El Niño as a Window of Opportunity for the Restoration of Degraded Arid Ecosystems

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ABSTRACT

Most arid ecosystems have suffered from severe overexploitation by excessive wood harvesting, overgrazing, and agriculture, resulting in depletion of vegetation biomass and soil erosion. These changes are often difficult to reverse due to positive feedbacks that tend to stabilize the new situation. In this paper, we briefly review evidence for the idea that different states in these ecosystems might represent alternative equilibria and present a graphic model that summarizes the implications for their response to changing environmental conditions. We show how, in the light of this theoretical framework, climatic oscillations such as El Niño Southern Oscillation (ENSO) could be used in combination with grazer control to restore degraded arid ecosystems. We also present evidence that, depending on grazing pressure, ENSO episodes can trigger structural and long-lasting changes in these ecosystems.

Key words: arid ecosystems; semiarid ecosystems; rangelands; alternative stable states; vegetation shifts; land degradation; desertification; El Niño; ENSO; climatic oscillation; ecosystem restoration.

INTRODUCTION

There is increasing evidence that the El Niño Southern Oscillation (ENSO) has strong effects on the dynamics of plant and animal populations in a wide range of terrestrial ecosystems ranging from arid and semiarid ecosystems to tropical and boreal forests (Holmgren and others 2001). During an El Niño episode, rainfall increases dramatically in certain areas of the world, while severe droughts occur in other regions. These increases in rainfall can be four to ten times that of a "normal" year. The phenomenon lasts approximately 1 year before the climate conditions reverse. The next phase, known as La Niña, produces climate patterns roughly opposite to those found during an El Niño episode. The oscillation between El Niño and La Niña is irregular but typically occurs once every 3–6 years (Allan and others 1996). Although the effect of global warming on ENSO oscillations are difficult to predict, recent high-resolution climatic models suggest that the frequency of El Niño–like conditions can be expected to increase over the coming decades (Timmermann and others 1999).

Interannual variability in precipitation is strongly associated with ENSO events in many arid and semiarid ecosystems. Increased rainfall during an ENSO event is crucial for plant recruitment and productivity in these ecosystems. Short-term responses are often spectacular due to an extraordinary increase in the cover of annual species as well as significant increases in growth, fruit, and seed production among perennial herbs and woody species (for example, see Gutiérrez and others 1997; Polis and others 1997). Higher trophic levels have also been observed to respond to the plant produc-

tivity pulse (Jaksic and others 1997; Meserve and others 1999; Grant and others 2000), leading to changes in ecosystem structure and functioning that can be quite intricate (Polis and others 1998).

One may imagine that an ecosystem essentially just tracks fluctuations in environmental conditions. Indeed, various long-term studies of El Niño effects on terrestrial ecosystems show such a tracing of environmental fluctuations with delays on different trophic levels (Holmgren and others 2001). However, this is not necessarily the case in ecosystems with alternative stable states or more appropriately, alternative "domains of attraction" or "dynamical regimes." Under the same environmental conditions (for example, rainfall), an ecosystem may be in either of two (or more) distinct states (for instance, bare soil or perennial grassland). Positive feedbacks may cause such multiple stable states, a concept now beginning to be recognized as an inherent property of a wide range of ecosystems (Carpenter forthcoming). In this case, a rare extreme event, such as high rainfall, may trigger structural shifts to a different ecosystem state, which remains extant even after the environmental conditions revert.

Here, we briefly review evidence for the hypothesis that arid ecosystems have alternative vegetation states depending on grazing and water availability and present a graphic model to summarize the implications for the response to El Niño Southern Oscillation. We then present several field observations that support the idea that, depending on grazing pressure, structural changes in arid ecosystems may be triggered by ENSO events.

ALTERNATIVE STABLE STATES IN ARID AND SEMIARID ECOSYSTEMS

Problems with the management of rangelands have led to a growing consensus that these ecosystems have distinct alternative stable states (for example see, Westoby and others 1989; Filet 1994). Numerous observations indicate that, rather than gradual responses to changing conditions, these systems experience sudden transitions from one state to the other when certain climatic conditions or management actions occur (Westoby and others 1989). It is also recognized that the ecosystem states are separated by critical thresholds and that transitions across such boundaries are extremely difficult to reverse (Friedel 1991; Laycock 1991).

On a small spatial scale, patch dynamics in drylands suggest the existence of alternative stable states. Arid and semiarid ecosystems often show a mosaic pattern, with patches that have a relatively high biomass dispersed in a matrix of poorly vegetated land (for example, see Aguiar and Sala 1999). Such patchy patterns can occur even on seemingly homogeneous landscapes and often remain remarkably constant over time, suggesting that the different patch types represent alternative stable states. For example, a comparison of the extension of woody patches in an otherwise herbaceous matrix in semiarid Chile revealed virtually no change over a 30-year time span (Fuentes and others 1984), indicating that both types of patches are highly resilient. Despite considerable variations in rainfall over the 30-year period, all woody spots remained woody and none of the open herbaceous areas was invaded by shrubs or trees.

Although numerous distinct vegetation states may be discerned in practice (Westoby and others 1989; Archer 1996), a rough simplification that captures the essence of much of the discussion is the one between woody, herbaceous, and bare vegetation states. In more disturbed and drier conditions, the herbaceous state becomes dominated by annual instead of perennial species (Fuentes and others 1984; Fuls 1992), which ultimately leads to a mostly bare condition. This is generally referred to as "land degradation" or "desertification" and is considered to be one of the main global ecological threats (Kassas 1995). We briefly review the mechanisms that are thought to be responsible for the stability of these distinct states, discuss the role of spatial heterogeneity, and highlight the interactive effects of water and grazing as major driving forces.

Mechanisms Stabilizing Alternative States

Overgrazing has become well known as a potential mechanism for explaining alternative stable states. The root of this theory is a classical graphic analysis by Noy-Meir (1975) showing that the amount of grazers needed to cause a collapse of vegetation biomass is much larger than the amount needed to subsequently suppress vegetation regrowth once it is in a low-biomass state. If grazing alone were responsible for maintaining vegetation in an over-exploited state, we would expect that removal of all grazers should eventually lead to recovery of the vegetation. However, although in some cases reduction of herbivore density has allowed for the recovery of degraded patches (for example, see McNaughton 1983; Belsky 1986), in other situations vegetation did not recover (for example, see Sinclair and Fryxell 1985; Friedel 1991; Laycock 1991). This implies that factors other than grazing could be responsible for the irreversability of vegetation loss.

Soil-plant interactions are thought to play a major role in determining the stability of perennial plant cover (for example, see Rietkerk and van de Koppel

1997; van de Koppel and others 1997; Shachak and others 1998). Perennial plants and their deposited litter allow precipitation to be absorbed by the topsoil and become available for uptake by plants. When vegetation cover is lost, infiltration decreases and water runoff increases. This triggers positive feedbacks (for example, see Graetz 1991). Bare ground enhances the formation of a soil crust by direct impact of raindrops, and this physical crust reduces further water infiltration. This reduction in water availability decreases the possibilities of plant establishment and growth and therefore of plant cover. In addition, bare soils are also very susceptible to erosion by water and wind, causing a net removal of nutrients from degraded patches. Due to the nonlinear response of erosion to plant cover, very small changes in plant cover close to a threshold can cause very large changes in erosion (Marshall 1973), which can precipitate a switch to a barren state.

Facilitative interactions between plants are also believed to play a major role in stabilizing different vegetation states. In arid ecosystems, even when plant recruitment does not occur in open spaces, seedling establishment is often possible under the shade of existing "nurse" shrubs or trees, allowing rejuvenation and long-term persistence of existing vegetation. One of the main reasons behind this nursing effect is an improvement in the seedling water relations (Holmgren and others 1997). In the shade of a nurse plant, air and soil temperatures are lower, and water content of the superficial soil layers tends to remain higher (for example, see Geiger 1965; Joffre and Rambal 1988). Therefore, seedlings experience less thermal and water stress (for example, see Valiente-Banuet and Ezcurra 1991; Aguiar and Sala 1994). Other factors often contribute to this nursing effect—for example, soil nutrient levels can be higher and herbivory levels lower under the nurse plant (for example, Callaway 1995)—but water availability is clearly a critical factor in arid ecosystems. The nursing effect, together with the fact that adult shrubs are relatively less sensitive to drought and herbivory explains why mature woody vegetation may persist and rejuvenate in climatic regions where the establishment of seedlings in the absence of nursing shade from woody vegetation is impossible.

Fire plays a special role because it may destroy woody plants that are relatively insensitive to grazing. If certain vegetation components facilitate fire ignition and are also relatively insensitive to fire effects, this implies another positive feedback (for example, see reviews in Westoby and others 1989; Carpenter forthcoming). For instance, grasses may produce a great deal of combustible litter, thus promoting fires. However, because grasses recover much faster from fires than shrubs, a positive feedback maintaining grass dominance is suggested.

In practice, a combination of factors is often responsible for observed shifts from one state to an alternative one and the subsequent maintenance of the latter state. For instance, human-induced fires are thought to have caused a major decline of Serengeti-Mara woodlands in Tanzania. However, grazing and trampling by elephants and other herbivores is likely to be the factor preventing recovery of the woodlands (Dublin and others 1990). Similarly, grazing by livestock in the Sahel region has caused vegetation loss, but the recovery of perennial plant cover is strongly prevented by soil–plant feedbacks.

Islands of Fertility and the Role of Shrubs and Trees

Perhaps one of the most confusing aspects in the study of land degradation is the fact that woody plants are often seen as indicators of desertification, whereas they also tend to provide a benign microclimate that facilitates the regeneration and growth of their own offspring as well as other perennial or annual plants. The key to understanding this paradox is spatial heterogeneity.

Runoff in degraded landscapes tends to lead to an accumulation of soil and water on lower sites, which become the most favorable places for plant growth and therefore may develop relatively lush vegetation. As perennial vegetation (herbaceous or woody) traps eroded soil and water, these patches tend to become "islands of fertility." This patchiness of resources and plant biomass is self-reinforcing. As the islands of fertility become more fertile, the desertic matrix becomes less fertile than in the situation in which resources are distributed evenly over the landscape. Because in several regions homogeneous perennial grass cover has broken up into a patchy mosaic of desert and fertile islands with woody cover, shrubs are often regarded as indicators of desertification (Schlesinger and others 1990). The new shrub state can be extraordinarily resilient. Cattle ranchers in such areas are constantly fighting against shrub encroachment to increase the carrying capacity for livestock (Page 1970).

It is important to note that despite the fact that in such disturbed landscapes, shrubs are indicators of desertification, they are not a cause. By contrast, in many regions, shrubs and trees may offer an important safeguard against land degradation, since they provide a crucially important protection
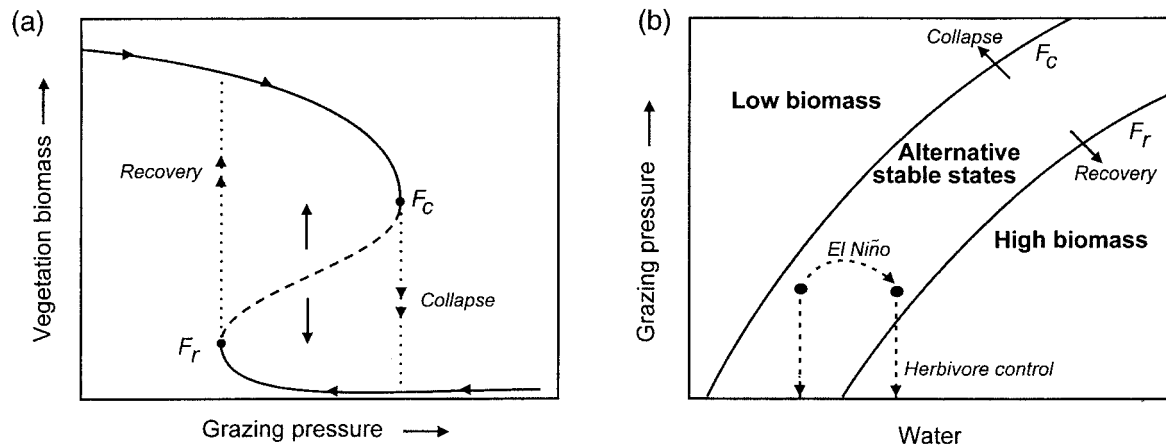
Figure 1. (a) Equilibrium biomass of vegetation in semiarid regions as a function of grazing pressure. The inflection points (dots) of the curve are fold bifurcations that mark critical biomass removal rates. At grazing pressures higher than F_c, the vegetation can only be in a state with low biomass. At grazing pressure lower than F_r, a high-biomass condition is the only stable state. At intermediate grazing pressure (between F_c and F_r), a high-biomass state and a low-biomass state are alternative equilibria (solid lines) of the system. Here, the dashed middle section of the sigmoidal curve represents an unstable equilibrium that marks the border of the basins of attraction of these two stable branches. (b) Critical thresholds of biomass removal (see 1a) as a function of water availability. Under wetter conditions, equilibrium biomass and the critical grazing pressure for collapse (F_c) or recovery (F_r) are higher. A certain reduction of biomass removal rate (for example, herbivory control) indicated by the vertical arrows may be sufficient to induce woodland recovery in a wet (El Niño) year but not in a dry year.

against soil erosion. Shachak and others (1998) have demonstrated that reduction of shrub cover increases nutrient leakage and desertification of shrublands. Indeed, loss of forests and shrublands has paved the way to historical land degradation in various semiarid areas of the world. For example, the destruction of evergreen forests in central Chile (Fuentes 1994) and the Mediterranean basin (Pignatti 1995) has led to a dramatic impoverishment of the soil and left the landscape dominated by bare soil and an annual flora, with dispersed shrub patches. Importantly, the invading shrubs in degraded shrublands usually belong to a different set of species than the mostly larger woody species dominating the original woodlands (see, for example, Bisigato and Bertiller 1997).

The switches between different vegetation states in the Mediterranean basin illustrate the effects of loss of semiarid woodlands. This region was once widely dominated by open woods and shrubs, but due to excessive firewood harvesting, the landscape has been progressively converted into one dominated by grasses. Later on, it becomes dominated by shrubs due to overgrazing. These transitions are probably irreversible. Because of the loss of organic soil and the failure of grasses to regenerate in open spaces without the protection of scattered trees, a shrub state cannot return, within an ecological time scale, to a grass state even when grazing is relieved.

And since the transition from a grass to an arboreal state is also very slow—if it is possible at all—the regeneration of the original woodlands seems extremely difficult (Puigdefabregas and Mendizabal 1998). Irreversible losses of Californian woodlands have been analyzed in this context as well (Huntsinger and Bartolome 1992).

A GRAPHIC MODEL

Despite confusing aspects such as the dual image of woody plants in the literature on desertification, the emerging grand picture is rather unambiguous. Arid ecosystems tend to have multiple stable states that are separated by critical thresholds of factors such as water availability and biomass removal (for example, through grazing). In this section, we condense this observation into a simple graphic hypothesis.

Woody Plants and Herbs as Alternative Stable States

First, we focus on a simple abstract model of alternative stable states in vegetation biomass that we think of as describing a single site (rather than a landscape average). As a starting point, we take the response of vegetation to grazing (Figure 1a) described by Noy-Meir (1975) and others (for exam-

ple, Rietkerk and van de Koppel 1997). In the absence of grazing, vegetation biomass is high, matching the carrying capacity of the environment. With increasing grazing pressure, vegetation biomass decreases gradually until a critical threshold (F_c) is reached, at which point the vegetation collapses to a very low level. Recovery from this overexploited state is only possible when grazing pressure falls below another, much lower critical level (F_r). Note that in addition to grazing, various mechanisms discussed earlier (facilitation, soil–plant interactions, and fire) may in practice contribute to such a hysteresis in the response of vegetation. Note also that this simple abrupt switching model is a starting point that can be modified for heterogeneous environments and more than two alternate states, as discussed later.

To see how the effects of grazing and rainfall may interact, we extend the previous model (Figure 1a) using the assumption that the critical grazing pressure for collapse and recovery will increase with the productivity of the environment. If conditions are moister, the maximum grazing pressure that can be sustained will be higher, implying that the critical point for collapse (F_c) will occur at higher grazing pressure. Likewise, recovery (F_r) may occur at higher grazing pressure than in a drier situation. The combined effects of water and grazing can best be summarized by a so-called bifurcation graph (Figure 1b). In terms of dynamic systems theory, the critical points F_c and F_r are "fold bifurcations." Plotting these bifurcations against water availability and grazing pressure gives a map of the system's behavior. In this case, the two bifurcation lines mark three different areas. Above the collapse bifurcation (F_c), only a degraded low-biomass state exists; whereas below the recovery bifurcation (F_r), the high-biomass situation is the only stable state. Between the two lines, the two states are alternative equilibria.

Note that, because we have not used an explicit quantitative model, the picture is not computed but rather inferred in a qualitative way from the information we have. There are only two essential features corresponding to two assumptions:

1. F_c is higher than F_r; this represents the alternative stable states assumption. The vegetation collapse occurs at higher levels of biomass removal and lower water availability than the recovery.

2. F_c and F_r have a positive slope; this represents the assumption that critical levels of biomass removal for both collapse and recovery are higher when water availability is higher.

El Niño Effects

From the resulting graph, we can infer the expected combined effects of altered levels of biomass removal and changes in rainfall conditions during El Niño. Where woodlands have been lost, they can recover if water increases and/or biomass removal decreases sufficiently to cross the critical line F_r (Figure 1b). In regions where El Niño years are wetter than intermittent periods, a rainy El Niño event will shift the system to the moister right-hand side of the graph. In some cases, this could be sufficient to allow the regeneration of some key species, triggering a recovery of the woodland. However, in other cases, the increased precipitation during El Niño alone will not be sufficient; a reduction of the grazer density (lower biomass removal, in general) would be needed to meet the critical requirements (F_r) for regeneration. Note that there can be situations in which the complete exclusion of grazers would be sufficient to allow regeneration during rainy El Niño years, yet it would have no effect during normal conditions (Figure 1b). Thus, in cases where neither herbivore control nor rainy El Niño events alone are sufficient to trigger woodland recovery, adjusting herbivore control to rainy El Niño events may result in vegetation regeneration. Note that although we use the term "El Niño," the idea applies to rainy events in general. It is important to remember that in various regions of the world, La Niña events are wet and El Niño episodes are dry.

Significantly, although the pulse of rainfall associated with an ENSO event is a temporal condition, a resulting recovery may be permanent due to the resilience of woodland (an alternative stable state). As long as the drought is not severe and biomass removal is moderate enough to remain below the critical line F_c even in dry years, a woodland will remain extant once it is well established. As mentioned earlier, this is due to the nursing effect of adult trees and shrubs on seedlings and to the relative tolerance of grown individuals to grazing. The potentially long-lasting effect of a brief regeneration episode makes it worthwhile to invest in making the most out of rainy years, such as the ones correlated to the ENSO events.

Most likely, grazer control is crucial to allow woodland regeneration during rainy years, even if the grazer density at the start of the year allows for initial seedling establishment. This is because not only plants but also herbivores respond to the increases in rainfall associated with El Niño. Farmers tend to increase the cattle stock in view of the lush growth of herbs and grasses; in addition, popula-

tions of natural herbivores increase following the productivity peak in plants (see, for example, Meserve and others 1999). Obviously, this may lead to elimination of established seedlings and potentially even leave the final condition of the vegetation deteriorated rather than improved after a rainy year.

Beyond Two Stable States

Under dry conditions, the perennial herbaceous vegetation can become prone to overgrazing and erosion, leading to patches of bare soil where only annual herbs will grow during short episodes following precipitation events. This bare state can be considered to be another stable state because recolonization by perennial plants is extremely difficult. The graphic model can be expanded to include this desertification process (Figure 2). Obviously, the absolute, but also the relative, position of the thresholds for catastrophic transitions between the three states may differ from case to case. The usual sequence with decreasing moisture and/or increasing biomass removal is probably woodlands > perennial herbs > annual herbs/bare soil. However, direct transitions from woodland to patches of annual herbs and/or bare soil may also occur, depending on the relative position of the three fold bifurcations in the system.

Distinguishing three alternative stable states also facilitates an understanding of the phenomenon in which homogeneous pastures have been replaced in some regions by woody patches in a matrix of bare soil (Schlesinger and others 1990). Indeed, if we plot equilibrium biomass as a function of availability of resources such as water or nutrients (Figure 2), it is easy to see that if the average resource level sustains herbaceous vegetation, concentration of the resource in fertile patches at the cost of resource depletion in the rest of the matrix could lead to bare soil with patches of woody vegetation. Wet years may induce shifts from bare to either herbaceous or woody vegetation depending on grazing and other properties of the ecosystem as reflected by the position of the bifurcation points in models such as the one presented. Obviously, the model is not intended to describe these complicated problems in any detail. The main point we wish to illustrate is that the basic idea of studying the effect of El Niño on systems with multiple equilibria can be easily extended beyond the simple case that we outlined previously.

An important general implication of spatial heterogeneity is that switches such as those depicted in Figure 1a may occur asynchronously at different sites in the landscape. Depending on variation in
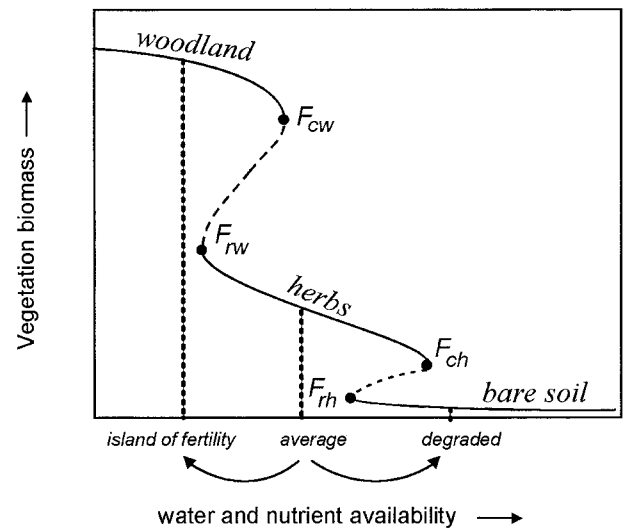

Figure 2. An extension of the model presented in Figure 1 to a situation with three alternative states— woodlands, herbs, and bare soil. Transitions between the states can now occur at four fold bifurcations. Critical removal rates are indicated for collapse of woodland (F_{cw}) or herbaceous vegetation (F_{ch}) and for recovery of woodland (F_{rw}) or herbaceous vegetation (F_{rh}). The three-alternative stable state model is consistent with the idea that if resources such as water and nutrients become patchily distributed, a homogeneous herbaceous vegetation that could be sustained by the average resource level (middle vertical dotted line) can be transformed in a matrix of bare soil (right-hand side) with woody patches (left-hand side). Wet years can allow the transformation of bare soil to either herbaceous vegetation or woodland depending on the position of the various fold bifurcations, which are affected (among other things) by grazer density.

factors such as topographical exposure, critical water and grazing levels leading to collapse or recovery (F_c and F_r) will, in practice, differ from site to site. Although a thorough treatment of the implications of such heterogeneity is beyond the scope of this paper, it is easy to see that the overall change in a heterogeneous landscape will be more gradual than in the simple model (Figure 1).

An example may help to clarify this. Suppose we have a hypothetical landscape that is homogeneous except that one half of it has a different, more fertile soil type than the other half. With gradually increasing grazing pressure, vegetation may then collapse first in the unfertile part and later in the fertile part due to the difference in plant growth rates (much as in the reasoning for the effects of water illustrated in Figure 1b). Thus, if we consider the average vegetation biomass in the entire landscape, vegetation decline occurs in two consecutive steps
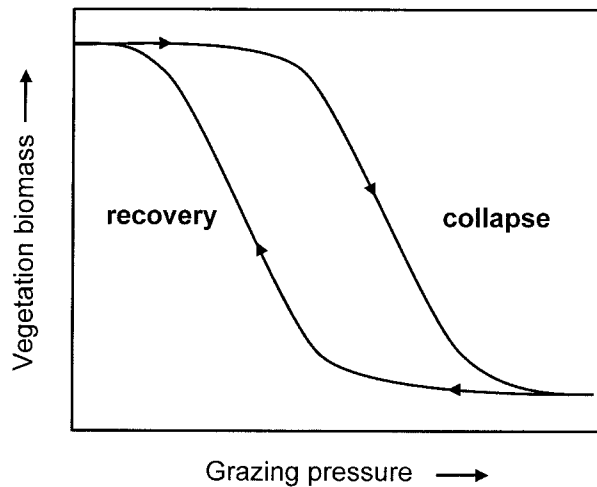
Figure 3. Vegetation biomass averaged over a heterogeneous landscape is predicted to show hysteresis, but it responds in a more gradual way than the simple base model to increases and decreases in grazing pressure (see Figure 1a).

rather than as one single collapse (as in Figure 1a). Extending this reasoning, if many soil types rather than just two distinct types exist, the response to increasing grazing pressure on a landscape scale will resemble a declining staircase with many small steps. By continuity, it follows that a landscape with a continuous range of local conditions will respond in a smooth way (Figure 3). Importantly, even if environmental heterogeneity is large, we should expect the essential aspect of hysteresis to be preserved in the sense that the paths of recovery and "collapse" are different. Obviously, real patch dynamics are more complicated due, for instance, to spatial interactions between adjacent areas. However, this line of reasoning suffices to explain that spatial heterogeneity will tend to make landscape-scale responses more gradual than local dynamics.

DISCUSSION

Field Evidence

Several observations support the idea that ENSO events can trigger long-lasting shifts in arid vegetation depending on grazing pressure. Rainy conditions during ENSO events have been shown to trigger the regeneration of woody vegetation in many arid ecosystems (Holmgren and others 2001). For example, in semiarid Australia, successful seedling establishment of mulga (Nicholls 1992), as well as *Eucalyptus* and conifer woodlands (Austin and Williams 1988), have been linked with wetter periods

during La Niña episodes. Similarly, in the shrubland–grassland transition zone of the Chihuahuan desert, large increases in shrub cover over the past decades have been related to episodes of increased winter precipitation that seem to correspond largely to El Niño events (Brown and others 1997). The interaction of El Niño effects with grazing is nicely illustrated by the dynamics in the Sonoran desert, where cactus seedlings establish during rainy El Niño years on ungrazed sites but not on sites grazed by burros, where the nurse shrubs under which cactus seedlings usually survive the drier periods have been extirpated (Bowers 1997). Moreover, long-term field experiments in northern Chile show that shrub cover can increase during a rainy El Niño event when the main herbivores are excluded or when predators are allowed to feed on the herbivores (Gutiérrez and others 1997).

Some of the most striking examples of the interactive effects of interannual variations in precipitation and grazing in plant recruitment and the subsequent switches in ecosystem state have been described for semiarid Australia (Austin and Williams 1988). In the 1830s, the Pilliga scrub was an open woodland of large *Eucalyptus* and *Callitris* trees and grasses. Over the next 40 years, the system was heavily invaded by shrubs due to management practices consisting of less frequent fires and increased grazing by cattle and sheep. The severe El Niño droughts of 1876–77 put an end to grazing. During the subsequent rainy year of 1878, regeneration of the original woodland trees was so dense that grazing became impossible. The system had switched into a very dense forest. A few years later, European rabbits invaded and made further regeneration of the original trees impossible. But the forest remained dense until the early 1950s due to slow sapling growth. The forest remained dense until the early 1950s. Then a second natural experiment occurred during the rainy aftermath of the 1951 ENSO when, coincidentally, rabbits were practically eliminated by the myxoma epizootic. Once again, the combined effects of rainy conditions and absence of grazing triggered the natural regeneration of the woodland trees, which since then has occurred in every suitable wet year.

Using El Niño for Ecosystem Restoration

These observations support the idea that the restoration of degraded arid ecosystems might be achieved in an efficient way by adjusting grazer control to the occurrence of temporal windows of opportunity opened by the ENSO phenomenon. However, to apply this idea in practice, the critical water and herbivory conditions (F_r) for the estab-

lishment of plant species in a given area must be known. Only this information can indicate the level of herbivory control that will be needed and whether it is essential to wait for El Niño or not. Field experiments with controlled herbivore density and water additions seem the most promising approach to establishing critical thresholds. But the ultimate test of the theory would be to perform grazer control experiments over a range of field sites during natural wet episodes. One such large-scale field experiment in northern Chile has already been following the effects of wet El Niño events on plants and animals for several years (Jaksic and others 1997). Past ENSO events may also be interpreted as natural experiments; consequently, dendrochronological databases could be used for testing the hypothesis that tree establishment in semiarid regions occurs in pulses associated with wet periods. Unfortunately, due to the lack of data on past grazing pressure, the link with herbivory is not easily established through this line of research (for example, see Milton and others 1997; Villalba and Veblen 1997).

Although the use of the windows of opportunity offered by El Niño still faces many challenges, the possibility merits further exploration. Grazer control appears to be an essential aspect, but measures other than reforestation and grazer control may also be used to stimulate recovery. For instance, the addition of large woody branches to degraded Australian areas has proved to be very effective in improving water infiltration rates as well as soil carbon and nitrogen, and in providing a modified microclimate in which the establishment and growth of perennial grasses is greatly enhanced (Ludwig and Tongway 1996; Tongway and Ludwig 1996). Regardless of the precise measures, the evidence summarized in our graphic model suggests that the multiplicity of stable states in arid vegetation makes it possible to design restoration strategies that can make use of wet ENSO years to induce vegetation and ecosystem restoration.

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