

A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands

Paolo D'Odorico,^{1,2*} Gregory S. Okin³ and Brandon T. Bestelmeyer⁴

¹ Department of Environmental Sciences, University of Virginia, Charlottesville, VA, 22904, USA

² Laboratory EFLUM, Faculté ENAC, Ecole Polytechnique Fédérale Lausanne, Lausanne, Switzerland

³ Department of Geography, University of California, Los Angeles, CA, 90095, USA

⁴ USDA-ARS, Jornada Experimental Range, Las Cruces, NM, 88003, USA

ABSTRACT

Many arid grasslands around the world are affected by woody plant encroachment and by the replacement of a relatively continuous grass cover with shrub patches bordered by bare soil. This shift in plant community composition is often abrupt in space and time, suggesting that it is likely sustained by positive feedbacks between vegetation and environmental conditions (e.g. resource availability) or disturbance regime (e.g. fire or freeze). These feedbacks amplify the effects of drivers of shrub encroachment, i.e. of conditions favouring a shift from grass to shrub dominance (e.g. overgrazing, climate change). Here, we review some major drivers and feedbacks and identify the basic stages in the transition from grassland to shrubland. We discuss some possible scenarios of interactions between drivers and feedbacks that could explain the transition from a stage to the next and the potential irreversibility of the shift from grass to shrub dominance. We introduce a simplistic modelling framework that can integrate the various drivers to explain the emergence of bistability for shrub-encroached grassland systems. Published 2011. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS shrub encroachment; fire ecology; climate change; soil erosion; spatial dynamics

Received 11 July 2011; Revised 3 September 2011; Accepted 4 September 2011

INTRODUCTION

Over the past 150 years, many arid and semiarid grasslands around the world have been encroached by shrubs. This phenomenon has been documented in Southern Africa, South America, Australia (van Vegten 1983, Adamoli *et al.*, 1990, Burrows *et al.*, 1990, Moleele *et al.*, 2002), and in the warm deserts of the southwestern United States (Archer *et al.*, 1995, Van Auken 2000, Ravi *et al.*, 2009a). In these continents, several hundred million hectares have been affected by shrub encroachment (e.g. Eldridge *et al.*, 2011) with important ecohydrological implications (e.g. Huxman *et al.*, 2005). In many cases, the shrub species are native to these landscapes and were already present at lower density or in restricted parts of the landscape (Van Auken 2000). The increase in shrub cover is often observed in conjunction with a decrease in grass cover and an overall increase in bare soil (Huenneke *et al.*, 2002, Gillette and Pitchford 2004).

The concern over this change in plant community composition and species dominance arises from the associated changes in ecosystem goods and services, often with serious implications on local pastoral economies. The loss of grass cover and the increase in bare soil typically leads to the intensification of water and wind erosion and the loss of nutrient-rich soil particles (Parsons *et al.*, 1996, Schlesinger *et al.*, 1999, Wainwright *et al.*, 2000, Li

et al., 2007, Li *et al.*, 2008), a process often termed *land degradation* (e.g. Millennium Ecosystem Assessment 2005; Reynolds *et al.*, 2007), although recent studies have shown that the association between shrub encroachment and land degradation is not universal (Eldridge *et al.*, 2011).

Moreover, the replacement of productive rangelands with shrublands involves a number of mechanisms, including (i) regional and global climate warming; (ii) increase in atmospheric CO₂ concentrations; (iii) fire management; and (iv) grazing management. The purpose of this report is to synthesize these mechanisms and the associated biotic and abiotic processes into a single framework and to examine the persistence of shrub-encroached landscapes.

The argument that climate warming may explain shrub encroachment arises from the observation that most of the encroaching shrub species are limited by low temperatures. For example, *Larrea tridentata* (or creosote bush), a major shrub species in the southwestern deserts of North America, is prone to stress and mortality from freezing-induced cavitation, which occurs with near surface temperatures close to $-18/-20^{\circ}\text{C}$ (Pockman and Sperry 2000, Martinez-Vilalta and Pockman 2002). The geographic distribution of this species appears to be controlled by low temperatures with the northern margins of *L. tridentata* in the Sonoran Desert coinciding with the -18°C minimum winter isotherm (Pockman and Sperry 1997). Climate warming could reduce the pressure from freezing-induced stress and favour the northward encroachment of *L. tridentata*. Sensitivity to low temperatures has been reported also for woody species contributing to shrub encroachment in other dryland

*Correspondence to: P. D'Odorico, Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904, USA.
E-mail: paolo@virginia.edu

regions, including, for example, *Prosopis glandulosa*, typical of south-west Texas and New Mexico (Felker *et al.*, 1982), or *Acacia mellifera*, encroaching in the savanna environments of southern Africa (Moleele *et al.*, 2002, Sekhwela and Yates 2007). Thus, the effect of climate warming on woody plant physiology has been often invoked as one of the drivers of woody plant encroachment, although it cannot explain why within a same climatic region, some areas have been affected by grass-to-shrub transition more than others (Archer 1989). Nor is there evidence of significant climate warming associated with historical shrub encroachment episodes (e.g. Gibbens *et al.*, 2005, Wainwright 2006). Thus, climate warming cannot alone explain landscape scale heterogeneities in grass–shrub cover (e.g. Bahre and Shelton 1993). However, this landscape-scale variability in vegetation cover can be better understood considering the possible existence of a positive feedback between vegetation and microclimate (D’Odorico *et al.*, 2010a, He *et al.*, 2010), whereby shrub dominance modifies local microclimate via increased nocturnal air temperatures during wintertime. The occurrence of this local warming effect – in addition to regional and global climate warming – can explain the existence of landscape-scale heterogeneities.

The argument that increasing atmospheric CO₂ may explain shrub encroachment arises from the observation that shrub species typically have a C₃ photosynthetic pathway, whereas in many ecosystems, a large variety of herbaceous species are C₄ grasses (e.g. Buffington and Herbel 1965). Because of their different physiology, C₄ plants have higher water-use efficiency (i.e. higher carbon assimilation with the same use of water) than C₃ shrubs. Thus, in arid and semiarid environments, C₄ grasses could be more competitive than shrubs (e.g. Polley *et al.*, 1992). However, the increase in atmospheric CO₂ concentration increases the gradients between ambient and intracellular CO₂ concentrations, thereby enhancing water-use efficiency (Mooney and Cleland 2001) and reducing the competitiveness of C₄ plants. Thus, the shift from grassland to shrubland conditions could have been favoured by the increase in the levels of atmospheric CO₂ (e.g. Idso 1992). This hypothesis has been challenged on the grounds that global-scale changes in atmospheric CO₂ concentrations could not explain local-scale heterogeneities in vegetation change, which seems to be more directly associated with land-use patterns (Archer *et al.*, 1995).

The argument that fire management may explain shrub encroachment arises from the observation that fires are a major disturbance to woody plants and may have historically contributed to the maintenance of low shrub densities in many arid and semiarid landscapes (e.g. Scholes and Archer 1997, du Toit *et al.*, 2003). In these environments, the fuel load is contributed mainly by grass biomass. Thus, fire suppression favours shrub encroachment at the expense of herbaceous vegetation, with the consequent loss of fuel load and the reduction in the rate and intensity of fire occurrence (D’Odorico *et al.*, 2006a). Overgrazing is hypothesized to have contributed to fire’s role in shrub encroachment by reducing the fuel load (Van Auken 2000).

Grazing livestock reduce aboveground grass biomass, and with the initial losses of herbaceous cover, overgrazing may become increasingly concentrated on the remaining grasses, resulting in the collapse of grass cover and leaving shrubs as the dominant vegetation (van de Koppel *et al.*, 2002). However, livestock will often consume and transport viable shrub seeds (Archer 1989, Brown and Archer 1999, Fredrickson *et al.*, 2006), thus serving as a vector and a facilitator for the establishment of the seeds of shrub species in the grazed area. Native mammal species, including deer (*Odocoileus virginianus*) and coyote (*Canis latrans*), have also been found to be effective shrub-seed vectors (Kramp *et al.*, 1998). Native grazers may also be involved in positive feedbacks that contribute to low levels of herbaceous cover once shrub cover increases and herbaceous cover decreases. In the Chihuahuan Desert, increasing shrub cover (and associated decreases in the continuity of herbaceous cover) is often associated with the increasing abundance of rodents by providing nest sites and escape space from predators (Whitford 1997, Bestelmeyer *et al.*, 2007). Certain rodents (e.g. *Dipodomys* spp.) and lagomorphs (e.g. *Lepus californicus*) are herbivores of grasses or damage their reproductive structures (Kerley *et al.*, 1997, Havstad *et al.*, 1999, Sipsos *et al.*, 2002). In Chihuahuan Desert savannas, rodent exclusion has been shown to increase the cover of the perennial grasses (Heske *et al.*, 1993, Curtin *et al.*, 2000). Shrub-seedling establishment, however, may also be reduced by rodents (Valone and Thornhill 2001). Thus, rodent herbivory seems unlikely alone to cause shifts from grassland to shrubland, but the persistence of desertified shrubland can clearly be reinforced by rodent herbivory (Bestelmeyer *et al.*, 2007, Kerley and Whitford 2009).

Although all these mechanisms are plausible, it is unclear how their relative importance may change under different environmental conditions. Moreover, the possible existence of different limiting factors for grasses and shrubs adds complexity to the way environmental conditions determine the competitive advantage of one life form over the other. The understanding of the mechanisms underlying the conversion to shrubland and of their dynamical implications is particularly important given the wide variety of environments in which shrub encroachment has been observed (Ravi *et al.*, 2009b). The wide variety of circumstances in which shrub encroachment occurs suggests that not all of the same processes are at work in every instance. On the basis of an understanding of the preceding mechanisms, it would be useful to develop a diagnostic framework to accept or rule out on a case-by-case basis the possibility that certain mechanisms might be at work. From a management perspective, it is crucial to know in a particular instance what the dominant processes are; and, on the basis of this, whether there is a practical method for stopping, or reversing, shrub encroachment (e.g. Briske *et al.*, 2008).

CATEGORIES OF SUGGESTED MECHANISMS

The mechanisms that have been suggested to explain the occurrence of shrub encroachment fall into two major

categories, depending on whether they are driven by exogenic or endogenic factors.

Exogenic factors are those associated with large-scale changes such as rising global CO₂ concentrations, (e.g. Polley 1997), large-scale fire suppression and overgrazing (Van Auken 2000, van de Koppel *et al.*, 2002) or regional/global changes in rainfall or temperature (e.g. Idso 1992, Brown *et al.*, 1997). What all of these proposed mechanisms have in common is that the large-scale exogenic driver determines a shift in competitive advantage from grasses to shrubs, with the inevitable consequence of replacement of grasslands with shrublands.

Endogenic mechanisms typically involve ecosystem feedbacks that may create bistability (e.g. Wilson and Agnew 1992, D'Odorico *et al.*, 2010b), with external drivers that determine the shift from one state to another. In these systems, a change in plant community composition may lead to a self-sustained sequence of processes (i.e. the positive feedback) that further enhance the initial change in vegetation until the system reaches the other stable state (Scheffer *et al.*, 2001). These state shifts are quite abrupt and difficult to reverse (Scheffer and Carpenter 2003). In the case of the southwestern United States, shrub encroachment has been relatively rapid, suggesting that the underlying dynamics might be bistable, with grass and shrub dominance representing alternative stable states of the system. In this case, the change in plant community composition could be triggered, for example, by a change in some external driver (e.g. disturbance) and sustained by the internal feedback. This type of state shift is difficult to reverse: even once the causes of the disturbance have been removed, the system will not return to its initial state (Figure 1). The limited or temporary success of many shrub-removal programmes tend to confirm that shrub encroachment is often irreversible (Whitford *et al.*, 1995, Havstad *et al.*, 1999, Rango *et al.*, 2005, Mata-Gonzalez *et al.*, 2007, Bestelmeyer *et al.*, 2009).

Four major feedback processes have been proposed as possible endogenic factors that could explain shrub encroachment as a state shift in bistable ecosystem

dynamics. These feedbacks involve interactions of vegetation cover with fire dynamic, soil erosion/water-resource loss, grazing by small mammals or microclimate.

The fire–grass feedback operates in environments where shrubs have a competitive advantage over grasses (e.g. D'Odorico *et al.*, 2006a, D'Odorico *et al.*, 2007). In this feedback, fire, sustained by a relatively continuous cover of flammable grass (e.g. Van Wilgen *et al.*, 2004), kills shrub seedlings, thus preventing shrubs from expanding in a landscape where, in the absence of fire, shrubs would be the dominant type of vegetation (Figure 2A).

In the erosion–vegetation feedback (e.g. Schlesinger *et al.*, 1990), a nearly continuous cover of grasses prevents redistribution of soil resources by wind and water erosion and promotes water infiltration that supports grass production. Because of their reliance on shallow soil nutrients and the fact that their meristems are in an air layer in which saltation occurs, grasses are more sensitive to soil erosion. In fact, soil erosion removes nutrient-rich soil particles from the soil surface, whereas sand blasting and burial cause serious injury to grasses. With the loss of grass, surface-soil resources are depleted by erosion and can be redistributed to shrubs (Figure 2B). This feedback plays a role in environments in which grasses maintain competitive advantage with respect to shrubs in the access to soil resources (Okin *et al.*, 2009b).

The third feedback involves small mammals grazing on small patches of grass amid a mosaic of shrubs that serve as both nesting and cover sites. These interactions between vegetation and small mammals serve as an internal feedback that tends to increase the ratio of shrub to grass cover (Bestelmeyer *et al.*, 2007, Kerley and Whitford 2009).

Finally, it has been recently observed that the increase in bare soil associated with shrub encroachment modifies the surface energy balance causing an increase in diurnal soil heat fluxes and an increase in nocturnal upward long-wave radiation. These changes in soil energy fluxes have the net effect of increasing the near-surface (nocturnal) air temperatures, thereby favouring shrub survival (Figure 2C, D'Odorico *et al.*, 2010a, He *et al.*, 2010).

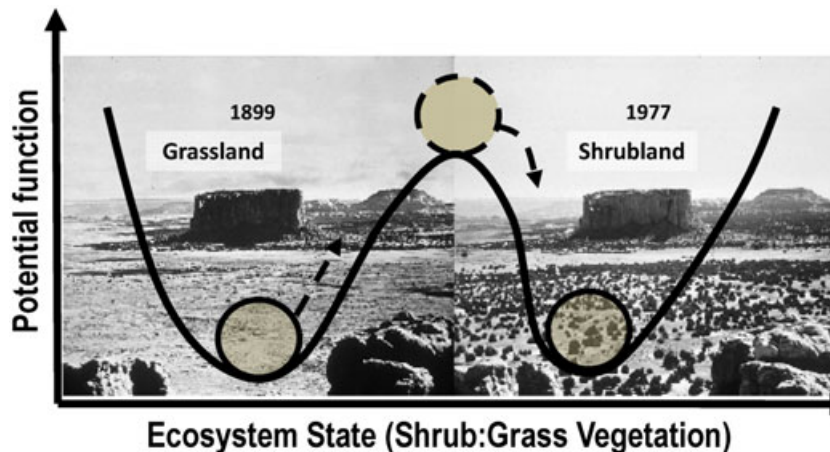


Figure 1. Shrubland and grassland as alternative stable states. In the background is a view from Acoma Pueblo to Enchanted Mesa, west of Albuquerque, NM. Photos by William H. Jackson (1899) and H.E. Malde (1977). Repeat photography source: Allen *et al.*, 1998 <http://biology.usgs.gov/luhna/chap9.html>

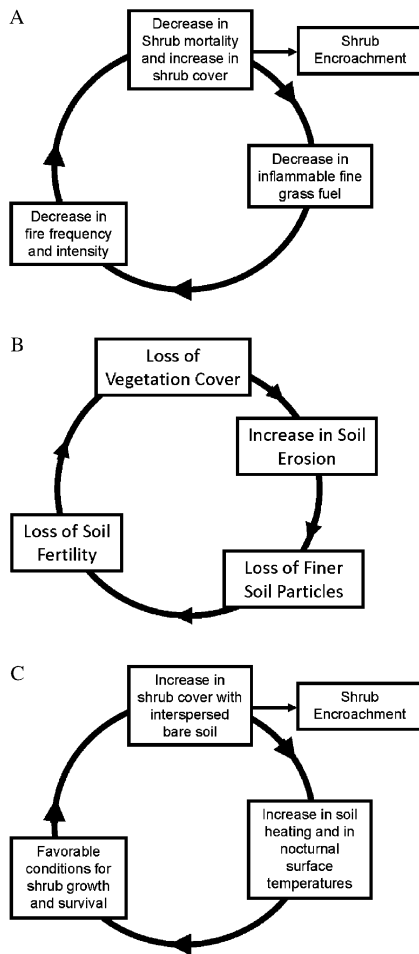


Figure 2. A: Fire-vegetation feedback. B: Soil Erosion-vegetation feedback. C: Vegetation-microclimate feedback.

As noted, these endogenic feedbacks can induce bistability in ecosystem dynamics, and shrub encroachment may result from a shift between the two stable states of landscapes dominated by shrub or grass (Anderies *et al.*, 2002, van Langevelde *et al.*, 2003, D’Odorico *et al.* 2006a, Ridolfi *et al.*, 2008, Okin *et al.*, 2009a). A driver is required to initiate the transition from one stable state to the other. In the case of the fire-grass feedback and the erosion-grass feedback, the driver of the transition could have been the factors leading to the loss of grass cover or climate change. Particularly instructive is the case of North American warm deserts: upon the arrival of European settlers and their cattle, intense grazing was a likely cause for this grass reduction. However, climate variability may have also played an important role in the recent history of vegetation succession in this region, as evidenced by the paleo record: in the mid-Holocene, the region was for the most part grass dominated (Van Devender and Spaulding 1979). A shift to shrub dominance occurred during the Medieval Warm Period (Stine 1994, Bradley *et al.*, 2003). A reconversion to grassland in the following century has been associated with the Little Ice Age (Neilson 1986). Shrub encroachment in southern New Mexico documented by Buffington and Herbel (1965) may have been underway when European settlers arrived in the 1800s, lagging behind changes in

climate that had already occurred (Cole 1985). In this way, the initiation of conversion of grasslands to shrublands could have echoed the warming-driven change that occurred near the beginning of the first millennium Common Era with the addition of intensive livestock grazing (e.g. Fredrickson *et al.*, 1998) likely accelerating the process by placing additional stress on grasses.

STAGES OF SHRUB ENCROACHMENT

Whatever the driver and regardless of the competitive advantage, several demographic changes must occur in order for the shift to shrubland to take place. First, pioneer shrubs must enter the landscape. During this initial colonization phase, the establishment rate of shrubs must exceed their mortality rate. In the following phase, the grass cover decreases until it almost disappears. The disappearance of grasses after the encroachment of shrubs indicates that the establishment rate of grasses is lower than the mortality rate.

The next transition is to a shrub duneland state, which appears to occur only on wind-erodible sandy soils. Coppice dunes or *nebkhas*, which can be found in many sandy deserts around the world, are the result of interactions between aeolian processes and shrub vegetation (Nickling and Wolfe 1994, Khalaf *et al.*, 1995, Dougill and Thomas 2002). Ecohydrological processes can also play a crucial role in coppice dune formation (e.g. Ravi *et al.*, 2007). We do not claim that all *nebkhas* necessarily originate from the degradation of desert grasslands; however, in some landscapes, their formation is observed as a late stage of the shrub encroachment process (e.g. Gibbens *et al.*, 2005, Ravi *et al.*, 2007).

On the basis of this analysis, we propose classifying grasslands that are undergoing shrub encroachment, or have done so in the past, into four stages (Figure 3): (I) pure grassland with almost no shrubs; (II) grassland with limited shrub cover; (III) shrublands where most grass cover is absent, and shrubs have increased in both size and density; (IV) shrub duneland. This fourth stage may not occur in all landscapes because coppice dunes are expected to develop mainly on sandy soils (Table I).

In the case of the Chihuahuan Desert, in North America, whichever mechanisms are responsible for shrub encroachment over the past ca. 150 years, the change in land cover included a transition from perennial *Bouteloua eriopoda* (black grama) grassland (State I) to a grass-shrub savanna (State II), a conversion to shrubland dominated primarily by *L. tridentata* (creosotebush) or *P. glandulosa* (mesquite) (State III), and the formation of *P. glandulosa* coppice dunelands (State IV) on sandy soils. The invasion of shrubs started with the colonization of grasslands by native species already present in the system. These native shrubs might have been dispersal limited prior to the introduction of domestic livestock to North America (e.g. Brown and Archer 1989), but in the case of *P. glandulosa*, the introduction of effective agents of seed dispersal (i.e. cattle, sheep and horses) would have increased the opportunities for woody plant establishment. This would have happened

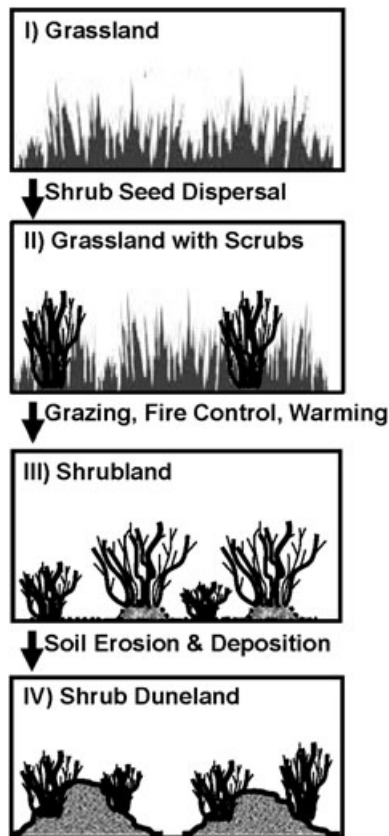


Figure 3. Stages of the shrub encroachment process.

regardless of effects of herbivory on grasses because even in undisturbed grasslands, sufficient microsites exist for woody seedling establishment (Jurena and Archer 2003). Indeed, many authors (e.g. Buffington and Herbel 1965, Van Auken 2000, Gibbens *et al.*, 2005, McGlynn and Okin 2006) have suggested that shrub seedlings and scattered mature individuals were present in grasslands prior to the arrival of Europeans (e.g. savanna physiognomy, State II),

although some *L. tridentata* shrublands already existed in the southwestern United States as early as in the 1860 (Buffington and Herbel 1965).

Thus, woody plant seedling establishment is a major demographic bottleneck in the state I → II transition that must have been overcome in the conversion of grasslands to shrublands, presumably by increased seed dispersal by domesticated animals, at least in the case of *P. glandulosa*. Theories explaining the state II → III transition can be classified into two major groups: (i) theories that postulate changes in competitive advantage caused by exogenic changes (e.g. climate warming, increase in nitrogen deposition or in CO₂ concentration), and (ii) theories that postulate an abrupt state shift in a bistable grasslands–shrubland system (Noy-Meir 1975, Walker *et al.*, 1981, Westoby *et al.* 1989, Anderies *et al.*, 2002, van Langevelde *et al.*, 2003, D'Odorico *et al.*, 2006a). In this second case, the bistability would be induced by endogenic processes, i.e. feedbacks internal to the system, whereas the transition could be initiated by exogenic changes in grass cover (e.g. intense grazing).

The invocation of various endogenic or exogenic factors has several implications for the processes that actually occur in the state transitions. In Table I, we summarize the major drivers of transitions among the four stages of the shrub encroachment process under different endogenic or exogenic mechanisms. Three different situations with respect to interspecific competition may exist: (i) in the course of the transition to shrubland, a shift in competitive advantage from grasses to shrubs occurs because of the changes in climatic conditions; (ii) grasses are able to outcompete shrubs in their use of soil resources, and no shift in this competitive advantage occurs in the course of the transition to shrubland; (iii) shrubs have always been in competitive advantage in their access to soil resources and in the absence of disturbances they tend to outcompete grasses.

Table I. State transitions in the shrub encroachment process.

	The competitive advantage shifts from grass to shrubs. Transition to shrubland due to exogenic factors	Grasses always in competitive advantage. Transition to shrubland due to exogenic factors with endogenic feedbacks on soil resources	Shrubs always in competitive advantage. Transition to shrubland due to exogenic factors with endogenic feedbacks on the disturbance regime
State I	Stable grassland (before exogenic changes)	Stable grassland	Stable grassland (maintained by fires, freeze, shrub seed predation or shrub dispersal limitation)
→ II	Shrubs increasingly favoured by exogenic changes in competitive relations	Limited shrub establishment due to decreased seed predation/increased seed dispersal	Shrubs outcompete grasses
II → III	Shrubs increasingly favoured	Erosion–vegetation feedback (triggered by grazing/decreased grass reproduction)	Shrubs outcompete grasses
III → IV	Erosion	Erosion	Erosion
Reversibility	I → II, II → III reversible if environment drivers reversed III → IV irreversible	I → II reversible II → III reversible if erosion decreases III → IV irreversible	I → II reversible if grass cover increases to allow fire II → III reversible if grass grows back to allow fire. Danger of nothing regrowing III → IV irreversible

In the first case (i), shrubs are increasingly favoured over grasses, and the transitions to states with higher shrub densities are driven by exogenic factors (warming, increasing levels of atmospheric carbon dioxide) causing the shift in competitive advantage from grasses to shrubs. In this case, the transition can occur gradually, i.e. with no abrupt state change and does not require the existence of any feedback mechanism. Therefore, the transitions I → II and II → III can be reversible if the competitive relations switch back before erosion in State III causes significant land degradation. The transition III → IV is generally irreversible.

In the second case (ii), in the absence of disturbances, grasses are always advantaged with respect to shrubs in current climate (Okin *et al.*, 2009a). This explains the stable existence of the initial grass cover. In the case of the Chihuahuan Desert, the transition I → II may have been favoured by an increase in shrub-seed dispersal associated with cattle grazing or by a decrease in seed predation by Native Americans. At this stage, the increase in shrub density did not occur at the expenses of grass cover in that sufficient sites were available for seedling establishment in the gaps of the grass canopy. The transition II → III was initiated by a loss in grass cover due to sustained intense grazing that permits shrubs to exploit water resources and is sustained by a positive feedback between soil erosion and loss of grass biomass (Okin *et al.*, 2009a; Ravi *et al.*, 2010). If an initial loss in grass cover causes soil erosion, the consequent loss of shallow soil resources and the damage of grass plants from sediment movement further decrease the grass cover, thereby exposing a larger fraction of the soil surface to wind and water erosion. Shrubs benefit from the weakening of the competition with grasses. Once all the grass cover is gone, the transition III → IV to coppice duneland is driven by physical processes: wind erosion removes soil from the bare interspaces and deposits the entrained sediments onto shrub colonized soil patches, thereby leading to the formation of nebkhas.

In the third case (iii), shrubs are always advantaged in the absence of fires or other disturbances. A stable grass cover initially exists because grasses provide the fuel load that sustains a vigorous fire regime. Frequent and intense fires kill or damage shrub plants. Shrub seed or seedling predation and limitations in seed dispersal might also contribute to the maintenance of the grassland state. Decrease in grass biomass (and fuel load) due to overgrazing or fire suppression reduces the fire-induced mortality of shrub seedlings, thereby allowing for the increase in shrub biomass (I → II transition). For instance, in the case of the southwestern United States, with the proliferation in the mid-1880s to late 1800s of domestic herbivores that preferentially utilize grasses, the mass and continuity of fine fuels decreased, leading to a virtual cessation of wildfire in many North American rangelands (e.g. Madany and West 1983, Savage and Swetnam 1990), thus removing a major constraint on woody plant establishment and growth (e.g. Madany and West 1983, Savage and Swetnam 1990). As the fire pressure is reduced, shrubs typically tend to outgrow grasses.

Sustained by the fire-vegetation feedback, this process leads to the shift to the stable shrubland State III. On sandy soils, erosion processes may then cause the formation of the nebkhas (State IV). In this case, the transition from grassland to shrubland is reversible as long as a sufficient grass cover exists for the occurrence and spread of fires across the landscape (Ravi *et al.*, 2009a). Whereas the I → II transition is likely to be reversible, the transition to coppice duneland (State IV), again, is irreversible. The shift to the State III can be reversible only if, once the native grass biomass has been removed, other grass species (most likely unpalatable exotic grasses) grow in the interspaces between shrubs. Invasive annual grasses are known for their ability to affect ecosystem dynamics by enhancing the rate of fire occurrence (e.g. McArthur *et al.*, 1990, D'Antonio and Vitousek 1992). In this case, the re-intensification of fires may reduce the shrub cover. Depending on whether the root systems and seed bank of native grasses are still present in the soil, the landscape might either return to the initial state of native grassland or shift to the undesirable state of soil covered by annual grasses, for which interannual climate variability means large interannual changes in vegetation cover and, hence, soil erosion. Notice that the reversibility of the transitions to States II and III depends also on the age of the shrub and shrub species, in that shrub mortality by fire may decrease with shrub age and size.

In cases where the shrubs are in competitive advantage [case (iii)] but their dominance is limited by frost occurrence, the transition II → III could also have been sustained by the microclimate feedback. In these cases, the shift in plant community composition would be enhanced by the nocturnal warming and reduced exposure to cold microclimates resulting from an initial increase in shrub cover in areas located close to the grass-shrub ecotone (D'Odorico *et al.*, 2010a, He *et al.*, 2010). If in a certain region the geographic distribution of shrubs is limited by freeze occurrences, even a short (<10 years) warm period could allow for the establishment of shrub seedlings in grasslands located in proximity to the ecotone. The associated increase in bare soil may then cause a local warming effect, thereby favouring shrub persistence and growth. In this case, the shift from State I to State II can be favoured by seed dispersal by herbivores in conjunction with the occurrence of warmer winters. The transition to State III is likely caused by the persistence of a warm period, which would allow shrubs to displace grasses. The stabilization of State III is favoured by the positive feedback between vegetation and microclimate conditions. Finally, the transition to State IV (coppice dunelands) is driven only by soil erosion and deposition as in the cases discussed before.

ROLE OF SPATIAL PROCESSES IN SHRUB ENCROACHMENT

The analysis presented in the previous sections did not stress the important role of spatial dynamics and heterogeneity, focusing rather on temporal dynamics of

shrub encroachment. Nonetheless, many of the processes related of shrub encroachment, such as fire and erosion, have clear spatial components (Bestelmeyer *et al.*, 2011). These spatial components are often, as with the previous discussion, implicit in the analysis of shrub encroachment processes. Here, we wish to make them explicit.

Both grasslands and shrublands are spatially heterogeneous, but the scale of heterogeneity depends on plant size and spacing. In grasslands, plant individuals are smaller and tend to be spaced closer together compared with shrublands; and therefore, the scale of spatial heterogeneity in grasslands is finer than in shrublands (c.f. Schlesinger *et al.*, 1996). As a consequence, the size of unvegetated gaps between plants in shrublands is larger than those in grasslands. Soil erosion, and the consequent removal of soil resources, can only occur from unvegetated portions of the landscape; wind transport increases nonlinearly with the size of unvegetated gaps (Okin *et al.*, 2006), whereas both the size and the connectivity of unvegetated patches influences the ability of water to transport soil resources (Mueller *et al.*, 2007). Thus, the contribution of resource removal by wind and water transport to shrub encroachment increases as bare gaps in the grassland state (State I) expand and become connected as the landscape moves through State II towards the shrubland state (State III), which has a large number of highly interconnected bare gaps. The extreme heterogenization that occurs in the coppice dunelands state (State IV) happens as a result of the ability of the wind to transport large amounts of material from unvegetated gaps to areas directly beneath shrub canopies.

Fire dynamics are also strongly affected by the spatial arrangement of vegetation on the landscape. For an ignition event to propagate, a largely continuous layer of fine fuel must exist. This continuous layer is provided by grass canopies, which can be highly continuous even if the basal cover of grasses is not. In grasslands (State I), large fires and high burn frequency can control the growth of shrub seedlings. However, as the continuity of the fine fuel layer is reduced, by grazing or drought, fires become less common and more patchy; and shrub seedlings are able to grow to maturity, leading to the transition of the landscape to a mixed grassland–shrubland state (State II) that does not have enough fuel connectivity for ignition events to propagate across the landscape.

Thus, the spatial arrangement of vegetation plays an important role in the conversion of grasslands and scrublands. Likewise, spatial dynamics also can influence the reversibility from States II or III to I. The transition back to the grassland state requires an increase in shrub mortality and the creation of a more homogeneous distribution of soil resources for grass regrowth. If shrub mortality is caused by fires, there would be a need for a relatively continuous grass cover to allow for fire spread across the landscape. Thus, grass/fire connectivity is an important requirement for a landscape to be able to revert back to the grassland state (Okin *et al.*, 2009b, Ravi *et al.*, 2009b). Alternatively, a change in climate or several contiguous wet years might allow grasses to establish and grow to the point that the fire cycle is restarted and shrubs and/or shrub seedlings

experience high levels of fire mortality. Indeed, even human intervention might be able to encourage the transition from States II or III to I. Treatments that reduced the size of interconnected bare patches might reduce losses of soil nutrients, causing the landscape to be retentive thus favouring the growth of grasses in formerly bare interspaces (Okin *et al.*, 2009b).

A SYNTHETIC MODELLING FRAMEWORK FOR GRASS–SHRUB TRANSITIONS

The purpose of the earlier discussions has been to integrate the varied explanations for shrub invasion into a single conceptual framework that describes how exogenic factors (climate change, grazing, CO₂ increases) interact with endogenic factors (fire, erosion, temperature) to give rise to the wide variety of instances in which shrub encroachment is observed worldwide. We also seek to describe why in some cases, shrub encroachment appears to be, on human timescales, irreversible (such as in the southwest United States) and in other cases, shrub encroachment appears to be reversible (such as the South African Karoo).

The conceptual framework that arises from our analysis has a counterpart in the mathematical modelling of systems susceptible to or undergoing shrub encroachment. There have been many efforts since Noy-Meir (1975) to model the nonlinear dynamics and emergence of bifurcations in rangeland ecosystems (May 1977, Walker *et al.*, 1981, Walker and Noy-Meir 1982, Anderies *et al.*, 2002, van Langevelde *et al.*, 2003, D'Odorico *et al.*, 2006a, Okin *et al.*, 2009a), and there is a rich literature on the mathematical modelling of a wide variety of ecosystems worldwide. Our purpose here is not to create a new approach for the modelling of rangeland ecosystems and their nonlinear dynamics but rather to show that these modelling approaches can provide a framework to explain how the transition from grassland and shrubland results from the interaction between the endogenic feedbacks and the exogenous drivers discussed in this paper.

If grasses are in competitive advantage, shrubs are by definition unable to limit grass access to the resources they share. In these conditions, shrubs may coexist with grasses only because some disturbance (e.g. grazing) prevents grasses from using all the existing resources. In this case, grass dynamics are completely independent of shrubs and can be modelled as a logistic growth with a harvest term expressing the effect of grazing

$$\frac{dG}{dt} = \alpha G \left(1 - \frac{G}{K}\right) - \gamma G \quad (1)$$

where G is grass biomass, K is the grass carrying capacity (the maximum value of G allowed by the limiting resources), γ is a parameter determining the grazing rate and α is a growth coefficient. The dynamics of shrub biomass, S , depend on those of grasses and can rely only on the resources, $(K - G)$, that are not used by grasses

$$\frac{dS}{dt} = \beta S \left(1 - \frac{G + S}{K}\right) - \delta S \quad (2)$$

where β determines the growth rate for shrubs and the linear term δS accounts for disturbance-induced losses of shrub biomass. In the absence of other drivers and feedbacks, over time, these dynamics tend to $G = K(1 - \gamma/\alpha)$ and $S = (\gamma/\alpha - \delta/\beta) K$. As the grazing rate increases, grass cover decreases and shrubs increase. This change in vegetation composition is not associated with an abrupt shift between two alternative stable states because the system (Equations (1) and (2)) is not bistable. However, bistability can exist if the dynamics undergo one of the positive feedbacks discussed in this review. For example, Okin *et al.*, (2009a) modelled the positive feedback between grasses and soil erosion by expressing the carrying capacity for grasses as a function of grass biomass. In fact, a loss of grass cover leads to the erosion-induced depletion of shallow soil resources, resulting in a decrease in carrying capacity, thereby preventing grass re-establishment. Thus, in this model, the existence of alternative stable states depends on the strength of the feedback, whereas the shift from a state to the other depends on exogenous drivers, such as grazing.

Similarly, if shrubs are in competitive advantage with respect to grasses, their dynamics are independent of G and can be expressed as a logistic growth with a linear harvest term accounting for disturbance-induced mortality (e.g. D’Odorico *et al.*, 2006a)

$$\frac{dS}{dt} = \beta S \left(1 - \frac{S}{K} \right) - \delta S \tag{3}$$

whereas grass dynamics depend on S as

$$\frac{dG}{dt} = \alpha G \left(1 - \frac{S + G}{K} \right) - \gamma G \tag{4}$$

In this case, bistability may emerge either because of the fire–vegetation feedback or because of the feedback between vegetation and microclimate. In the first case, as fire pressure increases, shrub biomass decreases, while grasses increase (D’Odorico *et al.*, 2006a). The higher grass fuel load, in turn, further enhances fires (van Wilgen *et al.*, 2003). In the second case, a loss in shrub biomass results in colder microclimate conditions, thereby enhancing cold-sensitive shrubs. Regardless of the particular feedback mechanism, in both cases the mortality rate, δ , is a decreasing function of S (e.g. D’Odorico *et al.*, 2006a). For example, this rate can be expressed as (e.g. Noy-Meir, 1975)

$$\delta = \frac{c}{1 + \phi S^2} \tag{5}$$

with ϕ expressing the strength of the feedback; in fact, the dependence of δ on S (i.e. the decrease in fire pressure with increasing shrub biomass) becomes stronger as ϕ increases.

Notice that both exogenous drivers and endogenous positive feedbacks are included in this set of equations. Grazing acts as an exogenous driver, which controls the value of γ in Equations (1) and (4). Climate acts as an exogenous driver in its influence on the vegetation growth parameters, alpha and beta for grasses and shrubs, respectively. Climate also

acts as an exogenic driver in areas where shrub growth is temperature limited (because of freezing) by influencing δ in Equations (2) and (3). Indeed, we see from this analysis that although the feedbacks are endogenic, they can be modulated by endogenic factors.

We can study the equilibrium states of S by setting the right-hand side of Equation (3) equal to zero and plotting the equilibrium points as a function of β/c and ϕ . The results are plotted in Figure 4, which shows how the feedback intensity, ϕ , controls the existence or non-existence of bistable behaviour, whereas changes in β/c – i.e. in the relative importance of growth and disturbance-induced mortality rates – may cause the shift from a state to the other with a clear hysteretic behaviour. A similar represen-

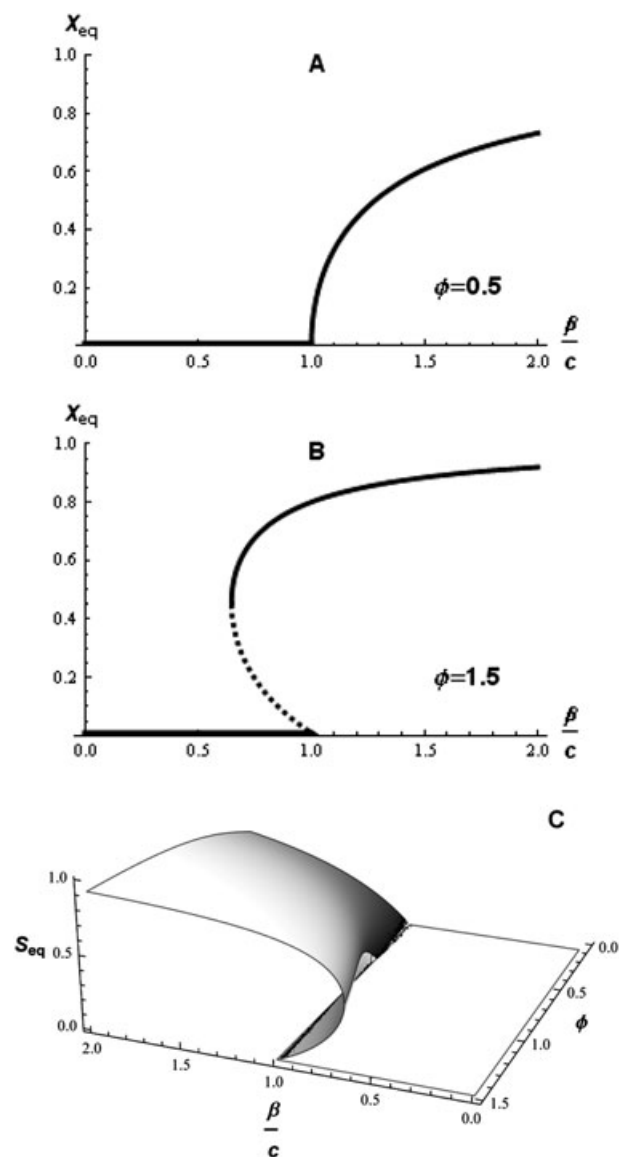


Figure 4. A and B: Stable (solid line) and unstable (dotted line) states of the system calculated with different strengths of the feedback. When the feedback is relatively weak (e.g. $\phi < 0.5$, Panel A), the dynamics exhibit only one stable state, whereas stronger feedbacks may induce the emergence of alternative stable states separated by an unstable equilibrium (e.g. $\phi = 1.5$, Panel B); C: Stable and unstable states of the system as a function of the strength, ϕ , of the internal feedback and of the relative growth rate, β/c , which is presumably controlled by exogenous drivers.

tation can be found in Turnbull *et al.* (2008). Thus, this modelling approach reiterates what was discussed in the previous sections: that endogenic feedbacks (expressed by ϕ in this case) determine the emergence of alternative stable states, whereas exogenous drivers (expressed by β/c) determine the shift from a state to another (i.e. they serve as triggers *sensu* Suding and Hobbs, 2009). Finally, according to some theories discussed previously, climate could also influence the competitive advantage of grasses or shrubs over the other, although CO₂ concentration has also been implicated in this control.

Even though these simplistic models provide useful indications of what processes and behaviours can explain the transition from grassland to shrubland, the explicitly spatial nature of the processes involved in shrub encroachment requires a spatial modelling approach (Ridolfi *et al.*, 2008; Ravi and D'Odorico, 2009c). In fact, the dispersal of grass and shrub seedlings, soil erosion and fire dynamics are inherently spatial processes, which depend on plant distribution and the connectivity of erosion pathways and of grass fuel (Okin *et al.*, 2009b).

CONCLUSIONS

A striking feature of shrub encroachment in many, but not all, drylands around the world has been its abruptness and apparent irreversibility. The irreversible nature of these transitions indicates that the shrubland state is a stable alternative to the grassland state. Bistable states arise from endogenic feedbacks, and the transition from one state to the other is driven by exogenic factors. The feedbacks are typically between the state of the system and its limiting resources or disturbance regime, mediated by processes that depend on large-scale environmental conditions such as climate, and CO₂ enrichment and land uses including the application of grazing, fire or shrub removal. The primary feedback processes involve fire, erosion and temperature regime, with shrubs primarily affected through feedbacks to the disturbance regime and grasses primarily affected through feedbacks that involve soil resources.

In this summary, we have focused on the feedbacks and the drivers that lead to shrub encroachment with the main goal of identifying the conditions under which management interventions have the potential to slow or reverse shrub encroachment and the cases in which the conversion may be, on human timescales, irreversible.

To this end, we have introduced an analysis of landscapes in several different states (States I–IV) and the conditions under which they may be reversible. We conclude that in cases where shrub encroachment is driven by changes in the competitive advantage of shrubs over grasses due to exogenous factors, there is very little chance for reversal unless there is a change in the exogenous factor itself. If shrubs are in competitive advantage, grasslands can be a metastable state in bistable dynamics induced by (positive) endogenic feedbacks. Once shrubs have encroached into the grassland (State II), fires or other disturbances (e.g. direct shrub removal) are needed to revert back to the grassland state. If, however, grasses remain in competitive advantage

over shrubs, there is the possibility of reversal through management, although management interventions must directly address the primary feedbacks. If erosion of soil resources is the dominant feedback, management interventions must focus on curtailing erosion. Because sediment transport depends on the details of the landscape connectivity, management interventions that change the connectedness of bare patches vulnerable to erosion is likely to be the best strategy for addressing shrub encroachment. Luckily, there has been significant research on soil erosion control, and appropriate methods from this field (e.g. Ravi *et al.*, 2011), as well as new methods, might be applied to the management of shrub encroachment. In cases where feedbacks on the disturbance regime (e.g. fire) are primarily responsible for shrub encroachment, its management should aim at the disturbance regime. In the early stages of shrub encroachment (e.g. State II), management interventions that encourage the growth of grass, such as reduction/cessation of grazing or seeding, might encourage the reestablishment of the grass–fire feedback, resulting in reduced shrub cover. These management interventions might be best timed to coincide with specific natural events, such as years of high rainfall followed by high grass cover. Active fire management, including prescribed burns, might be profitably employed to manage shrub encroachment. Modelling might also be utilized as a management tool to determine the times and places where interventions will have the greatest effect.

ACKNOWLEDGEMENT

This paper was funded by NSF under grant numbers EAR0746228, DEB0743678, EAR0720218, DEB0620482 (Sevilleta Long-term Ecological Research) and DEB0080412 (Jornada Long-term Ecological Research).

REFERENCES

- Adamoli J, Sennhauser E, Acero JM, Rescia A. 1990. Stress and disturbance - vegetation dynamics in the dry Chaco region of Argentina. *Journal of Biogeography* **17**: 491–500.
- Allen CD, Betancourt JL, Swetnam TW. 1998. Landscape changes in the southwestern United States: techniques, long-term data sets, and trends. In *Perspectives on the Land Use History of North America: A Context for Understanding our Changing Environment*, Sisk TD (ed). U.S. Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD/BSR-1998-0003 (Revised September 1999). Chapter 9 <http://biology.usgs.gov/luhna/chap9.html>.
- Anderies JM, Janssen MA, Walker BH. 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. *Ecosystems* **5**: 23–44.
- Archer S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *The American Naturalist* **134**: 545–561.
- Archer S, Schimel DS, Holland EA. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂. *Climatic Change* **29**: 91–99.
- Bahre CJ, Shelton ML. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography* **20**: 489–514.
- Bestelmeyer BT, Kalil NI, Peters DPC. 2007. Does shrub invasion indirectly limit grass establishment via seedling herbivory? A test at grassland–shrubland ecotones. *Journal of Vegetation Science* **18**: 363–370.
- Bestelmeyer BT, Tugel AJ, Peacock GL, Robinett DG, Sbaiver PL, Brown JR, Herrick JE, Sanchez H, Havstad KM. 2009. State-and-transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology & Management* **62**: 1–15.

- Bestelmeyer BT, Goolsby DP, Archer SR. 2011. Spatial patterns in state-and-transition models: a missing link to land management? *Journal of Applied Ecology* **48**: 746–757.
- Bradley RS, Hughes MK, Diaz HF. 2003. Climate in medieval time. *Science* **302**: 404–405.
- Briske DD, Bestelmeyer BT, Stringham TK, Shaver PL. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology and Management* **61**: 359–367.
- Brown JR, Archer S. 1989. Woody plant invasion of grasslands – establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* **80**: 19–26.
- Brown JR, Archer S. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* **80**: 2385–2396.
- Brown JH, Valone TJ, Curtin CG. 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Science* **94**: 9729–9733.
- Buffington LC, Herbel CH. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* **35**: 139–164.
- Burrows WH, Carter JO, Scanlan JC, Anderson ER. 1990. Management of savannas for livestock production in north-east Australia – contrasts across the tree grass continuum. *Journal of Biogeography* **17**: 503–512.
- Cole K. 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. *The American Naturalist* **125**: 289–303.
- Curtin CG, Kelt DA, Frey TC, Brown JH. 2000. On the role of small mammals in mediating climatically driven vegetation change. *Ecology Letters* **3**: 309–317.
- D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Reviews of Ecological Systems* **23**: 63–87.
- D'Odorico P, Laio F, Ridolfi L. 2006a. A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *The American Naturalist* **167**: E79–E87.
- D'Odorico P, Laio F, Ridolfi L. 2006b. Vegetation patterns induced by random climate fluctuations. *Geophysical Research Letters* **33**: L19404, doi: 10.1029/2006GL027499.
- D'Odorico P, Laio F, Porporato A, Ridolfi L, Barbier N. 2007. Noise-induced vegetation patterns in fire-prone savannas. *Journal of Geophysical Research-Biogeosciences* **112**: G02021, doi: 10.1029/2006JG000261.
- D'Odorico P, Fuentes JD, Pockman WT, Collins SL, He Y, Medeiros JA, De Wekker SFJ, Litvak ME. 2010a. Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. *Ecosphere* **1**: 17.
- D'Odorico P, Laio F, Porporato A, Ridolfi L, Rinaldo A, Iturbe IR. 2010b. Ecohydrology of terrestrial ecosystems. *Bioscience* **60**(11): 898–907.
- Dougill AJ, Thomas AD. 2002. Nebkha dunes in the Molopo Basin, South Africa and Botswana: formation controls and their validity as indicators of soil degradation. *Journal of Arid Environments* **50**: 413–428.
- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* **14**: 709–722.
- Felker P, Clark PR, Nash P, Osborn JF, Cannell GH. 1982. Screening *Prosopis* (mesquite) for cold tolerance. *Forest Science* **28**: 556–562.
- Fredrickson E, Havstad KM, Estell R. 1998. Perspectives on desertification: south-western United States. *Journal of Arid Environments* **39**: 191–207.
- Fredrickson EL, Estell RE, Laliberte A, Anderson DM. 2006. Mesquite recruitment in the Chihuahuan Desert: historic and prehistoric patterns with long-term impacts. *Journal of Arid Environments* **65**: 285–295.
- Gibbens RP, McNeely RP, Havstad KM, Beck RF, Nolen B. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. *Journal of Arid Environments* **61**: 651–668.
- Gillette DA, Pitchford AM. 2004. Sand flux in the northern Chihuahuan desert, New Mexico, USA, and the influence of mesquite-dominated landscapes. *Journal of Geophysical Research-Earth Surface* **109**: F04003.
- Havstad KM, Gibbens RP, Knorr CA, Murray LW. 1999. Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics. *Journal of Arid Environments* **42**: 155–166.
- He YF, D'Odorico P, De Wekker SFJ, Fuentes JD, Litvak M. 2010. On the impact of shrub encroachment on microclimate conditions in the northern Chihuahuan desert. *Journal of Geophysical Research-Atmospheres* **115**: D21120.
- Heske EJ, Brown JH, Guo QF. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant-species diversity in the Chihuahuan Desert. *Oecologia* **95**: 520–524.
- Huenneke LF, Anderson JP, Remmenga M, Schlesinger WH. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* **8**: 247–264.
- Huxman TE, Wilcox BP, Breshears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* **86**: 308–319.
- Idso SB. 1992. Shrubland expansion in the American Southwest. *Climatic Change* **22**: 85–86.
- Jurena PN, Archer S. 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* **84**: 907–919.
- Kerley GIH, Whitford WG. 2009. Can kangaroo rat graminivory contribute to the persistence of desertified shrublands? *Journal of Arid Environments* **73**: 651–657.
- Kerley GIH, Whitford WG, FR Kay. 1997. Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory? *Oecologia* **111**: 422–428.
- Khalaf FI, Misak R, Aldousari A. 1995. Sedimentological and morphological characteristics of some nabkha deposits in the northern coastal plain of Kuwait, Arabia. *Journal of Arid Environments* **29**: 267–292.
- Kramp BA, Ansley RJ, Tunnell TR. 1998. Survival of mesquite seedlings emerging from cattle and wildlife feces in a semi-arid grassland. *The Southwestern Naturalist* **43**: 300–312.
- Li J, Okin GS, Hartman LJ, Epstein HE. 2007. Quantitative assessment of wind erosion and soil nutrient loss in desert grasslands of southern New Mexico, USA. *Biogeochemistry* **85**: 317–332.
- Li J, Okin GS, Alvarez LJ, Epstein HE. 2008. Effects of wind erosion on the spatial heterogeneity of soil nutrients in two desert grassland communities. *Biogeochemistry* **88**: 73–88.
- Madany MH, West NE. 1983. Livestock grazing fire regime interactions within Montane Forests of Zion National Park, Utah. *Ecology* **64**: 661–667.
- Martinez-Vilalta J, Pockman WT. 2002. The vulnerability to freezing-induced xylem cavitation of *Larrea tridentata* (Zygophyllaceae) in the Chihuahuan desert. *American Journal of Botany* **89**: 1916–1924.
- Mata-Gonzalez R, Figueroa-Sandoval B, Clemente F, Manzano M. 2007. Vegetation changes after livestock grazing exclusion and shrub control in the southern Chihuahuan Desert. *Western North American Naturalist* **67**: 63–70.
- May RM. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**: 471–477.
- McArthur DE, Romney MN, Smith SD, Tueller PD. 1990. Cheatgrass invasion, shrub die off and other aspects of shrub biology and management. INT-276, USFS, Ogden, Utah.
- McGlynn IO, Okin GS. 2006. Characterization of shrub distribution using high spatial resolution remote sensing: ecosystem implication for a former Chihuahuan Desert grassland. *Remote Sensing of Environment* **101**: 554–566.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being: Synthesis*. Island Press: Washington, DC.
- Moleele NM, Ringrose S, Matheson W, Vanderpost C. 2002. More woody plants? The status of bush encroachment in Botswana's grazing areas. *Journal of Environmental Management* **64**: 3–11.
- Mooney HA, Cleland EE. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America* **98**: 5446–5451.
- Mueller EN, Wainwright J, Parsons AJ. 2007. Impact of connectivity on the modeling of overland flow within semiarid shrubland environments. *Water Resources Research* **43**: W09412.
- Neilson RP. 1986. High-resolution climatic analysis and southwest biogeography. *Science* **232**: 27–34.
- Nickling WG, Wolfe SA. 1994. The morphology and origins of nabkhas, region on Mopti, Mali, West Africa. *Journal of Arid Environments* **28**: 13–30.
- Noy-Meir I. 1975. Stability of grazing systems: application of predator-prey graphs. *Journal of Ecology* **63**: 459–481.
- Okin GS, Herrick JE, Gillette DA. 2006. Multiscale controls on and consequences of aeolian processes in landscape change in arid and semiarid environments. *Journal of Arid Environments* **65**: 253–275.
- Okin GS, D'Odorico P, Archer SR. 2009a. Impacts of feedbacks on Chihuahuan Desert grasslands: transience and metastability driven by grass recruitment. *Journal of Geophysical Research* **114**: G01004.
- Okin GS, Parsons AJ, Wainwright J, Herrick JE, Bestelmeyer BT, Peters DPC, EL Fredrickson. 2009b. Do changes in connectivity explain desertification? *Bioscience* **59**: 237–244.
- Parsons AJ, Abrahams AD, Wainwright J. 1996. Responses of interrill runoff and erosion rates to vegetation change in southern Arizona. *Geomorphology* **14**: 311–317.

- Pockman WT, Sperry JS. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* **109**: 19–27.
- Pockman WT, Sperry JS. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany* **87**: 1287–1299.
- Polley HW. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management* **50**: 562–577.
- Polley HW, Johnson HB, HS Mayeux. 1992. Carbon dioxide and water fluxes of C-3 annuals and C-3 and C-4 perennials at subambient Co-2 concentrations. *Functional Ecology* **6**: 693–703.
- Rango A, Huenneke L, Buonopane M, Herrick JE, KM Havstad. 2005. Using historic data to assess effectiveness of shrub removal in southern New Mexico. *Journal of Arid Environments* **62**: 75–91.
- Ravi S, D'Odorico P. 2009c. Post-fire resource redistribution and fertility island dynamics in shrub-encroached desert grasslands: a modeling approach. *Landscape Ecology*. doi: 10.1007/s10980-008-9307-7.
- Ravi S, D'Odorico P, Okin GS. 2007. Hydrologic and aeolian controls on vegetation patterns in arid landscapes. *Geophysical Research Letters* **34**: L24S23.
- Ravi S, D'Odorico P, Collins SL, Huxman TE. 2009a. Can biological invasions induce desertification? *The New Phytologist* **181**: 512–515.
- Ravi S, D'Odorico P, Wang LX, White CS, Okin GS, Macko SA, Collins SL. 2009b. Post-fire resource redistribution in desert grasslands: a possible negative feedback on land degradation. *Ecosystems* **12**: 434–444.
- Ravi S, Breshears DD, Huxman TE, D'Odorico P. 2010. Land degradation in drylands: interactions among hydrologic-aeolian erosion and vegetation dynamics. *Geomorphology* **216**: 236–245.
- Ravi S, D'Odorico P, Breshears DD, Field JP, Goudie AS, Huxman TE, Li J, Okin GS, Swap RJ, Thomas AD, Van Pelt S, Whicker JJ, Zobeck TM. 2011. Aeolian processes and the biosphere. *Reviews of Geophysics*. doi: 10.1029/2010RG000340.
- Reynolds JF, Smith DMS, Lambin EF, Turner BL, Mortimore M, Batterbury SPJ, Downing TE, Dowlatabadi H, Fernandez RJ, Herrick JE, Huber-Sannwald E, Jiang H, Leemans R, Lynam T, Maestre FT, Ayarza M, Walker B. 2007. Global desertification: building a science for dryland development. *Science* **316**: 847–851.
- Ridolfi L, D'Odorico P, Laio F, Tamea S, Rodriguez-Iturbe I. 2008. Coupled stochastic dynamics of water table and soil moisture in bare soil conditions. *Water Resources Research* **44**: W01425.
- Savage M, Swetnam TW. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo Ponderosa pine forest. *Ecology* **71**: 2374–2378.
- Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* **18**: 648–656.
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591–596.
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. *Science* **247**: 1043–1048.
- Schlesinger WH, Raikes JA, Hartley AE, Cross AF. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**: 364–374.
- Schlesinger WH, Abrahams AD, Parsons AJ, Wainwright J. 1999. Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. rainfall simulation experiments. *Biogeochemistry* **45**: 21–34.
- Scholes RJ, Archer SR. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**: 517–544.
- Sekhwela MBM, Yates DJ. 2007. A phenological study of dominant acacia tree species in areas with different rainfall regimes in the Kalahari of Botswana. *Journal of Arid Environments* **70**: 1–17.
- Sipos MP, Andersen MC, Whitford WG, Gould WR. 2002. Graminivory by *Dipodomys ordii* and *Dipodomys merriami* on four species of perennial grasses. *The Southwestern Naturalist* **47**: 276–281.
- Stine S. 1994. Extreme and persistent drought in California and Patagonia during medieval time. *Nature* **369**: 546–549.
- Suding KN, Hobbs RJ. 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution* **24**: 271–279.
- du Toit J, Biggs HC, Rogers KH. 2003. *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press: Washington, DC.
- Turnbull L, Wainwright J, Brazier RE. 2008. A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. *Ecohydrology* **1**: 23–34.
- Valone TJ, Thornhill D. 2001. Mesquite establishment in arid grasslands: an experimental investigation of the role of kangaroo rats. *Journal of Arid Environments* **48**: 281–288.
- Van Auken OW. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* **31**: 197–215.
- Van Devender TR, Spaulding WG. 1979. Development of vegetation and climate in the southwestern United States. *Science* **204**: 701–710.
- Van de Koppel J, Rietkerk M, van Langevelde F, Kumar L, Klausmeier CA, Fryxell JM, Hearne JW, van Andel J, de Ridder N, Skidmore A, Stroosnijder L, HHT Prins. 2002. Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. *The American Naturalist* **159**: 209–218.
- Van Langevelde F, van de Vijver C, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337–350.
- Van Wilgen BW, Govender N, Biggs HC, Ntsala D, Funda XN. 2004. Response of Savanna fire regimes to changing fire-management policies in a large African National Park. *Conservation Biology* **18**: 1533–1540.
- Van Wilgen BW, Trollope WSW, Biggs HC, Potgieter ALF, Brockett BH. 2003. Fire as a driver of ecosystem variability. In *The Kruger experience: ecology and management of savanna heterogeneity*, Du Toit JT, Rogers KH, Biggs HC (eds). Island: Washington, DC; 149–170.
- Van Vegten JA. 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* **56**: 3–7.
- Wainwright J. 2006. Climate and climatological variations in the Jornada Basin. In *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site*, Havstad KM, Huenneke LF, Schlesinger WH (eds). Oxford University Press: Oxford, UK; 44–80.
- Wainwright J, Parsons AJ, Abrahams AD. 2000. Plot-scale studies of vegetation, overland flow and erosion interactions: case studies from Arizona and New Mexico. *Hydrological Processes* **14**: 2921–2943.
- Walker BH, Noy-Meir I. 1982. Aspects of the stability and resilience of savanna ecosystems. In *Ecology of Tropical Savannas*, Huntley BJ, Walker BH(eds). Springer-Verlag: Berlin; 556–590.
- Walker BH, Ludwig D, Holling CS, Peterman RM. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**: 473–498.
- Westoby M, Walker B, Noy-Meir I. 1989. Opportunistic management of rangelands not at equilibrium. *Journal of Range Management* **42**: 266–274.
- Whitford WG. 1997. Desertification and animal biodiversity in the desert grasslands of North America. *Journal of Arid Environments* **37**: 709–720.
- Whitford WG, Martinez-Turanas G, Martinez-Meza E. 1995. Persistence of desertified ecosystems: explanations and implications. *Environmental Monitoring and Assessment* **37**: 319–322.
- Wilson JB, Agnew ADQ. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* **23**: 263–336.