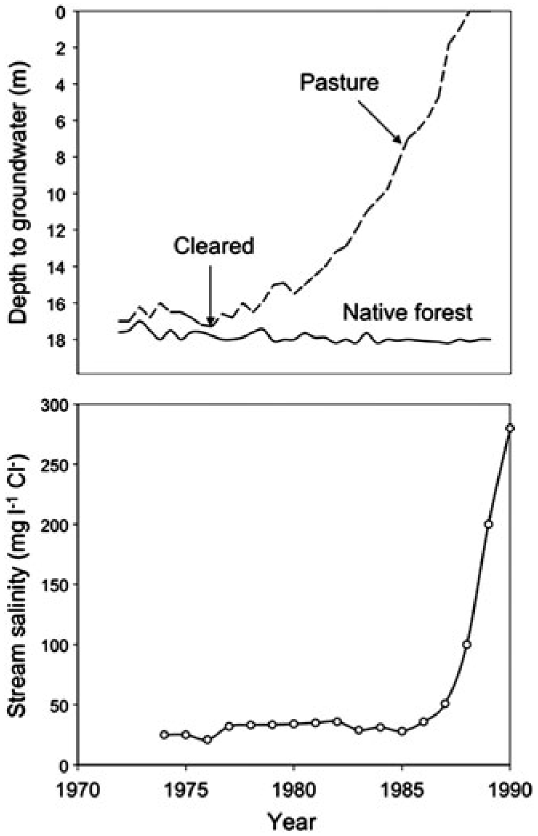

Figure 3. Groundwater-level changes and soil-salinity response following clearing of forest in Lemon Catchment, Western Australia. The catchment was cleared between November 1976 and March 1977. Sources: Top graphic from Schofield (1992), based on the data of Ruprecht and Schofield (1991); bottom graphic from Ruprecht and Schofield (1991).

In an attempt to prevent the salinization of surface soils caused by these amplifying ecohydrological feedbacks, strategies designed to mimic the water balance of the natural ecosystem were implemented. They included planting perennial pasture species and planting belts of trees to increase water use (George *et al*., 1999). Although these measures have brought about reductions in groundwater levels in some cases (e.g. Schofield, 1992; George *et al*., 1999), they have not been widely adopted because of socioeconomic factors, such as potential loss of agricultural land, cost, uncertainty, and negative attitudes.

Case Study 3: Ecohydrological feedbacks associated with desert crusts

Biological soil crusts (biocrusts) play a critical role in dryland ecosystems, influencing the fertility, stability, and hydrology of soils. In dryland regions, biocrusts may cover up to 70% of the soil surface and thus mediate the flow of most materials into and across the surface (2003a, 2003b). In all regions where crusts occur, they increase soil stability by binding soil particles together, which reduces erosion by wind and water. Crusts dominated by mosses and lichens provide greater stability than those dominated by cyanobacteria (Warren, 2003). Biocrusts have a range of external morphologies; the more developed they are, i.e. the greater the lichen, moss, or cyanobacterial biomass, the rougher the soil surface – and the greater its influence on hydrologic function (Belnap, 2006). Smooth biocrust surfaces (typical of hot deserts) retain less material, leading to a more heterogeneous distribution of nutrients, water, and plants, whereas rougher biocrust surfaces (typical of cool deserts) retain more material, leading to more homogeneous distributions. Disturbances such as compression of the soil surface, fire, and deposition of sediment via water or wind affect the morphology, biomass, and species composition of biocrusts – which in turn alter ecohydrological feedbacks at multiple spatial scales (Belnap *et al*., 2006).

In hot deserts, biocrusts are typically dominated by cyanobacteria, rendering the soil surface smooth (Figure 4a), which decreases both water retention times and surface permeability; as infiltration is decreased, runoff is increased, transporting sediment, seeds, and organic matter to downslope vegetation (Figures 5 and 6a; Belnap *et al*., 2005). If the biocrusts are disturbed, the cyanobacteria can die, leading to increased infiltration at the local scale. The impacts of such disturbances may then reverberate through the system via a series of amplifying feedbacks. For example, higher localized infiltration often means less runoff and, thus, less water reaching downslope vegetation. The resulting possible stress to or death of downslope vegetation may eventuate in a restructuring of the environment, as has been observed in the Negev, in the Sahel, and in Australian deserts, notably in banded vegetation (Tongway *et al*., 2001). Reduced runoff may also decrease the transport of seeds, organic matter, and nutrients from plant interspace areas to nearby fertile islands.

In cooler deserts, relatively undisturbed desert surfaces are partially to mostly covered with rough, erosion-resistant

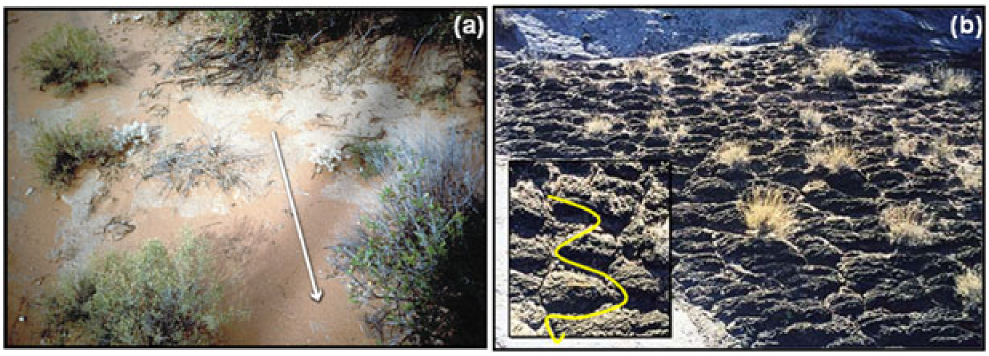

Figure 4. (a) Crusts in hot desert dominated by cyanobacteria. (b) Crusts in cold desert dominated by lichens and mosses. Arrows show how the direction of water flow over the crust-covered surfaces is influenced by surface morphology.

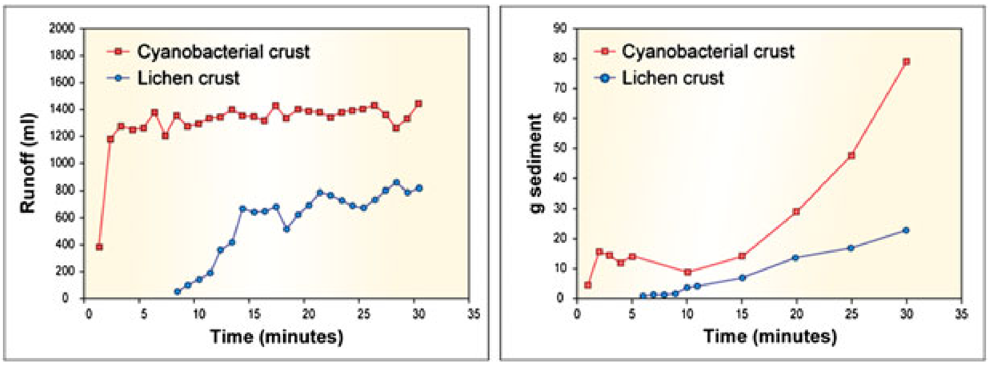

Figure 5. Runoff and sediment production during a 30-min rainfall simulation on two types of crusted surfaces: a disturbed, smooth cyanobacterial crust in a hot desert and an undisturbed, rough lichen crust in a cool desert. Runoff and sediment production were higher from the disturbed surfaces than from the undisturbed surfaces throughout the experiment.

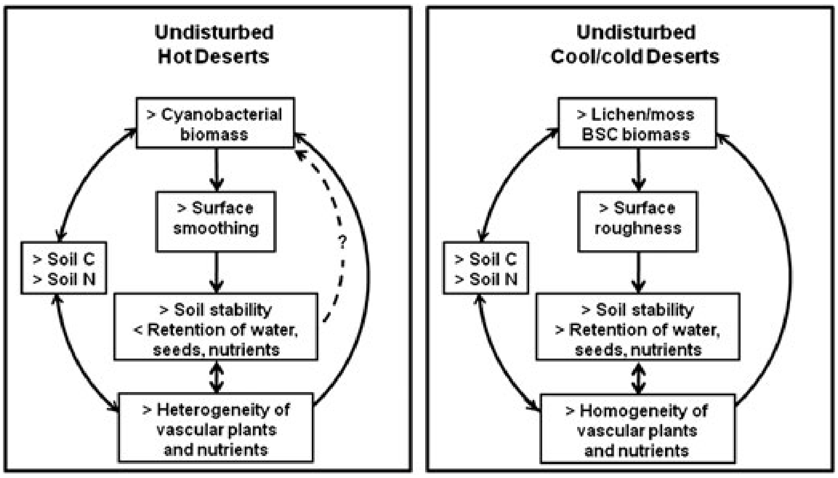

Figure 6. Conceptual models of the role of biocrusts in (a) hot and (b) cool-cold deserts. In hot deserts, biocrusts are dominated by cyanobacteria that smooth the soil surface (see Figure. 4a) and reduce retention of materials moving across it (e.g. water, seeds, soil). In cool/cold deserts, the much rougher lichen and moss biocrust surfaces (see Figure. 4b) enhance retention of materials.

biocrusts dominated by lichens and mosses (Figure 4b). This roughened surface slows overland flow, thereby increasing local infiltration and the retention of sediment and organic matter (Figure 5). A series of stabilizing ecohydrological feedbacks maintains such a crust-dominated ecosystem state (Figure 6b). If the biocrusts are disturbed and the soil surface flattened, infiltration decreases and soil-moisture content is reduced, breaking the stabilizing feedbacks. The volume of runoff then increases, enabling the onset of amplifying feedbacks such as rill formation, which further accelerates water and soil loss and leads to further reductions in infiltration. Biocrusts still present are undercut, leaving soils even more vulnerable to erosion during rainfall events. These changes also accelerate the loss of nutrients and organic matter, reducing soil fertility. In an amplifying feedback loop, reduced soil moisture and soil fertility limits the regrowth of crusts, which enables the processes of reduced infiltration/increased runoff and soil loss to continue. If water and soil losses are too great, biocrusts may not recover.

Regardless of desert type, disturbance of biocrusts reduces soil stability, which may alter hydrologic cycles and erodibility at both local and regional scales and leave the local site more vulnerable to rainfall and runoff events. Rainfall simulations show that regions dominated by disturbed biocrusts exhibit higher runoff and sediment loss than those dominated by undisturbed crusts (Figure 5), and their carbon and nitrogen losses are higher as well (Barger *et al*., 2006). Well-developed crusts can withstand the shear stress exerted by naturally occurring winds, producing little to no sediment; but once the crust is disturbed, wind action can produce up to 500 times more sediment than from an undisturbed crust (Field *et al*., 2010). Sediment blown from disturbed areas may bury nearby undisturbed biocrusts, further reducing stability, and/or may accumulate under plant canopies, increasing soil infiltration rates. The eventual result is a differential loss of fine soil materials over time, which reduces soil absorption, moisture-holding capacity, and fertility. By reducing plant productivity, these changes further alter the long-term hydrology of the site (Neff *et al*., 2005). An amplifying feedback contributes to the process: As more crusts are buried, they die, leading to further sediment production.

Loss of soil stability due to the disturbance of biocrusts at the local level has broader-scale ecohydrological consequences. For example, fine sediment eroded by wind from low-elevation lands is often deposited on the snowpack of nearby mountains, which decreases the albedo of the snowpack and thereby accelerates snowmelt (Painter *et al*., 2010). Early snowmelt leads to increased evapotranspiration, which translates to less water entering streams and large rivers. Water lost in this way is estimated to account for up to 8% of annual Colorado River flows.

Case Study 4: Ecohydrological feedbacks associated with encroachment of grasslands by woody plants in semiarid climates

The expansion of shrubs and woody plants into native semiarid grasslands has been widely observed – for instance, over large areas of the southwest United States. This rapid transformation from a grass-dominated state to a shrub-dominated state (woody plant encroachment) is largely irreversible on human timescales, and has ecohydrological, biogeochemical, and socioeconomic implications (Schlesinger *et al*., 1990; Huxman *et al*., 2005; Knapp *et al*., 2008; Ravi and D'Odorico, 2009). Woody plant encroachment is caused by multiple exogenous forces, including overgrazing, fire suppression, and climate change (Archer, 1989; Schlesinger *et al*., 1990; van Auken, 2000).

In semiarid climates, such as the southwestern United States, these exogenous forces initiate the shrub-encroachment process by decreasing the resilience of native grasslands (Archer *et al*., 2011). As shrubs encroach into grasslands, abiotic processes such as runoff and erosion are amplified and amplifying ecohydrological feedbacks increase in strength (Schlesinger *et al*., 1990; Parsons *et al*., 1996; Wainwright *et al*., 2000; Okin and Gillette, 2001; Turnbull *et al*., 2010a). Greater runoff and erosion further enhances the heterogeneities in nutrient distribution across the landscape (e.g. Okin *et al*., 2009; Turnbull *et al*., 2010b) and reinforces the stability of shrub domination through an amplifying ecohydrological feedback (Figure 7). The reduced connectivity of grass cover during the process of shrub encroachment decreases the ability of fire to spread across the landscape, again enhancing the stability of the shrub-dominated state (Anderies *et al*., 2002; Okin *et al*., 2009).

With the development of shrub-associated microtopography and rilled, nutrient-poor inter-shrub areas, the dynamics of this ecosystem state change are hysteretic, since a reversal of the exogenous forces to their former state does not facilitate a reversal to a grass-dominated

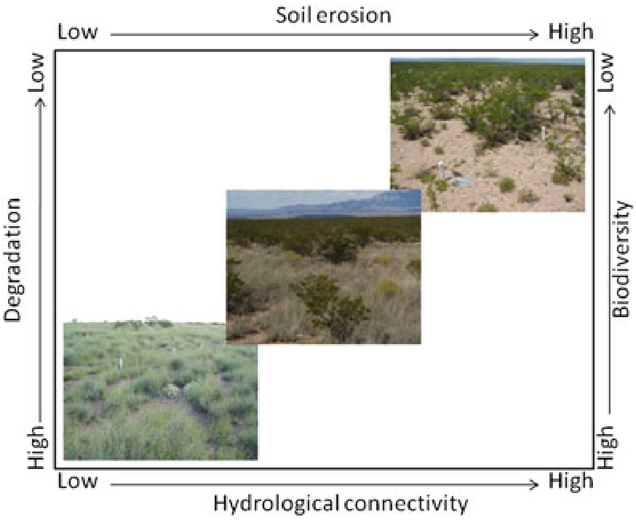

Figure 7. Conceptual diagram showing the stages of shrub encroachment in the Chihuahuan Desert and the associated changes in hydrological connectivity, soil erosion rates, and biodiversity (adapted from Ravi *et al*., 2010).

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state, at least on human timescales. In other words, in semiarid landscapes, changes in abiotic processes brought about by the shrub encroachment process leave a pronounced geomorphic imprint that is not readily overcome.

In a recent modelling study, Okin *et al.* (2009) investigated how soil erosion affects the stability of grasslands and shrublands. Seeking to ascertain the conditions under which a vegetation type having ecohydrological advantages would still succumb to invasion by another vegetation type not having the same ecohydrological advantages, the authors incorporated as an assumption that grasses had an ecohydrological advantage over shrubs. In the absence of an amplifying soil erosion feedback, their simulations showed – as expected – that even strong pulses of shrub invasion were reversible. The absence of pronounced amplifying soil erosion feedbacks appears to be the case in some drylands worldwide, especially the South African Karoo (Hoffman *et al.*, 1995), where shrubs and grasses are in dynamic equilibrium. However, when Okin *et al.* (2009) introduced a soil erosion feedback in their model (represented by a decrease in the ability of bare spaces to support grass due to soil erosion), the model exhibited bi-stable dynamics – the two alternative states of grass dominance and shrub dominance coexisting. Although conversion to the state of grass dominance alone was possible in the model, it required changes in exogenous forces and ecohydrological feedback mechanisms (such as reversion to a climate that facilitates the success of grass reproduction). This result is consistent with multiple grass–shrub–grass transitions seen during the Holocene, as responses to regional and global climate changes, and it is also consistent with the apparent irreversibility of shrub encroachment under present climatic conditions (Van Devender, 1990).

Case Study 5: Ecohydrological feedbacks associated with dune dynamics

The dynamics of vegetated dune systems in drylands is an excellent example of how ecohydrological processes and feedbacks control ecosystem state. Dune dynamics and ecosystem state are influenced by exogenous forces and the ways in which those forces shape amplifying and stabilizing ecohydrological feedbacks. A change in one or more exogenous forces that alters the strength of these amplifying and/or stabilizing feedbacks – for example, a change in wind strength or a change in vegetation cover by clear-cutting, overgrazing, or forced dune stabilization by planting (Yizhaq *et al.*, 2007) – may cause dunes to switch to a new state. Some dune fields subsequently revegetate and stabilize, whereas others do not. Precipitation contributes to vegetation growth, which reduces erosion through a stabilizing feedback (although initiation of this feedback appears to be governed by wind strength; if winds are strong enough to transport sand, the growth of vegetation may be reduced or even prevented).

Dunes such as those found south of the Negev–Sinai border are kept in an unstable state because of active grazing in this region. If grazing is halted, revegetation is likely to take place, as it did east of the border when grazing was discontinued in the 1980s. Although precipitation in this region is low, wind strength is also low, which allows regrowth to take place (Tsoar, 2005). In this case, the system is very resilient in that the landscape has only one stable state (i.e. vegetated dunes). In contrast, in The Netherlands, disturbed once-vegetated dunes do not revegetate even after the disturbance ceases. Even though precipitation is high, the wind is too strong to enable the initiation of a stabilizing feedback (Yizhaq *et al.*, 2007). The availability of water, then, is the major factor controlling vegetation growth, but wind force determines the strength of the feedbacks between vegetation and aeolian transport.

SUMMARY

The case studies illustrate that in drylands, stabilizing ecohydrological feedbacks, as the name suggests, are critical for maintaining a stable ecosystem state. From the case studies explored, it is apparent that at the plant-patch scale, the biotic (vegetation or biocrust) regulation of vertical water exchange and the concentration of plant-essential resources within the vicinity of the plants (Schlesinger *et al.*, 1990) is the most significant type of stabilizing ecohydrological feedback. At increasingly larger scales, ecohydrological feedbacks associated with lateral redistribution of materials, by both water and wind, become increasingly important in determining ecosystem state (as illustrated by the case study on shrub invasion in the southwest United States). Vegetation–fire feedbacks appear to be more significant at broader spatial scales, with connectivity of vegetation across broad areas a prerequisite for these feedbacks to become well established. We can surmise that in drylands, stabilizing feedbacks are generally associated with enhanced infiltration and the trapping of sediment and other resources that enable plant growth and continued retention of plant-essential resources. Amplifying ecohydrological feedbacks are generally associated with the strong predominance of abiotic processes, which control the broad-scale redistribution of plant-essential resources within the system. These abiotic processes often bring about a net loss of resources from the system – for example, wind, water, and fire can dramatically alter the structure of vegetation, leading to further changes in wind- and water-driven ecohydrological feedbacks.

In all case studies, exogenous forces that cause a change in the type and/or distribution of vegetation cover appear to break critical stabilizing feedbacks that maintain a stable system state. We anticipate that this is especially the case in drylands because of the scarcity of water. Without water-related stabilizing feedbacks, plants are unable to access all the resources they require. However, the breaking of a stabilizing feedback does not necessarily equate to the onset of an amplifying feedback, as is clearly illustrated by the Negev–Sinai dune case study and by the modelling study of Okin (2009), who looked at the dynamics of shrub encroachment into grasslands. Breaking of stabilizing feedbacks enables changes in vegetation to occur (loss of vegetation in the dune study, and rapid shrub encroachment in the modelling study); but without the onset of strong amplifying ecohydrological feedbacks, these changes in vegetation are potentially reversible. For amplifying ecohydrological feedbacks to be initiated, there needs to be a strong abiotic regime – increases in runoff and water-driven erosion, wind erosion, or fire. As demonstrated in the case studies, changes in ecohydrological feedbacks associated with one of these abiotic mechanisms will often lead to secondary changes in other ecohydrological feedbacks associated with a different abiotic mechanism. Our findings are supported by Didham *et al*., (2005), who suggest that systems with strong abiotic regimes may more readily switch to an alternative state following disturbance than systems with weaker abiotic regimes.

Although scale is not the primary focus of this paper, it is important to understand how spatial scale affects the ecohydrological feedbacks that govern ecosystem state. The biocrust and savanna case studies, in particular, shed light on this issue. For example, in the biocrust case study, the exogenous forces (in this instance, physical disturbance of the crusts) cause increased runoff and consequent erosion, which initiate amplifying ecohydrological feedbacks at the local scale. These local-scale feedbacks then reverberate through the system, affecting larger spatial scales through increases in wind-driven erosion because of reduced soil-surface stability. In the savanna case study, at the patch scale, stabilizing feedbacks are associated with the concentration of plant-essential resources that facilitate coexistence of grasses and shrubs, but these stabilizing feedbacks may be overcome by fire-driven amplifying ecohydrological feedbacks , which control ecosystem state at the landscape scale. In other words, the primary mechanisms controlling ecosystem state can change across different spatial scales. This insight highlights the challenges involved in attempting to predict future cross-scale responses of drylands to exogenous forces.

Future changes in climate, along with the likelihood of increased human-induced disturbance, will no doubt have a great effect on the type and strength of ecohydrological feedbacks in drylands. A major unknown is the different types of ecohydrological feedbacks that might ensue from changes in exogenous forces – in particular, simultaneous changes in multiple exogenous forces. For example, in the southwestern United States, recent decades have witnessed a great increase in invasive grasses that has enabled vegetation–fire–erosion amplifying feedbacks to control ecosystem state (Wilcox *et al*., 2011). These controlling feedbacks are very different from the stabilizing ecohydrological feedbacks that predominate in native grasslands. As another example, in regions such as the Negev–Sinai, an increase in wind speed is likely to alter the ecosystem state through increasing erosion, possibly to the point of hysteresis.

As noted above, a comprehensive understanding of how ecosystems respond to exogenous forces through changes in ecohydrological feedbacks is essential for successful environmental management, either to reduce the likelihood that a system will transition to a less desirable state or to shift a system back to a more desirable state. Recently, researchers have emphasized the importance of identifying leading indicators, and increases in the variability of these indicators, as early warning signs of hysteretic changes in ecosystem state (Carpenter and Brock, 2006; Scheffer, 2009). However, Hastings and Wysham (2010) show that such a strategy is not always applicable because some systems actually lack these leading indicators. Taking this into consideration, as well as the significance of ecohydrological feedbacks in changing ecosystem state as demonstrated in the case studies, we suggest the following guidelines for any future efforts in the management, restoration, or rehabilitation of dryland ecosystems:

1. Identify the key exogenous forces and how they are changing.
2. Pay attention to changes in ecohydrological feedbacks that cause significant changes in runoff and erosion.
3. Emphasize the modification or tweaking of key ecohydrological processes rather than of biotic structures (most restoration efforts already do this).
4. View current and future desirable ecosystem states as ‘moving targets’ and do not focus on returning to exact former states.
5. Include a socioecological ‘reality check’ to see whether the benefits/services desired from a given ecosystem state are realistic or even possible.

A focus on not striving to ‘relive the past’ is essential. In many cases, if an ecosystem has already changed state, a return to the exact former state may be highly unlikely because of the enduring legacy of amplifying feedbacks, which alter the geomorphic template of the ecosystem. For example, when soil is lost because of erosion, that condition cannot be readily reversed. Management planning must be in line with what is realistically achievable. To mitigate potential undesirable transitions in semiarid ecosystems following a change in exogenous forces, the operation of ecohydrological feedbacks needs to be considered in management strategies. How can we exploit the strength of stabilizing ecohydrological feedbacks to increase the resilience of a desired ecosystem state? How can we lessen the effects of amplifying ecohydrological feedbacks to keep the system from moving towards a new and less desirable state? Or, can exogenous forces be manipulated to prevent a desirable state from converting to a less desirable one?

The multiple ecohydrological feedbacks occurring in response to exogenous forces create multidimensional problems. We cannot surmount these problems simply by continuing along the same research trajectory, with a focus on ecological processes or hydrological processes alone. In future investigations of the role of ecohydrological feedbacks, we must:

1. *Learn the lessons of ecology* – to value truly coupled eco–hydro experiments, in which biogeochemistry, plants, geomorphology, soils, and hydrology are all well represented and experimentally manipulated.

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2. *Learn the lessons of hydrology and geomorphology* – to value observational experiments, in which ecological measurements are coupled with hydrological and geomorphological measurements, and the role of exogenous forces is explicitly recognized.

Adopting these two experimental approaches will enable us to isolate the effects of single and multiple types of exogenous forces on the type and strength of ecohydrological feedbacks. Further, carrying out these two approaches in tandem (experimental manipulations coupled with long-term observations) will pave the way for understanding the long-term dynamics of ecosystem state change in response to exogenous forces. The US Long-Term Ecological Research network has great potential to catalyse a new era of coupled eco–hydro experimental manipulations and long-term monitoring, but for this to actually happen, there needs to be an *a priori* recognition of the potential significance of ecohydrological processes in controlling ecosystem state in drylands. Without carrying out experiments in which ecological measurements of system processes are coupled with hydrological and geomorphic measurements, we simply cannot deduce how ecohydrological feedbacks will change in response to changes in one or more exogenous forces.

Future research efforts must also seek new experimental directions for studying processes across scales (e.g. water use efficiency from the plant scale to the landscape scale; runoff generation from patch to catchment). This added dimension will enable us to predict the general direction of responses to exogenous forces and ecohydrological feedbacks. Since it is potentially within the capabilities of land managers to alter ecohydrological feedbacks, but it is largely outside the capabilities of managers to alter exogenous forces, more attention needs be paid to assisting managers with science.

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