A multi-scale classification of vegetation dynamics in arid lands: What is the right scale for models, monitoring, and restoration? [☆]

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Abstract

Measurements of vegetation and soil dynamics used to anticipate (or reverse) catastrophic transitions in arid and semi-arid rangelands are often difficult to interpret. This situation is due, in part, to a lack of empirically based conceptual models that incorporate the effects of multiple processes, scale, spatio-temporal pattern, and soils. Using observations of multi-temporal data from the Chihuahuan Desert, we describe a new approach to classifying vegetation dynamics based on multiple scales of vegetation and soil pattern as well as cross-scale interactions. We propose the existence of six types of mechanisms driving vegetation change including (1) stability, (2) size oscillation of plants, (3) loss and reestablishment of plants within functional groups, (4) loss of one plant functional group and replacement by another, (5) spatial reorganization of vegetation patches, and (6) cascading transitions that spread from small to broad scales. We provide evidence for the existence of these mechanisms, the species involved, and the geomorphic components on which they are observed in the Chihuahuan Desert. These mechanisms highlight the kinds of multi-scale observations that are needed to detect or interpret change and emphasize the importance of soil surface properties for interpreting vegetation change. The classification is potentially general across arid and

semi-arid ecosystems and links spatial and temporal patterns in vegetation with ecological and geomorphic processes, monitoring, and restoration strategies.

1. Introduction

Catastrophic ecosystem transitions have been documented in several arid and semi-arid regions of the world (Scheffer et al., 2001; Walker, 2002; Gibbens et al., 2005). These transitions often involve the loss of perennial grasses and their replacement with shrubs and/or bare ground (Rietkerk et al., 1997). Such transitions are often governed by shifting feedbacks that create accelerating rates of change (thresholds) that cannot be reversed by lowering the magnitude of an external driver such as grazing pressure (i.e. hysteresis; Rietkerk et al., 2004). These processes occur across a range of spatial and temporal scales, from local soil degradation (Herrick et al., 2002) to water and sediment redistribution (Ludwig et al., 1997) to land–atmosphere feedbacks (Pielke et al., 1997). Transitions are often accompanied by persistent losses of soil fertility, plant community variability, biodiversity, and livestock production. Consequently, a broad range of public and private natural resource managers are interested in predicting, halting, and reversing vegetation transitions.

In considering the translation of research on vegetation transitions into conceptual and management tools, it has become clear that we do not fully understand the drivers that lead to spatio-temporal variation in landscape patterns (Peters and Havstad, 2006). Furthermore, we recognize that general models of the transition process cannot represent the variation observed within all land areas (Bestelmeyer et al., in press). Despite some general similarities (e.g. loss of grass), the patterns and causes of transitions vary widely, depending on soils, climate, and plant associations. Although variation in local properties of soils and climate have been recognized in scientific and management applications (Dyksterhuis, 1949; McAuliffe, 2003; Pringle and Tinley, 2003), the consequences of pattern–process relationships emphasized in landscape ecology (e.g. Watt, 1947; Ludwig et al., 1997) are only weakly linked to management approaches in many arid systems.

Information about the transition processes occurring in different soils is being summarized for land managers in state-and-transition models (Westoby et al., 1989). Models developed in the United States by the Natural Resources Conservation Service (NRCS) provide a simple description of alternative vegetation states as well as the transition drivers and feedbacks that move ecosystems between states (Stringham et al., 2003). These models are embedded within Ecological Site Descriptions that specify the different biophysical characteristics of land units derived from soil maps of the National Cooperative Soil Survey. The characteristics of the states and transition drivers described in current models reflect the variety of processes at work in different ecological sites (Bestelmeyer et al., 2004). Nonetheless,

these simplified depictions continue to be limited by their inability to represent the role of scale, spatial and temporal pattern, and multiple scales and types of processes.

Connecting state-and-transition models to on-the-ground activities such as assessment, monitoring, and management decisions will require attention to spatial and temporal patterns (Ares et al., 2003; Hobbs and Norton, 2004). The distinct processes driving vegetation change can be detected only by measuring particular parameters at specified scales. If measurements are taken at too fine a scale relative to the process driving change, then the data may indicate a trend unrelated or opposite to that observed at broader, management-relevant scales (e.g. Wiens, 1989) or simply indicate rapid transition with little warning or explanation (Peters et al., 2004). Alternatively, measurements gathered at a scale that is too coarse will not register significant changes in vegetation until it is too late to respond with a management adjustment. For these reasons, it is imperative that we match assessment and monitoring technologies (e.g. line-point intercept transects, remote sensing) and stratification strategies to the processes and patterns driving change in particular settings.

The prediction of vegetation transitions at broad scales requires an improved understanding of vegetation dynamics across a range of scales as well as an understanding of the role of spatial connections in vegetation dynamics (Peters and Havstad, 2006). To address this need, we propose a preliminary classification of vegetation transition patterns that have been derived from the literature and a repeat photography database from south-western New Mexico, USA. Our objective is to provide easily recognized distinctions of the mechanisms driving vegetation and soil behavior to aid in communication among stakeholders. We provide empirical examples of each of the mechanisms, identify geomorphic components on which they occur, and discuss implications of the mechanisms for development of state-and-transition models and monitoring strategies. Several of these mechanisms emphasize the need for information on soil-surface dynamics to refine inter-pretations of pattern (Tugel et al., 2005). Finally, we test for non-random associations of these vegetation dynamics mechanisms with particular geomorphic components.

2. Methods

2.1. Study area

Our observations are from the Chihuahuan Desert of south-western NM, USA. The region examined encompasses about $21,100 \, km^2$ of public land. Dominant soil suborders (Soil Survey Staff, 2003) include Argids (on hillslopes), Calcids (piedmont slopes and basin floors), and Orthents and Psamments (basin floors and valley terrace soils derived from recently deposited or exhumed sediments). Land cover/vegetation types include Apacherian–Chihuahuan Semi-Desert Grassland, Chihua-huan Sandy Plains Semi-Desert Grassland and Steppe, Chihuahuan–Sonoran Desert

Bottomland and Swale Grassland, and several desert scrub types (see Comer et al., 2003). Elevations in the areas examined range from 1202 to 1698 m. Mean annual rainfall from 1980 to 1997 ranged from 200 to 350 mm. Cattle grazing, supported largely by long-lived perennial grasses, has been a spatially dominant land use in this region since at least the late 1800s (Fredrickson et al., 1998).

2.2. Repeat photography data

We summarized observations from trend plot photograph sets from the United States Bureau of Land Management (BLM) allotment monitoring program for the Las Cruces, NM Field Office. In addition to their high number, broad spatial extent, and long duration (up to 36 years), these photographs permit observations of soil surface conditions and changes in individual plants. Trend plot photograph locations were selected by BLM personnel according to the 'key area concept' (Bureau of Land Management, 1996), in which the number and location of plots are chosen to (1) represent the variety of dominant ecological sites present on a grazing allotment and (2) adequately reflect management (usually grazing) impacts on the management unit (i.e. 0.8–1.6 km from livestock watering points). Trend plots were always placed in patches of locally dominant perennial grass species, and were marked by steel angle iron at two corners, over which a steel frame (91.4 × 91.4 cm) was placed. A third steel post identified where plot photographs were taken. At each plot, two photographs (one encompassing the trend plot frame and another of the landscape) were taken during each visit by BLM personnel. The plots we examined were established by BLM personnel between 1968 and 1986. When initially established, BLM personnel mapped and identified perennial plant species occurring within each plot. Plots were re-photographed no more than once per year between establishment year and 2003 (from 6 to 26 times), usually between October and December. Many plots were irregularly visited by BLM personnel due to periodic budget limitations.

We revisited and photographed 123 of these plots between March and December 2003, matching the orientation and field of view of previous photographs. We identified and mapped the plant species in each plot and identified species visible in the landscape photographs. To characterize the soil environment of each plot, we excavated a soil pit (50 cm wide × 80 cm deep, where restrictive horizons permitted) near each plot and characterized the soil pedon to soil taxonomic unit and series (following Soil Survey Staff, 2003). Assignments were based on estimated soil texture, coarse fragment volume, calcium carbonate content determined using an Eijkelkamp calcimeter, and in situ observations of soil structure, clay illuviation, carbonate accumulation, and horizon development. Each series of photographs was examined and the dominant plant species and soil surface conditions were used to identify the vegetation dynamics mechanisms following Table 1. In addition, we used repeat photography associated with the Desert Soil-Geomorphology Project (DSP; Gile et al., 2003) to detect and illustrate some of the dynamics reported here.

Table 1

Mechanisms of vegetation dynamics (bold italics) and their variants (indented) recognized in this study

Class	Criteria
Stability	Minimal change in size/cover or spatial position of plants over the time series.
Size oscillation	
Full size oscillation	Both reduction and growth of canopy cover observed in the series. At least some of a plant's initial ramets maintain their spatial position over a time series, and initial ramets are the source for vegetative colonization of formerly or newly occupied areas.
Growth or decline	Only one trend, either increase or decrease in plant canopy cover observed (e.g., a partial oscillation due to insufficient time).
Loss–reestablishment	
Full loss–reestablishment	Death of individuals within a species or functional group is followed by or coupled with colonization by individuals of the *same* species or functional group in distinct spatial positions.
Establishment	New propagules of existing species/functional groups appear in a field of view devoid of grasses, presumably due to colonization by seed or perhaps stolon for certain species.
Death (potential reestablishment)	Plants die with no recruitment observed. This may be loss–reestablishment or loss–replacement pattern, but if there is no evidence of soil degradation or replacement, then loss–reestablishment is assumed.
Loss–replacement	
Full loss–replacement	Death of individuals within a species or functional group that is followed by/coupled with colonization by individuals of a *different* functional group.
Death (little potential for reestablishment)	Plants die with no recruitment. This may be loss–reestablishment or loss–replacement pattern. If there is evidence of soil degradation (i.e., erosion), then loss–replacement assumed.
Patch reorganization	Death of individuals within a species or functional group that is coupled with colonization by individuals of the same or different species or functional group in other patches (i.e., coupled dynamics occur within an area $> 4 \ m^2$). The coupling should indicate redistribution of resources. Usually detectable only with time sequences of landscape or aerial photos.
Cascading transition	Death of individuals appears to be due to sand deposition from adjacent sites. Context indicating a cascade is apparent in aerial photographs or space-based imagery.

These criteria were used to assign repeat photographic or other data series to mechanisms (see Fig. 1).

3. Results

Based on BLM and DSP repeat photography and literature review, we identified and described six mechanisms of vegetation dynamics. The mechanisms include (1) stability, (2) size oscillation of perennial grasses, (3) loss and reestablishment of

grasses, (4) persistent loss of grasses with soil degradation and/or replacement by shrubs, (5) spatial reorganization of grass/shrub patches, and (6) cascading grassland–shrubland transitions that spread from small to broad scales (Table 1; Fig. 1). The temporal scale of the dynamics we classified ranged from approximately 20 to 40 years, although these dynamics may be expressed over shorter or longer intervals depending on a host of site-specific factors including land use and climatic events. Although our examples focus on perennial grasses, the concepts could be extended to other life-forms. Many details that we do not specifically address, such as plant life history and livestock behavior (see Westoby, 1980), are important to consider in explaining these dynamics.

3.1. Stability

This type denotes minimal change in size, position, or composition of plants observed over a time period. Stability may reflect an insufficient period of time to observe dynamics or other factors that constrain the growth or establishment of plants but do not cause plant mortality. Post-degradation mesquite (*Prosopis glandulosa*) coppice dunes often fall within this category because once mature, mesquite plants grow very slowly but are long-lived. Burrograss (*Scleropogon brevifolius*) patches persisting on calcareous silt loam soils (fine-silty, Ustic Haplocalcid; Reagan series) also exhibit this pattern (Fig. 2a and b). Burrograss stability may occur because infiltration rates are very low (constraining grass growth) and burrograss is drought resistant and often unpalatable (limiting grass mortality). Like mesquite, burrograss dominance is often considered to reflect a stable, degraded state on soils formerly dominated by more palatable grasses (Devine et al., 1998).

3.2. Size oscillation

This mechanism of vegetation dynamics involves large fluctuations in the canopy (e.g. from 5% to 30%) and basal cover of grasses, likely due to grazing and/or drought, without death of entire plants (Fig. 1a). Once the magnitude of these local drivers is lowered, canopy cover recovers rapidly (see Herbel and Gibbens, 1996). Grass basal cover may increase more slowly than canopy cover through tillering and spread of rhizomes or stolons. Invasion by shrubs or exotics does not occur with rainfall pulses, perhaps because surviving grass plants are able to rapidly monopolize resources and space (Mauchamp et al., 1993) or because the soil environment is not conducive to shrub establishment. Shrub propagule limitation, however, is not likely to be a constraint in the environments we examined. Soil degradation that would limit grass recruitment does not occur because the soil and landscape position impart low erodibility. Thus, this type of dynamics results in minimal turnover in species composition and is characterized as highly resilient behavior at the individual plant level. System resilience in this case is contingent on plant survival and vegetative reproduction. Plant location exhibits high spatial fidelity over time. This is a fine-scale mechanism operating at the scale of individual grass tussocks that can produce a continuous pattern over tens of hectares.
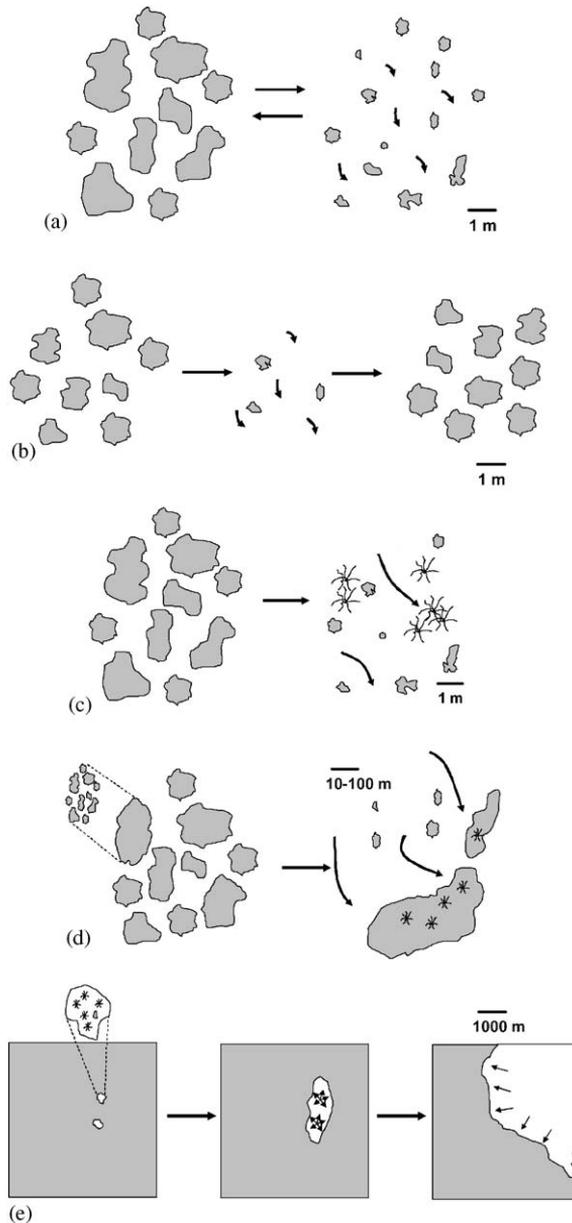
Fig. 1. A pictorial classification of Chihuahuan Desert vegetation dynamics into five of the six mechanisms (excluding stability), including (a) size oscillation of grasses, (b) loss and reestablishment of grasses, (c) loss of grasses with replacement by shrubs, (d) spatial reorganization of grass/shrub patches, and (e) cascading grass–shrub transitions that spread from small to broad scales. The grey areas represent perennial grass tussocks or patches composed of tussocks. Asterisk-shaped figures represent shrubs. Length of curved arrows indicates magnitude of the distance over which water-borne sediment may be translocated. Horizontal arrows show direction of patch change over time.
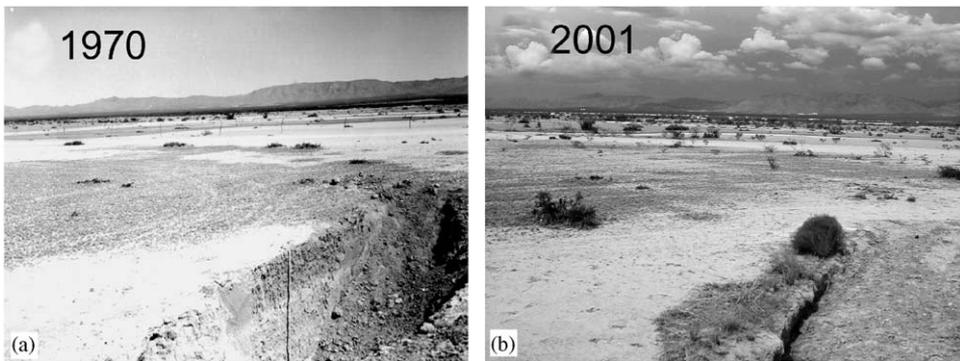
Fig. 2. Stability of a burrograss patch adjacent to a DSP soil pit (60-17) on Reagan clay loam. Note that grass in some areas of the patch around the pit has disappeared, but areas further away appear similar in 1970 and 2001. Colonization may have occurred in the background, so there may be similarities to the 'patch reorganization' type of change. Shrubs in the foreground are crucifixion thorn (*Koeberlinia spinosa*).

Size oscillation has been observed in many communities featuring black grama (*Bouteloua eriopoda*), tobosa (*Pleuraphis mutica*), and blue grama (*Bouteloua gracilis*) grasses. Perhaps the most dramatic examples are from tobosa-dominated communities in basin floor positions on loamy to silty or clayey soils (e.g. fine-silty Ustic Haplocalcid; Reagan series; Fig. 3). Resilience is common in these communities, but once tobosa plants are completely lost, the reliance of this species on vegetative reproduction rather than seed production leads to persistent absence (see Section 3.4; Campbell, 1931; Brown and Coe, 1951). Size oscillation is also common in blue grama communities on hills with lithic and/or clayey-skeletal Argids. Few long-term spatially explicit datasets exist that could be used to test for size oscillation. Detailed vegetation mapping efforts (e.g. Wondzell and Ludwig, 1995) would be required.

3.3. Loss–reestablishment

Like size oscillation, this mechanism features large fluctuations in canopy and basal cover of perennial grasses without apparent soil degradation (Fig. 1b). In this case, however, individual plants completely die. In some cases, all individuals of a species may die over broad areas. Reestablishment occurs primarily by the recruitment of individuals from the local seed pool or from seeds transported from elsewhere. Thus, system resilience is imparted not by the tolerances of individual plants but by the ability to rapidly establish from seed and by dispersal. Turnover in species composition of grasses may be high. Although shrubs may be present in these systems, they do not appear to spread and their presence does not seem to inhibit grass reestablishment.

Loss–reestablishment has been observed on deep loamy sand/sandy soils (coarse-loamy Petronodic Haplocalcids; Typic Torripsamments) in which dropseed species (*Sporobolus flexuosus, cryptandrus,* and *contractus*) rapidly reestablish with increases in rainfall (Herbel and Gibbens, 1996) or changes in its timing. In contrast to the
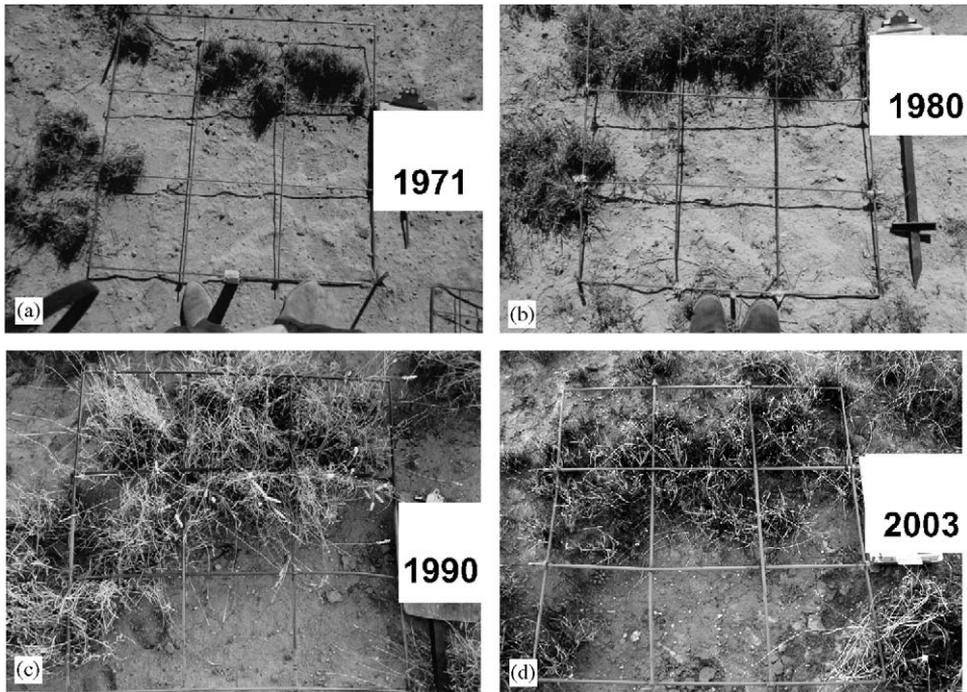
Fig. 3. Oscillation pattern of tobosa on Reagan silty clay loam, Dona Ana County, NM. Note also the recovery event in the lower right corner of the images, indicating that what might be regarded as litter is in fact a living plant.

tobosa example cited above, this pattern may be facilitated by the apparent ease with which dropseeds can establish from seed (Herbel et al., 1972). This pattern may have occurred over longer time scales (i.e. 15–40 years) in other studies involving species such as bush muhly (*Muhlenbergia porteri*), black grama, sideoats grama (*Bouteloua curtipendula*), and cool season grasses (Ludwig et al., 2000; Valone et al., 2002). Distinguishing loss–reestablishment patterns from size oscillation would require spatially explicit data.

3.4. Loss–replacement

As in the previously discussed cases, loss–replacement is driven by fine-scale processes. Unlike the previous situations, perennial grasses that are lost are replaced to varying degrees by distinct functional groups of plants. These plants are usually shrubs in the case of the Chihuahuan Desert. Grass recovery does not occur over long time periods (> 60 year), even after cessation of grazing and drought. Thus, this replacement process is referred to as 'crossing a threshold' to an alternative state and is associated with a 'transition' in state-and-transition models (Bestelmeyer et al., 2003; Stringham et al., 2003). In many cases, shrubs may establish prior to or

coincident with grass decline, perhaps due to seed introductions (Brown and Archer, 1999; Fredrickson et al., 2006) and rainfall pulse events (Brown et al., 1997; Reynolds et al., 2004). In addition, soil degradation in bare areas between existing grasses and shrubs is often observed (Rietkerk et al., 1997; Herrick et al., 2002) and runoff and erosion may be significant. A number of fine-scale positive feedbacks associated with low grass cover and the existence of drought-resistant shrubs may preclude grass reestablishment and shrub decline, including competition for, and redistribution of, limiting resources (Schlesinger et al., 1990), reduced fire frequency (Wright et al., 1976), or more native grass herbivores with shrub increases (Kerley et al., 1997). Demographic limitations to grasses, such as a reliance on vegetative reproduction, may also maintain their absence. Several mathematical modeling approaches have been used to describe these thresholds and feedbacks based on a number of mechanisms (Rietkerk et al., 1997; Anderies et al., 2002; van Langevelde et al., 2003). Thus, sparsely vegetated shrubland is considered to be a classical alternative stable state (Fig. 1c).

Loss–replacement is perhaps the most commonly used description of grassland to shrubland transitions (Van Auken, 2000). The pattern may apply to black grama grasslands occupying gravelly soils on upper piedmont slopes and relict piedmont surfaces (loamy-skeletal Calciargids) that have been replaced by creosotebush (*Larrea tridentata*; Fig. 4) and, more recently, viscid acacia (*Acacia neovernicosa*). This replacement is often accompanied by soil erosion. Some sandy basin floor positions where mesquite and snakeweed (*Gutierrezia* spp.) have increased may also conform to this mechanism (coarse-loamy Petrocalcids and Calciargids). Tarbush (*Flourensia cernua*) has replaced mixtures of tobosa, black grama, and other grasses on fine-loamy Calciargids of lower piedmont slopes. In these cases, the degree to which local grass loss is coupled to local shrub establishment appears to vary: in many cases grasses disappear without local increases in shrubs.

3.5. Patch reorganization

This mechanism is typically expressed at broader scales within which smaller units (patches) of grass tussocks and/or shrubs occur (Fig. 1d). The boundaries of the grass or shrub-dominated patch are sometimes clearly demarcated by areas of bare ground (Bertiller et al., 2002). In other cases, patches may be recognized at several hierarchical levels (Kotliar and Wiens, 1990).

When viewed at the scale of meters, patch reorganization may initially appear similar to be loss–replacement, but in the case of reorganization, grass loss and soil degradation in one area are coupled to grass increases and soil improvement in another part of the landscape, following the erosion–deposition or erosion cell concept (Pickup, 1985). Surface water runoff and sediment that were formerly captured and stabilized by a vegetation patch are free to be redistributed to other patches. This shift may depend strongly on the pattern and directional connectivity of bare-ground patches with respect to slope gradients across a range of vegetation cover values (Davenport et al., 1998; Ludwig et al., 2002).
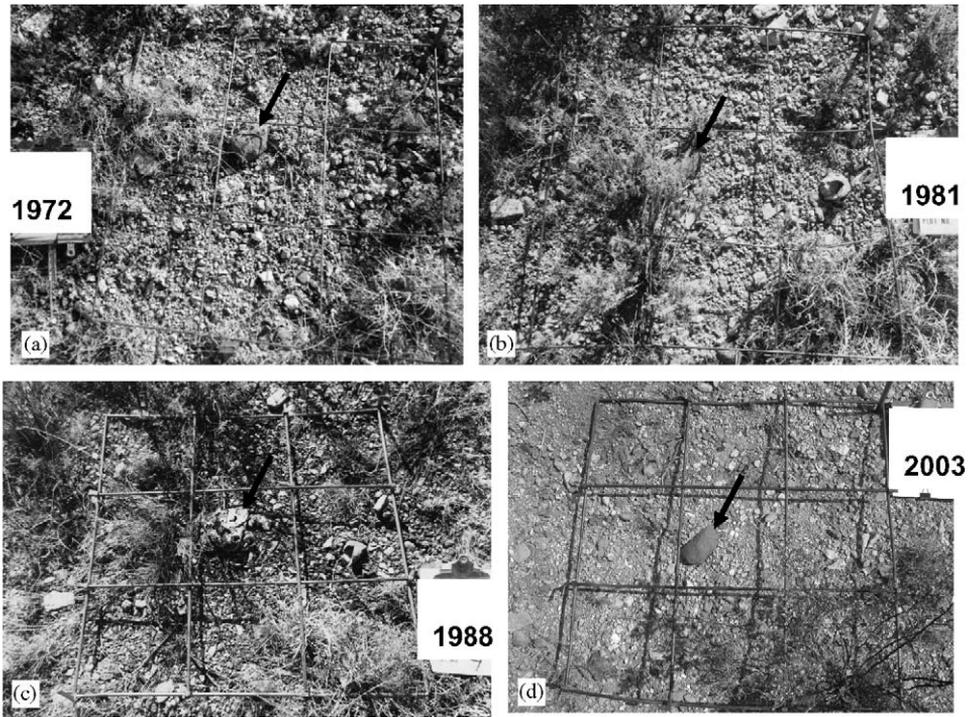
Fig. 4. Loss–replacement pattern on Tres Hermanos gravelly clay loam, Sierra County, NM. Ground cover was dominated by black grama from 1972 to 1988. By 2003, most of the black grama has disappeared and a creosotebush has established in the lower right corner of the plot. The arrow indicates the position of a single clast. In 1972 and 1981, the clast appears partially concealed by sediment, beneath a cow fecal pat in 1988, and exposed in 2003. Soil loss between other surface clasts indicates erosion.

In 'banded landscapes', redistribution may occur among patches expressed as parallel bands on gentle slopes ($<1\%$), such that loss of vegetation at the downslope edge of a band is coupled with increased vegetation at the upslope edge of the band directly below (Tongway et al., 2001). This reorganization process, however, may not necessarily result in bands, but can lead to an irregular pattern (Ludwig et al., 2005). Variably shaped patches may disappear in one part of the landscape and reappear in another, governed by local micro-topography, hydrology, sedimentation patterns, and episodic, high-intensity rainfall events (Pickup et al., 1994; Ludwig et al., 1997). Thus, fine-scale patch dynamics may be coupled with stability at a broader (landscape) scale (deAngelis and Waterhouse, 1987; Watt, 1947).

Bands in the fine-loamy soils of lower piedmont slopes of the Chihuahuan Desert (fine to fine-loamy Typic Calciargids) often feature both grasses (e.g. tobosa) and shrubs (e.g. tarbush) co-occurring (and competing) in bands (Mauchamp et al., 1993). Repeat aerial photography studies in similar communities near Las Cruces, New Mexico suggest that patch loss and creation are associated with one another
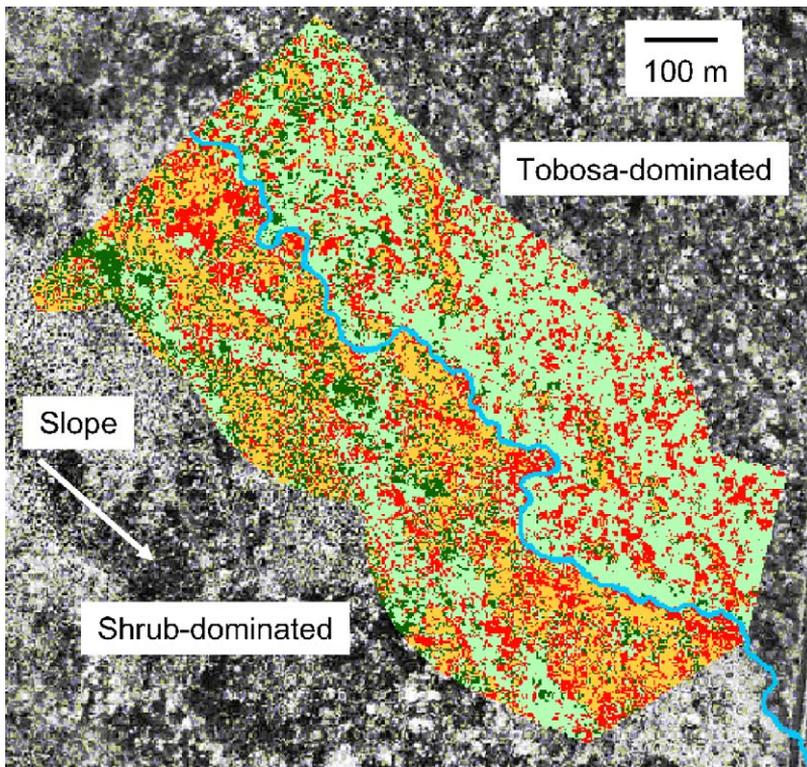
Fig. 5. Patch reorganization pattern occurring at the Corralitos Ranch, Dona Ana County, New Mexico between 1936 and 1996 on fine and fine-loamy Calciargids (Dona Ana, Berino, and Stellar series). Polygon classes are vegetated in 1936 and 1996 (light green), unvegetated in 1936 and 1996 (yellow), vegetated in 1936 but not in 1996 (red), and unvegetated in 1936 but vegetated in 1996 (dark green). Classes were based on unsupervised classification of 1936 Soil Conservation Service aerial photographs and 1996 US Geological Survey Digital Ortho Quarter Quads into vegetated and unvegetated classes using Erdas Imagine 8.6. Images were georegistered and overlain to create the polygons/classes. The blue line indicates a sharp demarcation between generally tobosa-dominated and shrub-dominated sides and the area analysed is a 200-m buffer around this line. Note that the classes are finely intermingled in many areas and the presence of relatively large patches on the shrub-dominated side where revegetation and vegetation loss have occurred.

over tens of meters, although patches are not organized in bands (Fig. 5). Despite localized appearance of vegetation between 1936 and 1996, overall vegetation cover within the study area declined by about 10%. The small-scale consequences of patch reorganization are illustrated in a grazing exclosure established in 1911 on the Jornada Experimental Range on a gravelly, middle piedmont location (Fig. 6). A comparison of 1969 and 2002 photographs at this site indicated colonization of bush muhly and approximately 12.5 cm of accumulated sediment deposited from a barren and eroded upslope area. The causes of this apparently spontaneous patch creation are unknown, but grazing rest is likely to have been a necessary precondition.
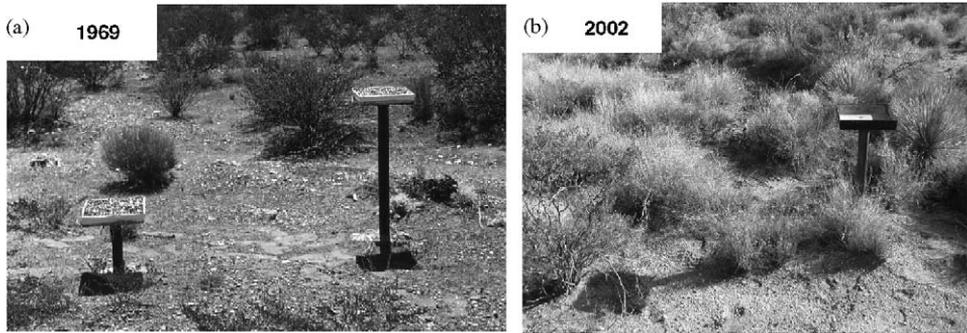
Fig. 6. Colonization of bush muhly and *Yucca elata* in conjunction with 12.5 cm of sediment accumulation at DSP dust trap site 5, on piedmont with gravelly sandy loam soil (see Gile and Grossman, 1997). This site is located within a large grazing exclosure on the Jornada Experimental Range that has been ungrazed since 1911. Note also the growth of the creosotebush in the lower left of the images. Sediment accumulation was measured from the top of the two dust trap posts, which were anchored in concrete at a fixed height above the soil surface in 1969. Adjacent areas were highly eroded, and the localized sedimentation and colonization indicate the 'patch reorganization' pattern.

There is also evidence that patch reorganization may occur between major landforms (Wondzell et al., 1996). Observations from long-term chart quadrats on the Jornada Experimental Range indicate that loss of grass from a piedmont slope position was coupled with increased grass cover at the margin of the basin floor, several km away (see Herbel et al., 1972; Gile and Grossman, 1997). Defining the scale at which water and sediment redistribution processes can create stability or buffer loss in vegetation cover or production is a critical problem that has yet to be addressed.

3.6. Cascading transition

Like patch reorganization, cascading transitions are initiated by loss–replacement dynamics but occur in areas dominated by sandy soils (e.g. coarse-loamy Typic Calciargids) of relict basin floor river alluvium. Once shrubs (especially mesquite) dominate patches, subsequent degradation of perennial grasses (primarily black grama and threeawns; *Aristida* spp.) is spatially contagious (Fig. 1e) due to feedbacks with broad-scale drivers (Peters et al., 2004). Heavy grazing, trampling, and drought are coupled with rainfall pulse events that favor local mesquite establishment (Snyder and Tartowski, 2006), leading to bare-ground expansion and decreased stability of highly erodible soils. Wind is increasingly able to remove fine particles from the local ecosystem, a process that is highly dependent on self-organizing increases in bare-ground connectivity as mesquite become dominant (Gillette and Monger, in press). Larger sand particles are moved over shorter distances, abrading, burying, and killing grass plants (Okin et al., 2001; Okin et al., 2006; Fig. 7a). Sand and other resources accumulate under shrubs (Schlesinger et al., 1990). Once continuous, bare areas are sufficiently large (e.g. 100 km^2),
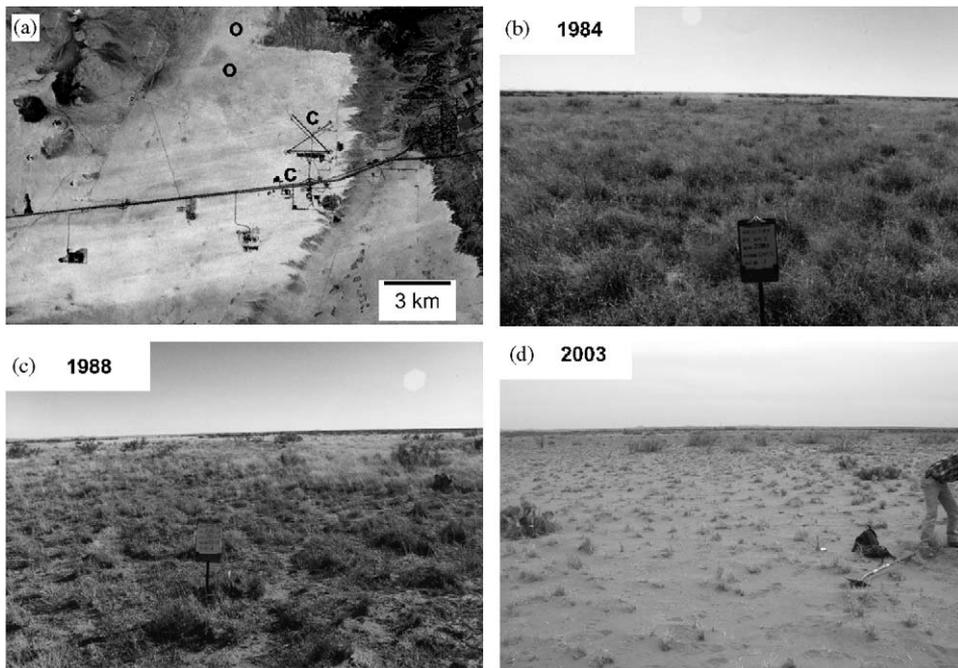
Fig. 7. Indicators of cascading transitions. (a) Illustrates the broad-scale pattern of sand redistribution on the Rio Grande valley border, west of Las Cruces, NM. The sand ridges appear as light colored bands oriented in the direction of prevailing winds (SWW–NEE; north is top of image). The horizontal linear feature is US Interstate 10 and the vertical breaks are valley rim scarps. Note also the mountains in the upper left quadrant of the image. The image was produced using orthorectified Landsat ETM data, courtesy of the University of Maryland Global Land Cover Facility. The source image was acquired on 13 June 2001. Principal components analysis was conducted on raw digital number data for image bands 1–5 and 7. The image is derived from principal component 2. The letter 'c' denotes plots on sandy soils where cascading transitions are suspected to have occurred and 'o' indicates plots on sandy soils exhibiting oscillation. (b–d) Are a series of repeat photographs showing the progressive burial of a tobosa grassland on Berino sandy loam by aeolian sand deposits from a degraded mesquite coppice dune (behind photographer). Soil characterization indicated 23 cm of sediment had accumulated on the original surface.

land–atmosphere feedbacks (Pielke et al., 1997) may create an increasingly inhospitable environment for grass survival and establishment by accelerating wind-driven erosion. Thus, ongoing transitions in existing grasslands may have been initiated more than a century ago and be independent of current local management. This process may explain why long-term grazing exclosures established around grass patches on sandy soils at the Jornada and elsewhere in southern New Mexico have been unable to prevent grass loss. Longer term climatic change and its effects on hillslope erosion and other geomorphic processes may also drive cascading transitions independent of human impacts (e.g. McFadden and McAuliffe, 1997).

Cascading transitions may have been historically important on sandy soils in southern New Mexico and extreme west Texas (Gile, 1999; Okin et al., 2001) and the

process is ongoing in other areas. The position of mountain ranges relative to prevailing winds may determine whether particular points are susceptible to cascading transitions (Fig. 7a). We have also observed that sand deposition from degrading coarse-loamy/sandy sites is causing tobosa mortality on adjacent fine-loamy soils (Figs. 7b–d). Thus, cascading transitions may also affect heterogeneous land mosaics in which sandy soils are a component.

3.7. Analysis

Of the 123 trend plot photograph series examined, the predominant mechanism was oscillation, followed by loss-reestablishment (Table 2). Patch reorganization and cascading transitions were observed in only a few cases; however, their detectability is limited using only small-scale photographs. Excluding these rare cases, Fisher's exact test ($p = 0.05$, $n = 118$) indicated a significant association of vegetation dynamics mechanisms with geomorphic components. The coarse-textured, basin floor soils were more prone to grass loss over the last 20–40 years than were Lithic/skeletal hill soils or fine-textured, basin floor soils, while gravelly/skeletal piedmont soils were intermediate. Piedmont soils also exhibited the highest frequency of obvious soil degradation and species replacements.

4. Discussion

4.1. A classification of vegetation dynamics

The science linking spatial and temporal patterns to the processes driving reversible vs. catastrophic ecosystem transition is in its infancy (Tongway et al., 2001; Rietkerk et al., 2004). Progress will necessitate the linkage of several spatial and temporal processes, including the effects of herbivore distribution and behavior (Fredrickson et al., 2006), the role of precipitation pulse events and disturbance on the differential growth and survival of plant species (Reynolds et al., 2004), the effects of disturbances on soil change and soil–plant interactions (Tugel et al., 2005), the eco-hydrological and 'eco-aeolian' effects of plant patch pattern (Breshears et al., 2003; Okin et al., 2006), the influence of broad-scale land cover patterns on climate (Pielke et al., 1997), and geomorphic evolution in response to climate and vegetation (Thomas, 2004; Monger and Bestelmeyer, 2006). These linkages will provide fertile research directions of immeasurable value to land managers.

We have taken a first step towards this synthesis by summarizing empirical observations about the scale and pattern of ecosystem change in the Chihuahuan Desert. The general mechanisms resulting from this synthesis may be applied to many specific state and transition models (or parts within models) developed for particular soils and regions (Stringham et al., 2003). The mechanisms also illustrate that thresholds associated with catastrophic transitions may have several distinct causes that can be detected at different spatial scales, including demographic and

Table 2
Number (and percentage) of plots classified into different types of vegetation dynamics on different geomorphic components (see text and Table 1)

Geomorphic component	Stability	Oscillation (full)	Oscillation (decline)	Loss (A) (no soil loss)	Loss (A) (reestablish-ment)	Loss (B) (soil loss/replacement)	Patch Reorganiz-ation	Cascade
Lithic, skeletal hillslope soils	1 (3)	16 (55)	8 (27)	2 (7)	1 (3)	1 (3)	0	0
Gravelly or skeletal piedmont soils	5 (8)	23 (39)	10 (17)	10 (17)	2 (3)	8 (14)	0	1 (2)
Non-gravelly, coarse, basin floor soils	0	4 (24)	3 (18)	8 (47)	0	0	0	2 (12)
Non-gravelly, fine, basin floor, inset fans	1 (6)	7 (39)	5 (28)	2 (11)	1 (6)	1 (6)	1 (6)	0

Loss A refers to the loss–reestablishment dynamics class and Loss B refers to loss–replacement dynamics. Soil terminology follows Soil Survey Staff (2003).

competitive constraints, soil degradation, local to landscape resource redistribution, and wind-driven, cascading erosion.

Thus, research on a suite of general processes (Peters and Havstad, 2006) can be applied to land areas that share similar properties. For example, size oscillation and loss–replacement mechanisms are associated with fine-scale disturbance and demographic processes, the shift from loss–reestablishment to loss–replacement involves threshold behavior, and patch reorganization and cascading transitions are driven by transport processes. Applications of general principles will be successful only when species–soil combinations are matched with appropriate processes and scales.

4.2. Dynamics observed on different geomorphic components

The repeat photography data confirm that different geomorphic components are prone to exhibit different types of dynamics. Overall, patterns associated with resilience (mostly oscillation) were dominant. One possible explanation for this result is that most of the grazing- or drought-susceptible sites were already devoid of grasses when the BLM studies were initiated and those sites were therefore excluded. Thus, the population of points we examined may be a resilient subset of the population that existed prior to wide-spread livestock grazing and prolonged droughts of the 1950s (Herbel and Gibbens, 1996).

Nonetheless, patterns of ongoing grass loss are predictable and tend to occur on gravelly piedmont slopes and coarsely textured basin floor soils. The long-term significance of most grass loss, however, is unclear. Some losses were associated with obvious signs of local erosion and soil degradation, hydrologically driven patch reorganization, or sand deposition occurring in areas dominated by aeolian forces. Subsequent monitoring will reveal whether the other plots in which grasses were lost, tentatively classified as 'loss–reestablishment' (Table 1), will recover. Indeed, many of these plots may be at a threshold of irreversible change in which management practices and/or rainfall patterns over the next several years will determine their fate.

Although factors affecting the processes leading to grass mortality or recovery (e.g. local grazing intensity, shrub seed deposition, local drought) may be effectively stochastic at the plot scale (but see Fredrickson et al., 2006), the processes themselves can be linked mechanistically to the multivariate properties of particular soils and landscape positions (Tongway et al., 2001; Tugel et al., 2005; Gillette and Monger, in press) and the traits of particular plants (Allred, 1989; Hamerlynck et al., 2000; Gibbens and Lenz, 2001). Disentangling these relationships will require more intensive sampling of our study area. Nonetheless, this idea offers hope that careful stratification of observations by soils, geomorphic surface, and plant community composition may lead to monitoring strategies and management decisions that utilize quantitative data to a greater degree than is currently possible (see McFadden and McAuliffe, 1997; Holm et al., 2002).

4.3. Implications for monitoring, assessment, and restoration

Differing spatial and temporal patterns of change associated with these mechanisms suggest that different monitoring strategies and interpretations are required to detect vegetation change in arid lands. For example, line–point intercept transects or photopoints (Herrick et al., 2005) deployed haphazardly in a pasture may be adequate to detect size oscillation, loss–reestablishment, and loss–replacement dynamics, but would be incapable of detecting patch reorganization. Carefully stratified transects based on micro- and macro-topography and remote-sensed data would be needed to detect these larger scale processes (Tongway and Hindley, 2004). For example, given a scenario involving patch reorganization, plots could be stratified among areas predicted to lose grass and erode and areas predicted to accumulate sediment and exhibit increased grass production. This stratification protocol could also be used to predict locations where local restoration manipulations (Rango et al., 2006) would be most likely to succeed.

In the case of cascading transitions, transects that happen to be located in areas in which cascade-initiating loss–replacement dynamics are occurring could provide warning of an imminent cascade. Transects or manipulations located away from initiation areas would simply document the pattern and rate of spatial contagion, with little opportunity for meaningful management response. Close attention to areas where cascades may be initiated (e.g. along livestock trails or at water points) often requires the broad-scale perspective provided by remote sensing approaches (e.g. Ares et al., 2003).

Understanding the likelihood that particular processes are operating at a site is also essential for the interpretation of monitoring data. A grass cover increase detected using a 100-m transect in an area undergoing patch reorganization might be interpreted as restoration success when it may actually reflect degradation occurring at a broader scale (Pickup et al., 1994). Conversely, pastures exhibiting extremely altered composition or low grass cover and large bare patches may be condemned as having 'crossed a threshold' when they are fully capable of being restored with appropriate grazing management or increased rainfall (loss–reestablishment; see also Fuhlendorf et al., 2001). In yet other cases, the disappearance of grasses in a system previously exhibiting size oscillation may herald the start of a decades-long recovery process.

5. Conclusions

This analysis indicates that although several soil-contingent mechanisms drive vegetation change in arid lands, these mechanisms can be classified into a few types and we need not descend into the 'black hole of reductionism' (Wiens, 1992) to accommodate some complexity. From a practical standpoint, the typology indicates that vegetation pattern (e.g. high or low grass cover) observed at a point in time or space may have very different interpretations with respect to future dynamics depending on context. Uncertainty about which dynamics a system will exhibit in the

future can be reduced with an understanding of plant life history, soil properties, precipitation patterns, and grazing behavior and management (Westoby, 1980; Archer and Bowman, 2002). To this list, we add the multi-scale structure of spatial and temporal pattern in vegetation and soil surface conditions.

Concepts that recognize multiple processes and scales of spatial pattern of vegetation and soils need to be better incorporated into models and assessment/monitoring designs (Ludwig et al., 1997). The breadth of processes employed in quantitative models of aridland behavior (e.g. van de Koppel and Reitkerk, 2004) is limited, due in part to model complexity and also to the lack of empirically derived frameworks. Recognition that qualitatively different processes may regulate vegetation change on different geomorphic components will challenge the fundamental (and implicit) assumptions of many modeling and monitoring approaches. Conceptual state-and-transition models used by managers, for example, emphasize local processes (disturbance, competition) and vegetation composition (e.g. Bestelmeyer et al., 2003). These models should be reformulated to better incorporate spatial patterns and multiple scales of process that will require the synthesis of spatially explicit, multi-temporal data.

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References

Allred, K.W., 1989. Observations on seed dispersal and implantation in burrograss (*Scleropogon brevifolius*—Gramineae). Sida 13, 493–496.

Anderies, J.M., Janssen, M.A., Walker, B.H., 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. Ecosystems 5, 23–44.

Archer, S., Bowman, A., 2002. Understanding and managing rangeland plant communities. In: Grice, A.C., Hodgkinson, K.C. (Eds.), Global Rangelands: Progress and Prospects. CAB International, Wallingford, UK, pp. 63–80.

Ares, J., del Valle, H., Bisigato, A., 2003. Detection of process-related changes in plant patterns at extended spatial scales during early dryland desertification. Global Change Biology 9, 1643–1659.

Bertiller, M.B., Ares, J.O., Bisigato, A.J., 2002. Multiscale indicators of land degradation in the Patagonian Monte, Argentina. Environmental Management 30, 704–715.

Bestelmeyer, B.T., Brown, J.R., Havstad, K.M., Chavez, G., Alexander, R., Herrick, J.E., 2003. Development and use of state-and-transition models for rangelands. Journal of Range Management 56, 114–126.

Bestelmeyer, B.T., Brown, J.R., Havstad, K.M., Fredrickson, E.L. A holistic view of desert grassland: a synthesis of multidisciplinary research and management applications. In: Havstad, K.M., Schlesinger, W.H., Huenneke, L.F. (Eds.), Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin LTER. Oxford University Press, Oxford, UK, in press.

Bestelmeyer, B.T., Herrick, J.E., Brown, J.R., Trujillo, D.A., Havstad, K.M., 2004. Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. Environmental Management 34, 38–51.

Breshears, D.D., Whicker, J.J., Johansen, M.P., Pinder III, J.E., 2003. Wind and water erosion and transport in semiarid shrubland, grassland, and forest ecosystems: quantifying dominance of horizontal wind-driven transport. Earth Surface Processes and Landforms 28, 1189–1209.

Brown, J.R., Archer, S., 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. Ecology 80, 2385–2396.

Brown, W.V., Coe, G.E., 1951. A study of sterility in *Hilaria belangeri* (Steud) Nash and *Hilaria mutica* (Buckl.) Benth. American Journal of Botany 38, 823–830.

Brown, J.H., Valone, T.J., Curtin, C.G., 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceedings of the National Academy of Sciences USA 94, 9729–9733.

Bureau of Land Management, 1996. Sampling vegetation attributes. Interagency Technical Reference, BLM/RS/ST-96/002 + 1730, pp. 2–3.

Campbell, R.S., 1931. Plant succession and grazing capacity on clay soils in southern New Mexico. Journal of Agricultural Research 43, 1027–1051.

Comer, P., Faber-Langendoen, D., Evans, R., Gawler, S., Josse, C., Kittel, G., Menard, S., Pyne, M., Reid, M., Schulz, K., Snow, K., Teague, J., 2003. Ecological Systems of the United States: A Working Classification of US Terrestrial Systems. NatureServe, Arlington, VA, USA.

Davenport, D.W., Breshears, D.D., Wilcox, B.P., Allen, C.D., 1998. Viewpoint: sustainability of piñon–juniper ecosystems—a unifying perspective of soil erosion thresholds. Journal of Range Management 51, 231–240.

deAngelis, D.L., Waterhouse, J.C., 1987. Equilibrium models and nonequilibrium concepts in ecological models. Ecological Monographs 57, 1–21.

Devine, D.D., Wood, M.K., Donart, G.B., 1998. Runoff and erosion from a mosaic tobosagrass and burrograss community in the northern Chihuahuan Desert grassland. Journal of Arid Environments 39, 11–19.

Dyksterhuis, E.J., 1949. Condition and management of rangeland based on quantitative ecology. Journal of Range Management 2, 104–115.

Fredrickson, E.L., Havstad, K.M., Estell, R.E., Hyder, P.W., 1998. Perspectives on desertification: south-western United States. Journal of Arid Environments 39, 191–207.

Fredrickson, E.L., Estell, R.E., Laliberte, A., Anderson, D.M., 2006. Mesquite recruitment in the Chihuahuan Desert: historic and prehistoric patterns with long term impacts. Journal of Arid Environments 65, 285–295.

Fuhlendorf, S.D., Briske, D.D., Smeins, F.E., 2001. Herbaceous vegetation change in variable rangeland environments: the relative contributions of grazing and climatic variability. Applied Vegetation Science 4, 177–188.

Gibbens, R.P., Lenz, J.M., 2001. Root systems of some Chihuahuan Desert plants. Journal of Arid Environments 48, 221–263.

Gibbens, R.P., McNeely, R.P., Havstad, K.M., Beck, R.F., Nolen, B., 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. Journal of Arid Environments 61, 651–668.

Gile, L.H., 1999. Eolian and associated pedogenic features of the Jornada basin floor, southern New Mexico. Soil Science Society of America Journal 63, 151–163.

Gile, L.H., Grossman, R.B., 1997. The Desert Project Soil Monograph. United States Department of Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE, USA.

Gile, L.H., Ahrens, R.J., Anderson, S.P., 2003. Supplement to the Desert Project Soil Monograph: Soils and Landscapes of a Desert Region Astride the Rio Grande Valley Near Las Cruces, New Mexico. United States Department of Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE, USA.

Gillette, D., Monger, H.C. Aeolian processes. In: Havstad, K.M., Schlesinger, W.H., Huenneke, L.F. (Eds.), Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin LTER. Oxford University Press, Oxford, UK, in press.

Hamerlynck, E.P., McAuliffe, J.R., Smith, S.D., 2000. Effects of surface and sub-surface soil horizons on the seasonal performance of *Larrea tridentata* (creosotebush). Functional Ecology 14, 596–606.

Herbel, C.H., Gibbens, R.P., 1996. Post-drought Vegetation Dynamics on Arid Rangelands in Southern New Mexico. New Mexico Agricultural Experiment Station Bulletin 776, Las Cruces, NM, USA.

Herbel, C.H., Ares, F.N., Wright, R.H., 1972. Drought effects on a semidesert grassland range. Ecology 53, 1084–1093.

Herrick, J.E., Brown, J.R., Tugel, A.J., Shaver, P.L., Havstad, K.M., 2002. Application of soil quality to monitoring and management: paradigms from rangeland ecology. Agronomy Journal 94, 3–11.

Herrick, J.E., Van Zee, J.W., Havstad, K.M., Whitford, W.G., 2005. Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems. USDA-ARS Jornada Experimental Range, Las Cruces, NM. University of Arizona Press, Tucson, AZ, USA.

Hobbs, R.J., Norton, D.A., 2004. Ecological filters, thresholds and gradients in resistance to ecosystem reassembly. In: Temperton, V.M., Hobbs, R.J., Nuttle, T.J., Halle, S. (Eds.), Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Island Press, Washington, DC, USA, pp. 72–96.

Holm, A.M., Loneragan, W.A., Adams, M.A., 2002. Do variations on a model of landscape function assist in interpreting the growth response of vegetation to rainfall in arid environments? Journal of Arid Environments 50, 23–52.

Kerley, G.I.H., Whitford, W.G., Kay, F.R., 1997. Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory? Oecologia 111, 422–428.

Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59, 253–260.

Ludwig, J.A., Tongway, D.J., Freudenberger, D.O., Noble, J.C., Hodgkinson, K.C. (Eds.), 1997. Landscape Ecology, Function and Management: Principles from Australia's Rangelands. CSIRO Publishing, Melbourne, Australia.

Ludwig, J.A., Muldavin, E., Blanche, K.R., 2000. Vegetation change and surface erosion in desert grasslands of Otero Mesa, southern New Mexico: 1982 to 1995. American Midland Naturalist 144, 273–285.

Ludwig, J.A., Eager, R.W., Bastin, G.N., Chewings, V.H., Liedloff, A.C., 2002. A leakiness index for assessing landscape function using remote sensing. Landscape Ecology 17, 157–171.

Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., Imeson, A.C., 2005. Vegetation patches and runoff-erosion as interacting eco-hydrological processes in semiarid landscapes. Ecology 86, 288–297.

Mauchamp, A., Montaña, C., Lepart, J., Rambal, S., 1993. Ecotone dependent recruitment of a desert shrub, *Flourensia cernua*, in vegetation stripes. Oikos 68, 107–116.

McAuliffe, J.R., 2003. The interface between precipitation and vegetation: the importance of soils in arid and semiarid environments. In: Weltzin, J.F., McPherson, G.R. (Eds.), Changing Precipitation Regimes and Terrestrial Ecosystems. University of Arizona Press, Tucson, AZ, USA, pp. 9–27.

McFadden, L.D., McAuliffe, J.R., 1997. Lithologically influenced geomorphic responses to Holocene climatic changes in the Southern Colorado Plateau, Arizona: a soil-geomorphic and ecologic perspective. Geomorphology 19, 303–332.

Monger, H.C., Bestelmeyer, B.T., 2006. The soil-geomorphic template and biotic change in arid and semiarid ecosystems. Journal of Arid Environments 65, 207–218.

Okin, G.S., Gillette, D.A., Herrick, J.E., 2006. Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semiarid environments. Journal of Arid Environments 65, 253–275.

Okin, G.S., Murray, B., Schlesinger, W.H., 2001. Degradation of sandy arid shrubland environments: observations, process modeling, and management implications. Journal of Arid Environments 47, 123–144.

Peters, D.P.C., Havstad, K.M., 2006. Nonlinear dynamics in arid and semiarid ecosystems: interactions among drivers and processes across scales. Journal of Arid Environments 65, 196–206.

Peters, D.P.C., Pielke Sr., R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S., Havstad, K.M., 2004. Cross scale interactions, nonlinearities, and forecasting catastrophic events. Proceedings of the National Academy of Science USA 101, 15130–15135.

Pickup, G., 1985. The erosion cell—a geomorphic approach to landscape classification in range assessment. Australian Rangeland Journal 7, 114–121.

Pickup, G., Bastin, G.N., Chewings, V.H., 1994. Remote sensing-based condition assessment for nonequilibrium rangelands under large-scale commercial grazing. Ecological Applications 4, 497–517.

Pielke, R.A., Lee, T.J., Copeland, J.H., Eastman, J.L., Ziegler, C.L., Finley, C.A., 1997. Use of USGS-provided data to improve weather and climate simulations. Ecological Applications 7, 3–21.

Pringle, H., Tinley, K., 2003. Are we overlooking critical geomorphic determinants of landscape change in Australian rangelands? Ecological Management and Restoration 4, 180–186.

Rango, A., Tartowski, S.L., Laliberte, A., Wainwright, J., Parsons, A.J., 2006. Islands of hydrologically enhanced biotic productivity in natural and managed arid ecosystems. Journal of Arid Environments 65, 235–252.

Reynolds, J.F., Kemp, P.R., Ogle, K., Fernandez, R.J., 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141, 194–210.

Rietkerk, M., van den Bosch, F., van de Koppel, J., 1997. Site-specific properties and irreversible vegetation changes in semi-arid grazing systems. Oikos 80, 241–252.

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

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrel, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. Science 247, 1043–1048.

Snyder, K.A., Tartowski, S.L., 2006. Multi-scale temporal variation in water availability: implications for vegetation dynamics in arid and semiarid ecosystems. Journal of Arid Environments 65, 219–234.

Soil Survey Staff, 2003. Keys to Soil Taxonomy, ninth ed. United States Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.

Stringham, T.K., Krueger, W.C., Shaver, P.L., 2003. State and transition modeling: an ecological process approach. Journal of Range Management 56, 106–113.

Thomas, M.F., 2004. Landscape sensitivity to rapid environmental change—a Quaternary perspective with examples from tropical areas. Catena 55, 107–124.

Tongway, D.J., Hindley, N.L., 2004. Landscape Function Analysis Manual: Procedures for Monitoring and Assessing Landscapes with Special Reference to Minesites and Rangelands. Version 3.1. CSIRO Sustainable Ecosystems, Canberra, Australia.

Tongway, D.J., Valentin, C., Seghieri, J. (Eds.), 2001. Banded Vegetation Patterning in Arid and Semiarid Environments: Ecological Processes and Consequences for Management. Ecological Studies, vol. 149. Springer, New York, USA.

Tugel, A.J., Herrick, J.E., Brown, J.R., Mausbach, M.J., Puckett, W., Hipple, K., 2005. Soil change, soil survey, and natural resources decision making: a blueprint for action. Soil Science Society of America Journal 69, 738–747.

Valone, T.J., Meyer, M., Brown, J.H., Chew, R.M., 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. Conservation Biology 16, 995–1002.

Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31, 197–216.

Van de Koppel, J., Reitkerk, M., 2004. Spatial interactions and resilience in arid ecosystems. American Naturalist 163, 113–121.

Van Langevelde, F., van de Vijver, C.A.D.M., Kumar, L., van de Koppel, J., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84, 337–350.

Walker, B.H., 2002. Ecological resilience in grazed rangeland: a generic case study. In: Gunderson, L.H., Pritchard, Jr., L. (Eds.), Resilience and the Behavior of Large-Scale Systems. Island Press, Washington, DC, USA, pp. 183–194.

Watt, A.S., 1947. Pattern and process in the plant community. Journal of Ecology 35, 1–22.

Westoby, M., 1980. Elements of a theory of vegetation dynamics in arid rangelands. Israeli Journal of Botany 28, 169–194.

Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42, 266–274.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3, 385–397.

Wiens, J.A., 1992. Ecology 2000: an essay on future directions in ecology. Ecological Society of America Bulletin 73, 165–170.

Wondzell, S., Ludwig, J.A., 1995. Community dynamics of desert grasslands: influence of climate, landforms, and soils. Journal of Vegetation Science 6, 377–390.

Wondzell, S.M., Cunningham, G.L., Bachelet, D., 1996. Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert. Landscape Ecology 11, 351–362.

Wright, H.A., Bunting, S.C., Neuenschwander, L.F., 1976. Effect of fire on honey mesquite. Journal of Range Management 29, 467–471.