Disentangling Complex Landscapes: New Insights into Arid and Semiarid System Dynamics

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Although desertification is a global phenomenon and numerous studies have provided information on dynamics at specific sites, spatial and temporal variations in response to desertification have led to alternative, and often controversial, hypotheses about the key factors that determine these dynamics. We present a new research framework that includes five interacting elements to explain these variable dynamics: (1) historical legacies, (2) environmental driving variables, (3) a soil-geomorphic template of patterns in local properties and their spatial context, (4) multiple horizontal and vertical transport vectors (water, wind, animals), and (5) redistribution of resources within and among spatial units by the transport vectors, in interaction with other drivers. Interactions and feedbacks among these elements within and across spatial scales generate threshold changes in pattern and dynamics that can result in alternative future states, from grasslands to shrublands, and a reorganization of the landscape. We offer a six-step operational approach that is applicable to many complex landscapes, and illustrate its utility for understanding present-day landscape organization, forecasting future dynamics, and making more effective management decisions.

Keywords: alternative states, cross-scale interactions, desertification, feedbacks and thresholds, nonlinear dynamics

Desertification is a worldwide phenomenon in arid and semiarid regions. In many areas, it is manifested by the broadscale expansion of woody plants into perennial grasslands, with associated grass loss and soil degradation. Nearly 40% of the land's surface and a fifth of the world's human population occur in regions that are directly susceptible to desertification (Reynolds and Stafford Smith 2002). Conversion from grasslands to woody plant–dominated landscapes has important local, regional, and global consequences, including changes in carbon dynamics (Jackson et al. 2002), loss of biodiversity and forage production (Ricketts et al. 1999), spread of invasive exotic species (Masters and Sheley 2001), changes in the partitioning of hydrological budgets (Wilcox et al. 2003), and wind and water erosion of soil and nutrients (Okin and Gillette 2001, Wainwright et al. 2002). Although desertification is recognized as an important issue, and numerous studies have provided information on the dynamics of particular sites (Havstad et al. 2006), spatial and temporal variations in rates and patterns of woody plant invasion and grass loss (or conversely, grass recovery) have led to alternative, and often controversial, hypotheses about the key factors that determine desertification dynamics (Archer 1994, Van Auken 2000). In addition, such variation results in complex landscapes that are mosaics of vegetation types, including grasslands, savannas, and woodlands. These mosaics are influenced by different processes, and are expected to have very different dynamics in response to changes in environmental driving variables, such as climate (figure 1).

Given that landscapes include the scales at which humans interact with their environment and at which most management and policy decisions are made, it is imperative that scientists and managers understand current landscape complexity well enough to make reliable forecasts of ecosystem dynamics under changing environmental conditions (Turner 2005). An ability to generate effective forecasts is critical to managing natural resources to minimize human impacts on them and to sustain their use. Several compelling and important questions need to be addressed: For example, how can researchers disentangle landscape complexity in structure and dynamics? How and under what conditions do

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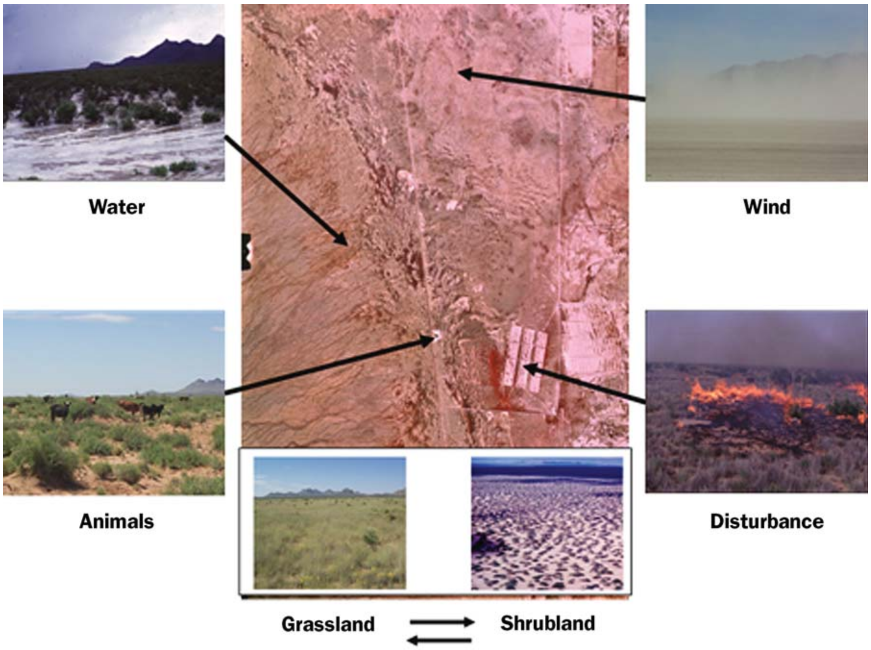

Figure 1. Landscapes in arid and semiarid systems consist of a mosaic of vegetation types, such as grasslands and shrublands, dominated by different species, controlled by different ecological processes (e.g., competition for resources; redistribution of nutrients, seeds, and other materials by wind, water, and animals), and expected to have different responses to environmental drivers (e.g., climate, disturbance). Photographs: Jornada Experimental Range photo gallery.

dynamics and decisions made at fine scales influence dynamics at broader scales? How and under what conditions do broadscale dynamics overwhelm fine-scale processes to influence landscape patterns?

In this article, we first discuss current conceptual frameworks developed to understand desertification and the types of dynamics that cannot be explained within these frameworks. We then discuss an integrated conceptual framework and operational scheme for understanding and forecasting spatial and temporal variations in desertification dynamics across a range of scales. Finally, we illustrate how this framework provides new insights into disentangling complexity in current landscape structure and predicting alternative states and responses under changing environmental conditions. Although we illustrate our framework using arid and semiarid systems, it is applicable to many landscapes that exhibit spatial and temporal variations in dynamics.

Current conceptual frameworks for desertification

A number of conceptual frameworks have been proposed to explain desertification dynamics. Most frameworks emphasize drought and livestock grazing as the key factors that affect competitive interactions between plants and act to shift grasslands to woody plant dominance (Schlesinger et al. 1990, Archer 1994). Vertical redistribution of water and differences in rooting depth were used in early attempts to explain competitive interactions and patterns in grass, forb, and woody plant cover and abundance (Weaver and Darland 1949, Weaver 1958, Walter 1971). Deep-rooted woody plants are expected to exploit deeper, more reliable water sources and withstand drought better than shallow-rooted grasses. The framework of Schlesinger and colleagues (1990) incorporated both drought and grazing, as well as horizontal redistribution of resources and positive feedback mechanisms between individual plants and soil properties. As woody plants expand into grasslands, areas of bare soil increase in spatial extent and frequency of occurrence, and wind and water redistribute soil nutrients horizontally from bare areas to locations beneath woody plants to create local "islands of fertility" (Wright 1982, Schlesinger et al. 1990). Livestock grazing and drought act to move grasslands toward a desertified landscape dominated by woody plants, whereas extended wet periods and the exclusion of grazers maintain grasses. This framework has been successful in comparing individual grass and woody plant dynamics, and in comparing the dynamics of large areas of relatively uniform grasslands and woody plant–dominated areas. However, it does not consider emergent properties at intermediate scales (e.g., ecohydrological patterns), and it assumes that the effects of drought and grazing are uniformly important across scales. These deficiencies may limit the usefulness of this framework (Peters et al. 2006).

Other desertification frameworks combine vertical and horizontal redistribution of water at the plant scale (Breshears and Barnes 1999) or include spatial and temporal heterogeneity in physical factors and disturbances at multiple spatial scales in addition to the redistribution of materials within and among spatial units (Ludwig et al. 1997, Reynolds and Wu 1999). These landscape-based frameworks are hierarchically organized: Each spatial scale has a set of characteristics that interact with finer spatial units and are constrained by conditions expressed at broader spatial scales (*sensu* O'Neill et al. 1986). Transfers of materials between spatial units can affect landscape function and response to disturbance, and can create distinct patterns in vegetation and soils at multiple scales (Tongway et al. 2001). Threshold behavior and feedbacks between vegetation and soil properties are important components of these types of conceptual frameworks (van de Koppel et al. 2002, Rietkerk et al. 2004).

Perplexing dynamics

Although existing frameworks are successful in explaining many dynamics of arid and semiarid ecosystems at fine and broad scales, they do not account for observed variation at scales intermediate between plants and landscapes, in large part because they do not consider the full range of important processes and their interactions deriving from interactions across spatial scales. For example, studies have shown that drought and grazing alone cannot explain spatial variation in woody plant success (Knapp and Soulé 1998), and that the impacts of drought and grazing are not uniformly distributed in time or space (Lyford et al. 2003). Fences designed to exclude livestock and limit the spread of woody plants can be unsuccessful if processes occurring outside an exclosure are ignored (figure 2). Spatial variation in perennial grass persistence through time often can not be explained on the basis of grazing history, precipitation patterns, and soil texture alone (Yao et al. 2006). Interactions among processes occurring at different scales are important to these dynamics. Recent analyses show that drought cannot explain temporal variation in grass loss (figure 3). Furthermore, high spatial and temporal variations in aboveground net primary production, or ANPP, often observed in arid and semiarid systems (Le Houérou et al. 1988) cannot be explained using traditional measures of precipitation (Huenneke et al. 2002); a consideration of water redistribution across spatial scales is needed to explain these dynamics (figure 4).

Figure 2. Protection from cattle is not always sufficient to inhibit woody plant dominance. A 250-hectare exclosure constructed at the Jornada Basin in 1933 (left) was designed as a "natural revegetation" site. The exclosure, located along an ecotone between black grama and honey mesquite (an important native shrub), was designed to protect an area of grassland from cattle grazing, thus allowing grasses to increase in cover and biomass through time. However, the exclosure was located near a historic mesquite dune field that overtook the exclosure by 1998. Contagious processes associated with dune expansion overwhelmed fine-scale interactions between grasses and shrubs that were operating within the exclosure. A ground photo from the same location in 2001 (right) shows dominance by mesquite inside the exclosure, even without grazing since 1933. Photographs: Jornada Experimental Range photo gallery (left) and Debra Peters (right).

In addition to drought and grazing, other explanatory variables for grassland–shrubland transitions include climate change, reduction in fire frequency, increase in atmospheric carbon dioxide, and change in small animal populations (Schmutz et al. 1992). These variables may be important under certain conditions; however, their effects cannot be generalized. Thus, a new framework is needed that considers the full range of potentially important processes and their multiscale interactions in order to explain spatial variation in patterns and dynamics of woody plant encroachment. More important, this understanding will increase researchers' ability to predict future dynamics and to promote recovery of desertified areas.

Landscape linkage framework

Our approach to disentangling landscape complexity in arid and semiarid systems builds on previous frameworks that use a hierarchy of spatial units (e.g., individual plants and associated bare interspaces, groups of plants and interspaces, and ecological sites or landscape units on distinct soil-geomorphic units) and the redistribution of resources within and between units (figure 5). We include interactions among five key elements of ecological systems that connect scales of the hierarchy and lead to complex landscapes (figure 6): (1) historical legacies that include climate and past disturbances; (2) environmental driving variables, such as weather, climate modes, and current natural and anthropogenic disturbance regimes; (3) a soil-geomorphic template of patterns in ecological variables that includes both local properties (e.g., soil texture, chemistry, microtopography) and their spatial context and arrangement; (4) multiple horizontal and vertical transport vectors (fluvial, aeolian, animal); and (5) the redistribution of resources by these vectors within and among spatial units. We focus on quantifying ecosystem processes in the context of patch structure (i.e., area or size, composition, and spatial arrangement of bare and vegetated patches at multiple scales) as a means of improving our mechanistic understanding and ability to integrate, predict, and extrapolate across spatial and temporal scales up to and including those relevant to land management and policy. Interactions and feedbacks among these elements within and across spatial scales generate threshold changes in patch structure and associated process rates that result in a reorganization of the landscape and lead to alternative future states. The relative importance of these elements is expected to depend on specific environmental conditions that may change through time. These mechanisms operate across multiple scales: Plants, animals, and soils influence transport vectors and resource redistribution within each spatial scale and, via the hierarchical spatial arrangement of vegetation patches, among scales as well.

The integration of all five elements into our landscape linkage framework provides a powerful approach for disentangling landscape patterns and dynamics. In addition, we emphasize three aspects that are missing from most previous desertification approaches. First, spatial context (i.e., the spatial arrangement and location or adjacency of spatial units)

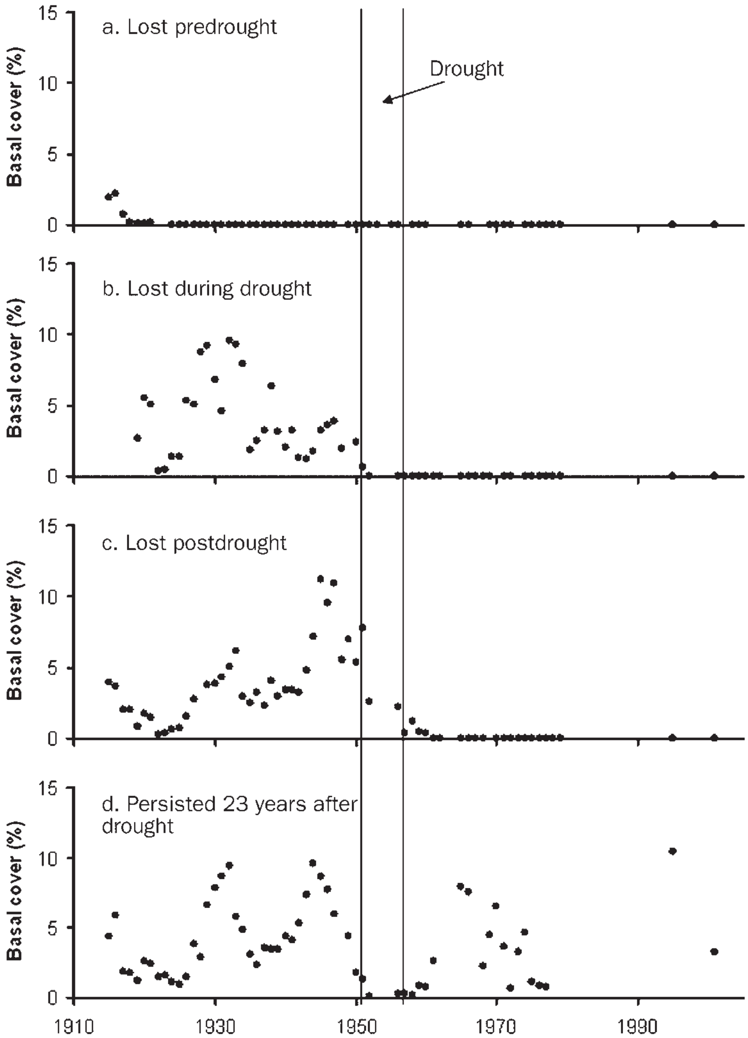

*Figure 3. Basal cover (percentage) of black grama (**Bouteloua eriopoda**), a dominant upland perennial grass in the Chihuahuan Desert, on four individual 1-square-meter quadrats, each representing a class of quadrats with different dynamics. These findings indicate that drought alone cannot explain temporal variation in grass loss across the Jornada Basin. Black grama went locally extinct on most quadrats (64%) either during (b) or shortly after (c) the 1950s drought. However, this species went locally extinct on 21% of research quadrats before the drought (a), and persists to the present day on 15% of the quadrats (d). Grass persistence was related to landscape context: Quadrats located farther from historic shrublands persisted longer than quadrats adjacent to shrublands (Yao et al. 2006).*

is an integral part of landscape structure and dynamics that influences resource redistribution between spatial units, both within and among spatial scales, to generate cross-scale interactions. These cross-scale interactions often generate surprising or unexpected dynamics (Peters et al. 2004a). Second, historic legacies from before 1900 have often been ignored in analyses of North American systems, yet they can provide important long-term signatures (Peters et al. 2006) and are critical to how landscapes change through time (Turner 2005). Third, soil-geomorphic organization is widely viewed as a primary determinant of the importance of particular vectors and spatial context to resource redistribution. The spatial context of geomorphic units in arid and semiarid systems is predictable within physiographic regions, and these units have predictable relationships with climate and soil development (Monger and Bestelmeyer 2006). Each element is described in more detail below.

Historical legacies. Past climate and disturbances, including land use and other human activities, can have a significant influence on the current state of the system (figure 6). Because legacies are nonuniformly distributed in both space and time, they have the potential for major impacts on current landscape complexity. In addition, time lags in the expression of the effects of past events on current spatial patterns and dynamics often result in historical legacies being overlooked as key elements in ecological frameworks, yet evidence of their long-term importance is increasing (Foster et al. 2003).

Legacies in arid and semiarid systems have most often been examined at the scale of landscape units and with respect to management that occurred within the past century, such as livestock grazing or mechanical and chemical treatments for woody plant control (Rango et al. 2002). These treatments were often small (1 to 100 hectares) and distributed across the landscape on the basis of woody plant density and cover (Herrick et al. 2006). However, legacies can also predate recent settlement to include the effects of indigenous peoples. For example, encampments by Native Americans over 600 years ago have had long-lasting impacts on vegetation dynamics and patterns in water erosion in the southwestern United States (York and Dick-Peddie 1969).

Climatic and geomorphic signatures can also be important to current landscape patterns and dynamics. Historic climate can be important at multiple temporal scales: Long periods (decades to centuries) of above average precipitation interspersed with periods of below average precipitation (e.g., drought) can have effects on the dominance by different life forms at broad scales (grasses or woody plants; Van Devender 1995). Short-term drought at the scale of decades can also affect vegetation dynamics for decades or longer. For example, after the extreme drought of the 1950s in southern New Mexico reduced cover of perennial grasses, some species have failed to recover over the past 50 years (Yao et al. 2006).

Environmental driving variables. Our view of environmental driving variables, such as weather and disturbance, is broader than previous hierarchically based frameworks in which

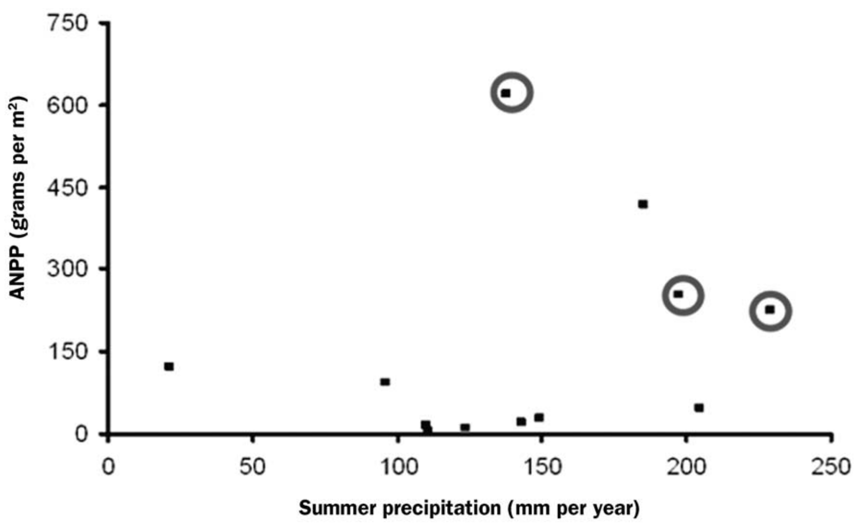

Figure 4. Relationship between summer precipitation (millimeters per year) and aboveground net primary production (ANPP) at the Jornada Basin site (1989–2000). The variation in ANPP cannot be explained by nonspatial explanatory variables, such as summer precipitation (Huenneke et al. 2002; http://jornada-www.nmsu.edu/). Water redistribution from upslope positions that results in flooding events (circled) can explain most of the high values of ANPP.

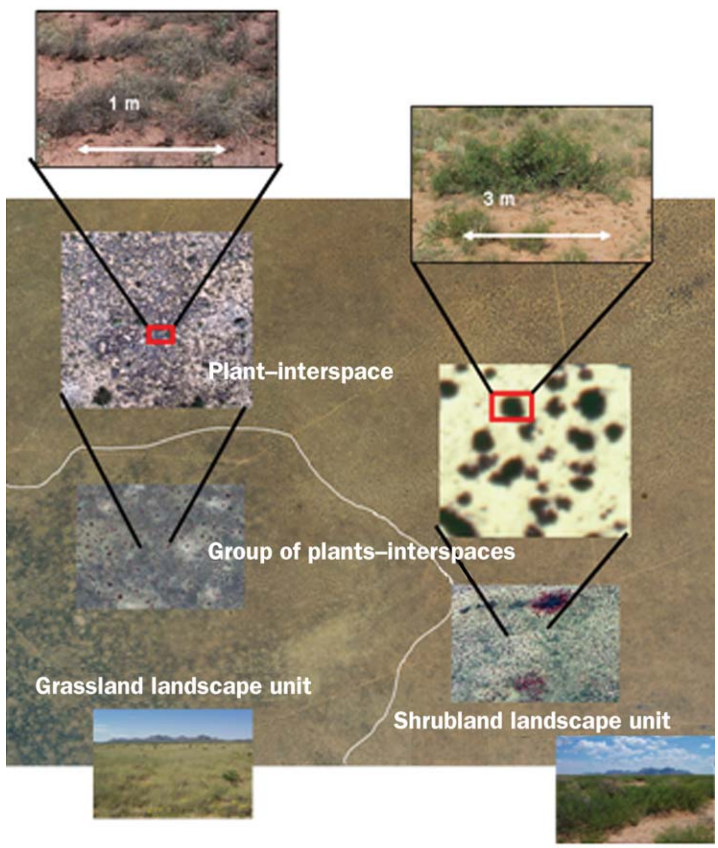

Figure 5. A hierarchy of spatial units is involved in our landscape linkage framework for arid and semiarid systems. Spatial units range from individual plants and their associated bare interspaces (above) to groups of plants and interspaces (center) to landscape units dominated by grasses or shrubs (below). Photographs: Jornada Experimental Range photo gallery.

broadscale phenomena provide constraints on fine-scale processes (O'Neill et al. 1986). In our framework, environmental drivers can either constrain, overwhelm, or interact with fine-scale processes to generate complex dynamics. Furthermore, these alternative conditions can occur within the same system at different points in time or at different locations on the landscape (Peters et al. 2004a).

Environmental drivers can have important direct and indirect effects on past, present, and future states of the system through influences on the soil-geomorphic template, transport vectors, and resource redistribution (figure 6). For example, high-intensity, short-duration thunderstorms and changes in climate modes can directly affect the rate and magnitude of material transfer by water and wind (Breshears et al. 2003, Wang and Schimel 2003). Disturbances, including fire, overgrazing, and some human activities such as driving off-road vehicles, have indirect effects on transport vectors by reducing plant cover and thereby increasing the potential for movement of soil particles through wind and water erosion (Okin and Gillette 2001, Wainwright et al. 2002). Because these driving variables are expected to continue to change in the future, we need to account for their current spatial and temporal variations and for how their characteristics may change in the future.

Soil-geomorphic template and spatial context. The soil-geomorphic template interacts with, and often regulates, transport vectors and environmental drivers to determine the redistribution of resources within and among spatial scales (figure 6). Both fast- and slow-moving ecological variables that change in response to environmental drivers (Carpenter and Turner 2000) result in a template of ecological properties with high spatial variation (Hamerlynck et al. 2002). Slow-moving variables include system properties that change over long time periods (centuries), such as geomorphology, parent material, topography, slope, aspect, and other relatively static soil properties. Fast-moving variables, which fluctuate widely over short time periods (hours or days to decades), include biotic properties and more dynamic soil parameters (e.g., labile soil organic matter; plant

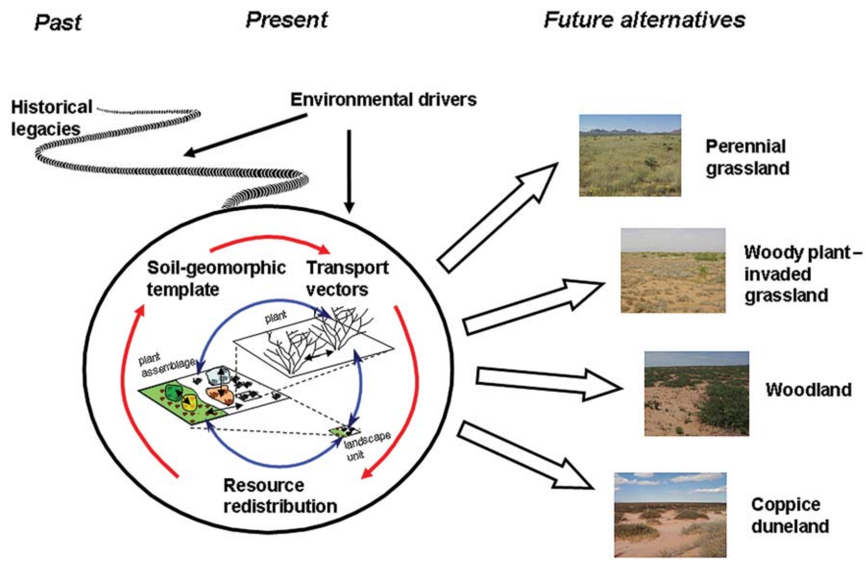

Figure 6. Interactions among five key elements connect scales of the hierarchy in our framework and lead to complex landscape dynamics. Historical legacies and environmental drivers affect critical scales of fast- and slow-moving ecological variables as well as their spatial distribution and context (soil-geomorphic template). The soil-geomorphic template interacts with horizontal and vertical transport vectors (fluvial, aeolian, animal) to influence the rate, direction, and amount of resource redistribution within and among spatial units. Cross-scale interactions generate nonlinear dynamics and threshold behavior in the reorganization of landscapes between an array of alternative grass- and woody plant–dominated states. Photographs: Jornada Experimental Range photo gallery.

species biomass, cover, and composition; density of plant, animal, and microbial species).

A key characteristic of this template is the arrangement or distribution of spatial units that influence their connectivity via transport vectors. Spatial context refers to the arrangement of similar types of interacting units and to the location of a unit with respect to other kinds of units (i.e., adjacency). The number, size, and arrangement of spatial units influence system dynamics through their interactions with transport vectors that connect spatial units, with the result that the area adjacent to or surrounding the study plot of interest can have large and significant effects on finer-scale patterns and dynamics (Ludwig et al. 1997). In addition, broadscale dynamics can be determined by the propagation of dynamics across scales. The rate and extent of these propagating events are influenced by the properties of the spatial units interacting with transport vectors, with fast- and slow-moving variables, and with environmental drivers (Peters et al. 2004a).

Transport vectors. Wind, water, and animals are dominant vectors for the movement of resources (water, nutrients) and materials (soil particles, plant litter, seeds) both within and among spatial units (figure 6). Although these vectors are often considered independently, in some cases desertification dynamics can be explained only by examining interactions among transport vectors (Breshears et al. 2003). For example, recent results show that cattle movement can be highly variable within a pasture over short time periods that are related to spatial context and redistribution of resources by transport vectors. The high densities of individual animals found near water sources and preferred plant communities in one time period follow the traditional view of cattle distribution patterns (figure 7a; Vallentine 1989, Holochek et al. 1998). However, cattle densities two weeks later show a very different pattern that cannot be explained by patterns in precipitation within the pasture (figure 7b). Movement to locations in the pasture containing normally less palatable grasses occurred after a thunderstorm upslope from the target pasture resulted in run-on of water and increased growth of those grasses. Cattle responded to this increase in forage by moving to those locations to graze. Thus, the impacts of cattle on grasses involve interactions among multiple transport vectors and spatial context. Furthermore, management decisions related to grazing animals need to account for the dynamics and transport of materials from adjacent pastures as well as for within-pasture properties and dynamics.

Resource redistribution. The redistribution of resources within and among spatial units is affected by transport vectors interacting with fast- and slow-moving variables, with environmental drivers, and with feedback mechanisms among plants, animals, and soils (figure 6). The movement of resources and materials from low to high concentrations (e.g., from a bare interspace to beneath a shrub canopy to produce an island of fertility) or vice versa (e.g., dispersal of seeds by rodents) results in a nonuniform, nonrandom distribution of materials and in high spatial variation in resources, with important consequences for desertification dynamics. For example, transfers within a spatial unit include the vertical movement of water and nutrients in the soil profile as affected by interactions among soil properties (texture, soil organic matter), roots, and microbial activity. These interactions generate feedbacks to future rooting distributions, soil structure, and microbial densities. Horizontal transfers between units include the movement of seeds, water, or nutrients from one plant to another plant.

In summary, alternative future states and landscape reorganization can result from interactions and feedbacks among the five key elements and from the propagation of effects across scales (figure 6). In many cases, multiple future states are possible, depending on interactions among past and current states of the system resulting from changes in the environmental drivers. In arid and semiarid regions, alternative states based on life form range from grasslands to savannas to shrublands and woodlands. Within each life form, alternative states are possible based on land cover and species composition as well as spatial restructuring of vegetation. This reorganization of states has feedbacks to ecological variables and transport vectors, and produces spatial and temporal variability in ecological responses as a result of threshold behavior and nonlinear dynamics. The importance of threshold behavior in producing spatial variability and nonlinear rates of change has been recognized for a variety of response variables at many scales (Groffman et al. 2006). Our framework explicitly includes threshold changes that occur as a result of cross-scale interactions that produce variation in ecosystem dynamics across landscapes.

Cross-scale interactions can refer to the ability of fine-scale processes to propagate nonlinearly and influence broader spatial extents or, alternatively, to the ability of broadscale processes or drivers to overwhelm fine-scale processes. Thresholds (i.e., discontinuous changes in a state variable) occur as the relative importance of fine- and broadscale processes changes with spatial extent and time (Peters et al. 2004a). For example, the initial expansion of woody plants involves few individuals at low densities within an herbaceous community (Goslee et al. 2003). These dynamics are often controlled by fine-scale processes, such as seed availability and competition with herbaceous plants. As the density of woody plants increases through time, the number and size of bare interspaces also increase until a threshold is reached where wind and water erosion become the dominant processes that overwhelm the importance of finer-scale processes. As the spatial extent of woody plant–dominated area increases to the regional scale, another threshold is reached where interactions between the land surface and atmosphere can become the dominant process driving changes in vegetation (Claussen et al. 1999). At this point, landscape characteristics that affect erosion, and plant life history traits that influence plant competition, are no longer important (Peters et al. 2004a). In addition, broadscale drivers, such as extended periods of extreme drought or overgrazing, can also overwhelm fine-scale processes (Yao et al. 2006).

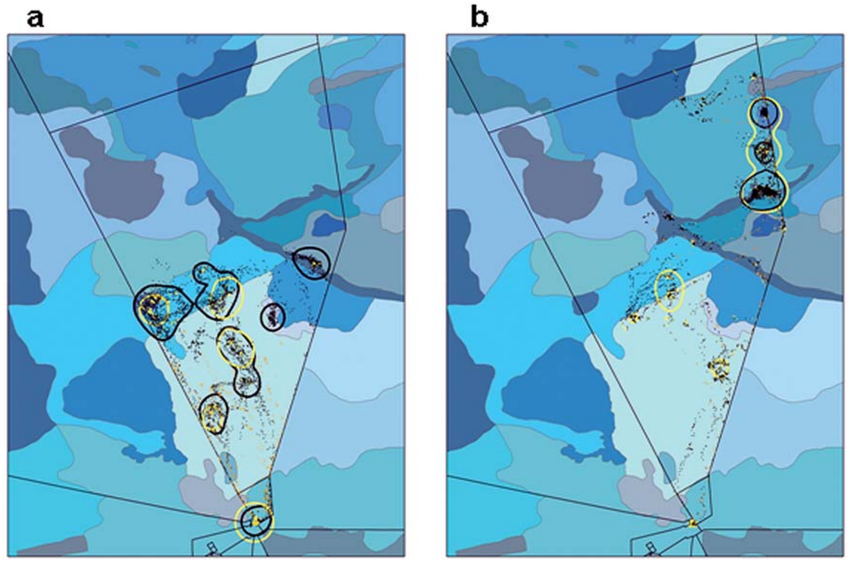

Figure 7. Position of 12 cows in one 1174-hectare pasture at the Jornada Basin, recorded at five-minute intervals. Cattle movement within a pasture can be related to spatial context and redistribution of resources from adjacent pastures. Maps show three behaviors—grazing (black), resting (yellow), and traveling (goldenrod)—at two time periods: (a) 17–20 June 2002, with no rainfall measured at the Jornada; and (b) 29 June–2 July 2002, following an isolated thunderstorm upslope (east) of the pasture. Blue polygons represent the area with 80% of the resting observations, whereas red polygons encompass 80% of the grazing observations. The only reliable source of water is in the southern part of the pasture.

New insights into current landscape dynamics

Although broadscale woody plant expansion has been well documented in the northern Chihuahuan Desert (Grover and Musick 1990), the process of woody plant expansion is poorly understood. Our framework sheds new light on the current pattern of grasslands and shrublands, and the likely trajectories of land-cover change in particular areas. At the Jornada Experimental Range, a small (1-square-kilometer) isolated area dominated by a shrub, honey mesquite (*Prosopis glandulosa*), was surrounded by perennial grasslands in 1858 (figure 8a). The presence of mesquite in this location cannot be explained by soil properties, geomorphic features, or local climate (Buffington and Herbel 1965). A plausible explanation for this mesquite-dominated area is the activity of indigenous people, the Jornada Mogollon, who existed in the region from AD 850 through 1400 and used mesquite for many purposes (Bell and Castetter 1937). The area of mesquite is located about halfway between two known Jornada Mogollon encampments (Lekson and Rorex 1980). We postulate that this isolated area of mesquite was a stopping point for these people as they moved seasonally between the San Andres Mountains and the Rio Grande.

There is evidence that this relatively small area of mesquite colonization expanded through time to influence current patterns in vegetation and soil: More than 80% of the west side of the Jornada Basin was dominated by this species by 1998 (figure 8b; Gibbens et al. 2005). Although early records do not exist, recent small-scale experiments and broadscale monitoring suggest that this change from grassland to shrubland on the west side of the Jornada Basin could have been initiated by changes in a limited area. Analyses of aerial photographs indicate that mesquite spreads from livestock trails where seeds are deposited (Laliberte et al. 2004). Thus, concentration of mesquite seeds by human activities most likely

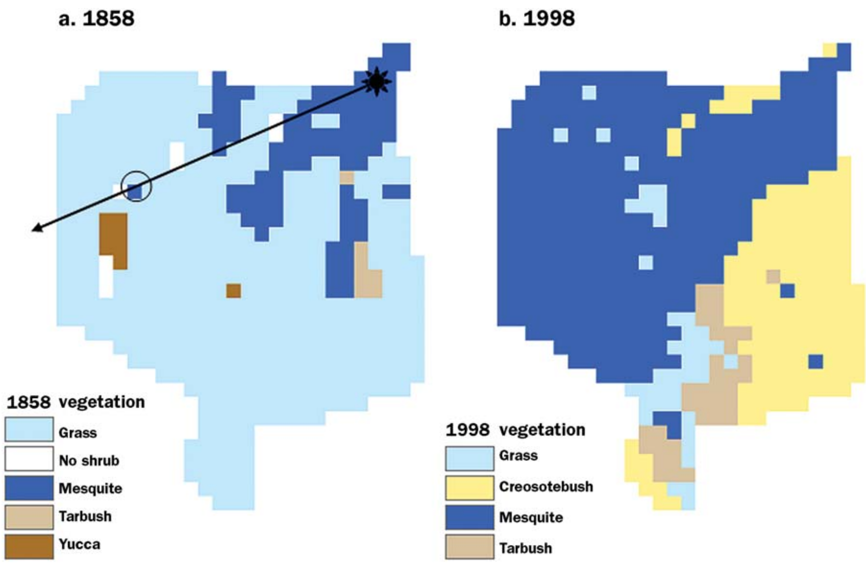

Figure 8. Vegetation maps of the Jornada Basin Agricultural Research Service–Long Term Ecological Research site illustrate the importance of historic legacies for current vegetation patterns in (a) 1858 and (b) 1998, showing the cover of perennial grasses, shrub species (tarbush, mesquite), or yucca using 1-square-kilometer grid cells. The 1858 map (modified from Buffington and Herbel 1965) shows perennial grasses as the dominant functional group. This map assumes that all areas that contained shrubs and had fair or poor grass cover were dominated by shrubs. The location of one major Jornada Mogollan encampment is highlighted with an asterisk (*); the location of a second major encampment is along the line and off the map. An isolated grid cell dominated by mesquite, located halfway between the two major encampments, is circled. (b) The 1998 map (modified from Gibbens et al. 2005) shows the western half of the Jornada dominated by mesquite.

resulted in a seed source for the spatial expansion of this species through time. Positive feedbacks between woody plants and the redistribution of resources (water, nutrients) at local scales, exacerbated by livestock overgrazing and loss of grasses, would have allowed woody plant survival and dominance after establishment (Schlesinger et al. 1990). Furthermore, bare areas created around mesquite plants as a result of local resource redistribution and competition with subdominant plants (Gibbens et al. 1983, Schlesinger et al. 1990) can aggregate to a point where soil surface stability is compromised at broader scales. When this occurs, soil is transported by wind to adjacent areas, causing the burial and abrasion of the remaining perennial grasses (Okin and Gillette 2001). Erosional and depositional processes favor taller woody plants over shorter grasses, thus promoting continued woody plant expansion. In some cases, this expansion can lead to coppice dunes. More recently, disturbance and seed dispersal associated with the movement of Europeans and their livestock along the Camino Real, starting in the 1500s and lasting more than 300 years, left a legacy of increased mesquite density and cover.

We postulate that the nonlinear rate of spread and increase in spatial extent exhibited three thresholds as the dominant process driving these dynamics changed through time and across space (Peters et al. 2004a). Cross-scale interactions resulted in fine-scale processes dominating initially and cascading to influence larger spatial extents. Because this particular sequence of mechanisms is likely to be constrained to deep, sandy soils where wind erosion is prevalent (e.g., much of the west side of the Jornada), a broad-scale spatial limit is imposed on these dynamics. Thus, the expansion of mesquite to the east was limited by soil properties that reflect, at least in part, geomorphology associated with the historic location of the Rio Grande (Mack et al. 1996, Monger 2006).

Forecasting future dynamics

Landscapes in arid and semiarid regions have experienced dramatic changes as human population has increased, both within the western United States and globally in parts of Asia, Africa, Central and South America, and Australia (Reynolds and Stafford Smith 2002). These changes are expected to continue in the future. Although our framework was developed for ecosystems without a major urban influence, clearly future landscapes will increasingly consist of a mosaic of interconnected urban, suburban, and exurban areas interspersed with ecosystems of varying degrees of management. Although research sites have typically been considered isolated from adjacent urban areas, encroachment from cities is decreasing these sites' distance from direct human interactions and increasing connections. Forecasting alternative states within each type of land cover and land use will require an explicit consideration of both the ecological processes described earlier and the human cultural processes driving patterns of urban and suburban development. An examination of processes occurring at individual or multiple scales is insufficient to explain dynamics when processes interact across scales and when thresholds are crossed (Peters et al. 2004a, Groffman et al. 2006). New experiments will be needed that focus on cross-scale interactions, the integration of ecological and human systems, and the importance of spatial context. In addition, it will be critical to integrate short- and long-term experiments and observations with simulation models, geographic information systems, and remote sensing tools to forecast future dynamics. Nonlinearities and thresholds at broader scales can be incorporated by linking landscape models with atmospheric models. Because many of these interactions are nonlinear, an explicit consideration of uncertainty will be needed (Peterson et al. 2003).

Our framework can also be used in management decisions to forecast recovery of desertified landscapes. Land managers in arid and semiarid regions are confronted with a complex mosaic of soils and vegetation within the context of spatially and temporally variable weather. However, this natural variability across a landscape and through time can be used to our advantage (Landres et al. 1999). Human and financial resource limitations frequently constrain active management to a small fraction of this mosaic. Optimizing the impact of these limited resources depends on identifying (a) areas with a high probability of response and that are likely to experience threshold behavior, (b) key processes that must be manipulated either to maintain current conditions or to reverse a current undesirable trend, and (c) early warning indicators that can be used to monitor changes in critical processes (Bestelmeyer et al. 2003). An understanding of our landscape linkage framework can increase the ability of land managers to focus on the most dynamic areas and on those areas where nonlinear dynamics are likely to occur (Illius and O'Connor 1999, Holmgren and Scheffer 2001). For example, remediation treatments are more likely to be successful if effects of spatial context and distribution of plants are explicitly considered along with vegetation type and edaphic properties (Rango et al. 2002). In addition, variation in environmental drivers can be used opportunistically to target periods with high rainfall that can be used to initiate recovery of grasses.

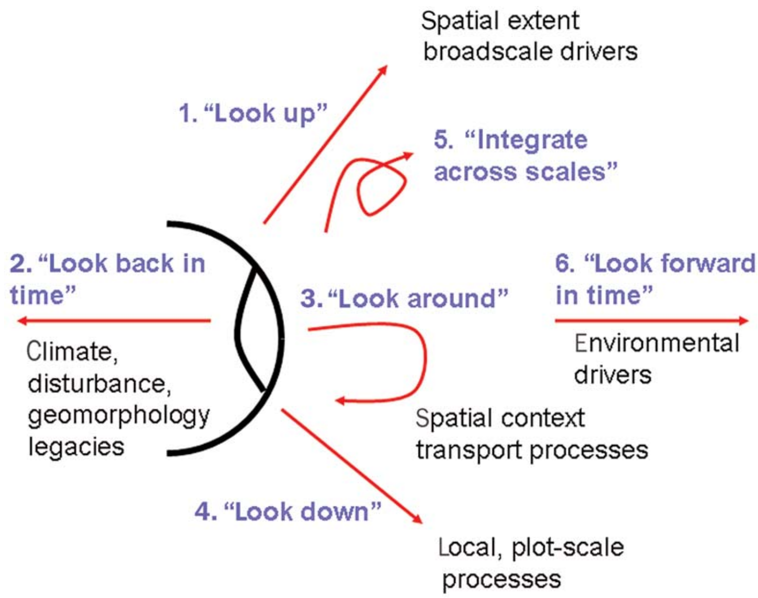

Figure 9. A six-step operational scheme can be used to disentangle landscape complexity. The first step is to "look up" and determine the broadscale variation in environmental drivers and spatial extent of connectivity associated with these drivers. The second step is to "look back" in time and determine the role of historical legacies in determining current patterns. The third step is to "look around" to determine the spatial properties of the units (arrangement, context, adjacency) and transport vectors (wind, water, animals) that connect spatial units across the landscape. The fourth step is to "look down" and determine the key local or fine-scale properties (fast- and slow-moving variables) and processes (plant, animal, soil) that influence patterns and dynamics. The fifth step is to integrate the information from each spatial scale to determine the key drivers, processes, and properties influencing spatial and temporal variations in landscape structure and dynamics. The final step is to "look forward" in time to the effects of changing environmental drivers and feedbacks from current landscape structure to future dynamics.

Disentangling landscape complexity: Operational scheme

Six steps can be used to disentangle complex landscapes and understand the key processes determining spatial and temporal variations (figure 9). The first step is to "look up" and determine the broadscale variation in environmental drivers and spatial extent of connectivity associated with these drivers. The second step is to "look back" in time and determine the role of historic legacies in determining current patterns. Researchers and managers need to know what happened, when, and where the event occurred. They also need to know how broadscale environmental drivers interact with historic legacies to generate current patterns. The third step is to "look around" to determine the spatial properties of the units (arrangement, context, adjacency) and transport vectors (wind, water, animals) that connect spatial units across the landscape. The fourth step is to "look down" and determine the key local or fine-scale properties (fast- and slow-moving variables) and processes (plant, animal, soil) that influence patterns and dynamics. The fifth step is to integrate the information from each spatial scale to determine the key drivers, processes, and properties influencing spatial and temporal variations in landscape structure and dynamics. The final step is to "look forward" in time to the effects of changing environmental drivers and feedbacks, from current landscape structure to future dynamics.

In some cases, spatial context and spatial processes are negligible, and only broadscale environmental drivers and local processes are sufficient to explain patterns and dynamics (see Schlesinger et al. 1990). Under these conditions, results obtained from fine-scale studies can be linearly extrapolated to the entire spatial extent. In other cases, spatial context interacting with transport vectors overwhelms the importance of local processes or broadscale drivers to generate nonlinear dynamics that cannot be explained by results obtained from fine-scale studies alone. Because explicitly accounting for spatial context, transport vectors, and historic legacies can be time-consuming and labor intensive, and can propagate errors in uncertainty associated with measuring additional variables (Peters et al. 2004b), researchers and managers need to identify the parts of the landscape and conditions under which local processes govern system behavior. Similarly, we need to identify the locations and conditions where it is necessary to measure spatial context, transport vectors, and time lag effects of historic legacies. Approaches such as our six-step operational scheme may be used to help disentangle the relative importance of key processes, vectors, and drivers in generating and maintaining complex landscapes.

Summary

Decades of research on desertification have provided a wealth of information on many aspects of arid and semiarid systems. However, researchers have been unsuccessful in developing sustainable strategies to combat desertification, and land managers' ability to mitigate and reverse degradation remains limited. High spatial and temporal variations in ecosystem patterns and dynamics across multiple scales cannot be explained using current conceptual frameworks. We developed an interactive landscape linkage framework that includes a spatial hierarchy and a process framework to connect these scales. Our perspective provides new insights into previously unexplained patterns and dynamics, improves researchers' ability to forecast future dynamics, and guides management decisions by selecting locations on the landscape that are most likely to respond to manipulations (Peters et al. 2006). At finer scales of resolution, the framework articulates a process-based understanding. At broad scales, it explains existing patterns and dynamics. At intermediate scales, it may increase the efficiency of resource management activities by matching actions with appropriate locations.

Our landscape linkage framework has counterparts in other ecosystems (Seastedt et al. 2004), although the dramatic, persistent, and nonlinear vegetation state changes associated with desertification add complexity that may not need to be addressed in other systems. Because the propagation of woody plants across landscapes shares processes and dynamics with other catastrophic events (Peters et al. 2004a), our framework has relevance to other types of systems where spatial and temporal nonlinearities are important. In addition, our focus on spatial heterogeneity, its modifications by environmental drivers, and its relationship to fluxes in resources is relevant to central questions in landscape ecology (Turner 2005).

It is becoming increasingly recognized that the full complexity and connectivity of landscapes is important, as human populations continue to rise and as globalization increases the frequency and magnitude of connections across a range of scales. Research sites are often viewed as isolated from the surrounding human-dominated landscapes when, in reality, these areas are becoming increasingly connected and dependent on each other for materials and information flow. It is only by integrating all aspects of landscapes through space and time that we can understand and disentangle these intricacies.

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References cited

Archer S. 1994. Woody plant encroachment into Southwestern grasslands and savannas: Rates, patterns and proximate causes. Pages 13–69 in Vavra M, Laycock WA, Pieper RD, eds. Ecological Implications of Livestock Herbivory in the West. Denver (CO): Society for Range Management.

Bell WH, Castetter EF. 1937. Ethnobiological studies in the American Southwest, V: The utilization of mesquite and screwbean by the aborigines in the American Southwest. University of New Mexico Bulletin, Biological Series 5: 1–55.

Bestelmeyer BT, Brown JR, Havstad KM, Chavez G, Alexander R, Herrick JE. 2003. Development and use of state-and-transition models for rangelands. Journal of Range Management 56: 114–126.

Breshears DD, Barnes FJ. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: A unified conceptual model. Landscape Ecology 14: 465–478.

Breshears DD, Whicker JJ, Johansen MP, Pinder JE. 2003. Wind and water erosion and transport in semi-arid shrubland, grassland and forest ecosystems: Quantifying dominance of horizontal wind-driven transport. Earth Surface Processes and Landforms 28: 1189–1209.

Buffington LC, Herbel CH. 1965. Vegetational change on a semidesert grassland range from 1858 to 1963. Ecological Monographs 35: 139–164.

Carpenter SR, Turner MG. 2000. Hares and tortoises: Interactions of fast and slow variables in ecosystems. Ecosystems 3: 495–497.

Claussen M, Kubatzki C, Brovkin V, Ganopolski A, Hoelzmann P, Pachur HJ. 1999. Simulation of an abrupt change in Saharan vegetation at the end of the mid-Holocene. Geophysical Research Letters 24: 2037–2040.

Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A. 2003. The importance of land-use legacies to ecology and conservation. BioScience 53: 77–88.

Gibbens RP, Tromble J, Hennessy JT, Cardenas M. 1983. Soil movement in mesquite dunelands and former grasslands of southern New Mexico from 1933 to 1980. Journal of Range Management 36: 145–148.

Gibbens RP, McNeely RP, Havstad KM, Beck RF, Nolen B. 2005. Vegetation change in the Jornada Basin from 1858 to 1998. Journal of Arid Environments 61: 651–668.

Goslee SC, Havstad KM, Peters DPC, Rango A, Schlesinger WH. 2003. High-resolution images reveal rate and pattern of shrub encroachment over six decades in New Mexico, U.S.A. Journal of Arid Environments 54: 755–767.

Groffman PM, et al. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems 9: 1–13.

Grover HD, Musick HB. 1990. Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American Southwest. Climatic Change 17: 305–330.

Hamerlynck EP, McAuliffe JR, McDonald EV, Smith SD. 2002. Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. Ecology 83: 768–779.

Havstad KM, Schlesinger WH, Huenneke LF, eds. 2006. Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin LTER. Oxford (United Kingdom): Oxford University Press. Forthcoming.

Herrick JE, Havstad KM, Rango A. 2006. Remediation research in the Jornada Basin: Past and future. In Havstad KM, Schlesinger WH, Huenneke LF, eds. Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin LTER. Oxford (United Kingdom): Oxford University Press. Forthcoming.

Holmgren M, Scheffer M. 2001. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. Ecosystems 4: 151–159.

Holochek JL, Pieper RD, Herbel CH. 1998. Range Management: Principles and Practices. Upper Saddle River (NJ): Prentice Hall.

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.

Illius AW, O'Connor TG. 1999. On the relevance of non-equilibrium concepts to arid and semi-arid grazing systems. Ecological Applications 9: 798–813.

Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418: 623–626.

Knapp PA, Soulé PT. 1998. Recent *Juniperus occidentalis* (Western juniper) expansion on a protected site in central Oregon. Global Change Biology 4: 347–357.

Laliberte AS, Rango A, Havstad KM, Paris JK, Beck RF, McNeely R, Gonzalez AL. 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. Remote Sensing of Environment 93: 198–210.

Landres PB, Morgan P, Swanson FJ. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179–1188.

Le Houérou HN, Bingham RL, Skerbek W. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. Journal of Arid Environments 15: 1–18.

Lekson SH, Rorex AS. 1980. The Cottonwood Spring and Indian Tank sites, Doña Ana County, New Mexico. The Artifact 33: 9–36.

Ludwig JA, Tongway D, Freudenberger D, Noble J, Hodgkinson K, eds. 1997. Landscape Ecology Function and Management: Principles from Australia's Rangelands. Melbourne (Australia): CSIRO.

Lyford ME, Jackson ST, Betancourt JL, Gray ST. 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. Ecological Monographs 73: 567–583.

Mack GH, McIntosh WC, Leeder MR, Monger HC. 1996. Plio-Pleistocene pumice floods in the ancestral Rio Grande, southern Rio Grande rift, USA. Sedimentary Geology 103: 1–8.

Masters RA, Sheley RL. 2001. Principles and practices for managing rangeland invasive plants. Journal of Range Management 54: 502–517.

Monger HC. 2006. Soil development of the Jornada Basin LTER site. In Havstad KM, Schlesinger WH, Huenneke LF, eds. Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin LTER. Oxford (United Kingdom): Oxford University Press. Forthcoming.

Monger HC, Bestelmeyer BT. 2006. The soil-geomorphic template and biotic change in deserts. Journal of Arid Environments 65: 207–218.

Okin GS, Gillette DA. 2001. Distribution of vegetation in wind-dominated landscapes: Implications for wind erosion modeling and landscape processes. Journal of Geophysical Research 106: 9673–9684.

O'Neill RV, DeAngelis DL, Waide JB, Allen TFH. 1986. A Hierarchical Concept of Ecosystems. Princeton (NJ): Princeton University Press.

Peters DPC, Pielke RA, Bestelmeyer BT, Allen CD, Munson-McGee S, Havstad KM. 2004a. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. Proceedings of the National Academy of Sciences 101: 15130–15135.

Peters DPC, Urban DL, Gardner RH, Breshears DD, Herrick JE. 2004b. Strategies for ecological extrapolation. Oikos 106: 627–636.

Peters DPC, Schlesinger WH, Herrick JE, Huenneke LF, Havstad KM. 2006. Future directions in Jornada research: Developing and applying an interactive landscape model to solve old and new problems. In Havstad KM, Schlesinger WH, Huenneke LF, eds. Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin LTER. Oxford (United Kingdom): Oxford University Press. Forthcoming.

Peterson GD, Carpenter SR, Brock WA. 2003. Uncertainty and the management of multistate ecosystems: An apparently rational route to collapse. Ecology 84: 1403–1411.

Rango A, Goslee S, Herrick JE, Chopping M, Havstad KM, Huenneke LF, Gibbens R, Beck R, McNeely R. 2002. Remote sensing documentation of historic rangeland remediation treatments in southern New Mexico. Journal of Arid Environments 50: 549–572.

Reynolds JF, Stafford Smith DM. 2002. Do humans cause deserts? Pages 1–21 in Reynolds JF, Stafford Smith DM, eds. Global Desertification: Do Humans Cause Deserts? Berlin: Dahlem University Press.

Reynolds JF, Wu J. 1999. Do landscape structural and functional units exist? Pages 273–298 in Tenhunen JD, Kabat P, eds. Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes. Chichester (United Kingdom): Wiley.

Ricketts TR, Loucks CJ, Dinerstein E, Olson DM. 1999. Terrestrial Ecoregions of North America: A Conservation Assessment. Washington (DC): Island Press.

Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305: 1926–1929.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. Science 247: 1043–1048.

Schmutz EM, Smith El, Cox ML, Klemmedson JO, Norris JJ, Fierro LC. 1992. Desert grassland. Pages 337–362 in Coupland RT, ed. Natural Grasslands, Ecosystems of the World, vol. 8A. Amsterdam: Elsevier Scientific Press.

Seastedt TR, Bowman WD, Caine TN, McKnight D, Townsend A, Williams MW. 2004. The landscape continuum: A model for high-elevation ecosystems. BioScience 54: 111–121.

Tongway DJ, Valentin C, Seghieri J, eds. 2001. Banded Vegetation Patterning in Arid and Semiarid Environments. Berlin: Springer-Verlag.

Turner M. 2005. Landscape ecology in North America: Past, present, and future. Ecology 86: 1967–1974.

Vallentine JF. 1989. Range Development and Improvements. 3rd ed. New York: Academic Press.

Van Auken OW. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31: 197–215.

van de Koppel J, et al. 2002. Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. American Naturalist 159: 209–218.

Van Devender TR. 1995. Desert grassland history. Pages 68–99 in McClaran MP, Van Devender TR, eds. The Desert Grassland. Tucson: University of Arizona Press.

Wainwright JA, Parsons AJ, Schlesinger WH, Abrahams AD. 2002. Hydrology–vegetation interactions in areas of discontinuous flow on a semi-arid bajada, southern New Mexico. Journal of Arid Environments 51: 219–258.

Walter H. 1971. Ecology of Tropical and Subtropical Vegetation. Edinburgh (Scotland): Oliver and Boyd.

Wang G, Schimel DS. 2003. Climate change, climate modes, and climate impacts. Annual Review of Environment Resources 28: 1–28.

Weaver JE. 1958. Classification of root systems of forbs of grassland and a consideration of their significance. Ecology 39: 393–401.

Weaver JE, Darland RW. 1949. Soil–root relationships of certain native grasses in various soil types. Ecological Monographs 19: 303–338.

Wilcox BP, Breshears DD, Allen CD. 2003. Ecohydrology of a resource-conserving semiarid woodland: Effects of scale and disturbance. Ecological Monographs 73: 223–239.

Wright RA. 1982. Aspects of desertification in *Prosopis* dunelands of southern New Mexico, U.S.A. Journal of Arid Environments 5: 277–284.

Yao J, Peters DPC, Havstad KM, Gibbens RP, Herrick JE. 2006. Multi-scale factors and long-term responses of Chihuahuan Desert grasses to drought. Landscape Ecology. Forthcoming.

York JC, Dick-Peddie WA. 1969. Vegetation changes in southern New Mexico during the past hundred years. Pages 157–166 in McGinnies WG, Goldman BJ, eds. Arid Lands in Perspective. Tucson: University of Arizona Press.