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Nonlinear dynamics in arid and semi-arid systems: Interactions among drivers and processes across scales

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Abstract

We discuss a new conceptual framework for arid and semi-arid systems that accounts for nonlinear dynamics and cross scale interactions in explaining landscape patterns and dynamics. Our framework includes a spatial and temporal hierarchy, and five key interacting components that connect scales of the hierarchy and generate threshold behaviors: (1) historical legacies that include climate, disturbance, and management regimes, (2) dynamic template of patterns in ecological variables and spatial context, (3) vertical and horizontal transport processes (fluvial, aeolian, animal), (4) rate, direction, and amount of resource redistribution between high and low resource areas, and (5) feedbacks among plants, animals, and soils. We illustrate how this framework can be used to understand, forecast, and manage ecological systems that exhibit nonlinear dynamics across a range of spatial and temporal scales. This paper provides the foundation for a series of papers from the Jornada Experimental Range ARS-LTER research site in southern New Mexico, USA that support this new conceptual framework.
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Keywords: Conceptual framework; Cross scale interactions; Historical legacies; Landscape context; Resource redistribution; Threshold behavior; Transport processes

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1. Introduction

Broad scale conversion of grasslands to shrublands has occurred throughout arid and semi-arid regions of the world over at least the past century (Buffington and Herbel, 1965; York and Dick-Peddie, 1969; Gibbens et al., 2005). Although a number of factors driving these conversions have been identified, there is not a clear consensus on the key factors or processes that produce different outcomes under seemingly similar conditions (Peters et al., in press a). The two most commonly cited drivers of this conversion are the separate and interactive effects of drought and livestock overgrazing (Archer, 1994; Buffington and Herbel, 1965; Grover and Musick, 1990; Humphrey, 1958; Van Auken, 2000). However, recent analyses show that these two factors are insufficient to account for observed responses in the Chihuahuan Desert of North America (Peters et al., unpublished data). For example, although the extreme drought of the 1950s had clear and measurable impacts on vegetation (Herbel et al., 1972), spatial and temporal variation in grass cover cannot be explained by the drought (Peters et al., unpublished data). In some locations, grass cover was reduced to zero before the drought occurred, and in other locations, grass cover remains high today. Similarly, intensive grazing by livestock in the 1800s and early 1900s led to decreased grass cover and increased shrub density through time (Paulsen and Ares, 1962). However, protection from cattle using exclosures was often unsuccessful in limiting the further spread of shrubs across the landscape (Peters et al., in press a, b). Including other factors that can influence grass–shrub interactions, such as changes in small animal activity, reductions in fire frequency, and directional changes in climate, is insufficient to explain this landscape scale heterogeneity in vegetation dynamics.

In this paper, we investigate explanations for this high spatial and temporal variation in vegetation dynamics for arid and semi-arid systems. We briefly describe a conceptual framework that focuses on factors and processes that generate heterogeneous spatial responses and nonlinear dynamics through time. We provide support for this framework from the other papers in this special issue with a focus on research conducted at the Jornada Experimental Range ARS-LTER site in southern New Mexico, USA (32.5°N, 106.8°W). Our goal is to improve our understanding of these systems in order to guide managers and decision-makers in effective use of arid and semi-arid resources and to provide useful forecasts of future system dynamics.

2. Landscape linkages conceptual framework

Our framework builds on existing conceptual frameworks of grass–shrub interactions in arid and semi-arid systems (i.e., Archer, 1994; Ludwig et al., 1997; Noy Meir, 1973; Reynolds et al., 1997, 2004; Schlesinger et al., 1990), yet explicitly includes five key elements that generate nonlinear dynamics (Fig. 1). Previous frameworks focused either on vertical redistribution of water and differences in rooting depth of grasses and shrubs (Walter, 1971, 1973) or consequences of grass or shrub plants or bare areas to horizontal movement of water and resulting feedbacks

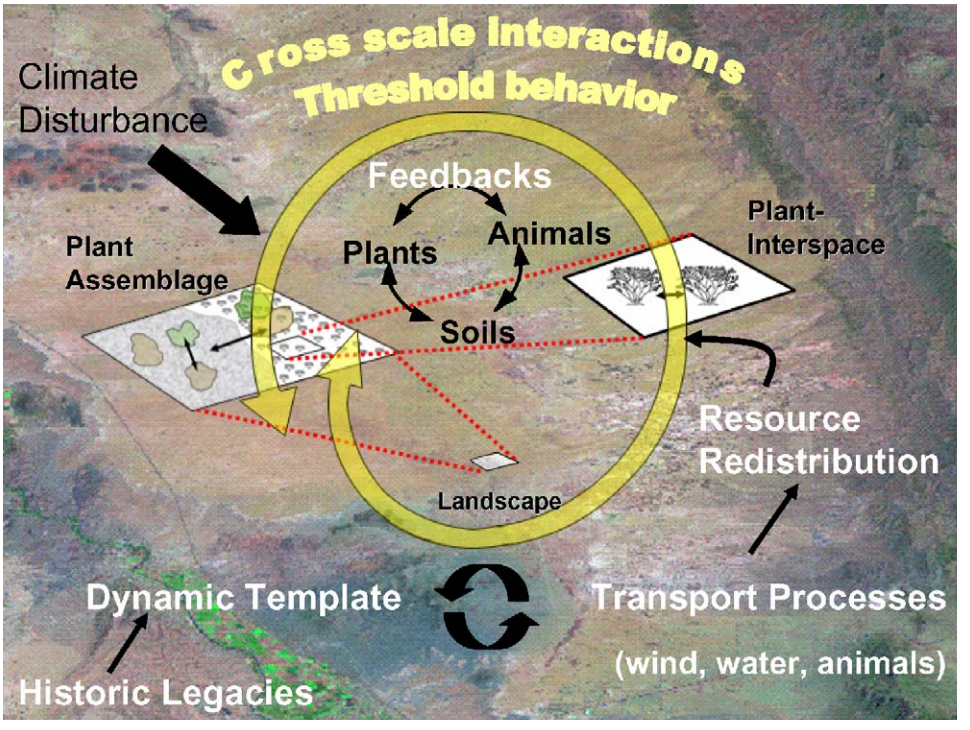

Fig. 1. Conceptual framework for arid and semi-arid systems includes a spatial and temporal hierarchy and five key interacting elements (historical legacies, dynamic template, transfer processes, resource redistribution, and plant–soil–animal feedbacks) that lead to nonlinear dynamics, thresholds, and cross scale interactions (depicted by the broad arrow that crosses spatial scales). Climate and disturbance are drivers that influence these interactions across a range of spatial and temporal scales. Our spatial hierarchy includes five spatial scales, although only three are shown for clarity (plant-interspace, plant assemblage, landscape). Spatial variation in vegetation and landforms at the Jornada Experimental Range are shown in the background image. The Jornada is bounded by the San Andres Mountains (right) and the Rio Grande (left with private irrigated land in green).

to vegetation (Schlesinger et al., 1990). More recent frameworks have combined vertical and horizontal redistribution of water at the plant scale (Breshears and Barnes, 1999) or focused on the importance of water runoff at patch scales to landscape scale processes (Ludwig et al., 2005). Multiple scales have also been examined (Reynolds et al., 1997, 2004) and the importance of thresholds has been identified (Archer, 1994).

Our framework differs from those mentioned above because we focus on cross scale interactions and nonlinear dynamics that result from five key interacting elements (Fig. 1). We combine a hierarchical framework of increasingly larger spatial and temporal units with a process framework that provides connections across scales. In this paper, we focus on spatial scales and recognize that temporal scales have a similar hierarchy. For example, temporal variability in water availability results from variation in climate and weather interacting with vegetation structure, the physical environment, and vegetation-soil water feedbacks at multiple scales to influence variation in ecosystem patterns through time (Snyder and Tartowski, 2006).

2.1. Hierarchical framework

Our spatial hierarchy includes five major scales, although we recognize that a continuum of scales is possible (see O'Neill et al., 1986). Our smallest spatial unit is an individual plant and its associated bare soil interspace. Smaller units (e.g., fungi) are often associated with plants and affect individual plant success as well as have consequences for vegetation dynamics at larger spatial scales (Lucero et al., 2006). These plant–fungal interactions are increasingly recognized as important to whole plant morphology, biomass, and reproductive success with consequences for ecological responses at broader spatial scales (Lucero et al., 2006).

The second scale of interest beyond an individual plant is a patch, a group of interacting plants and their interspaces. Patches throughout the Chihuahuan Desert are often dominated by one of several species of shrubs (e.g., mesquite [*Prosopis glandulosa*], creosotebush [*Larrea tridentata*], tarbush [*Flourensia cernua*]) or perennial grasses (e.g., black grama [*Bouteloua eriopoda*], tobosagrass [*Hilaria mutica*]). Patches vary in size from several plants ($< 5\,m^2$) to several hundred individuals ($> 1000\,m^2$).

Patch mosaics, the third scale, are composed of groups of patches dominated by different species or life-forms and inter-patch areas. At the fourth scale, landscape units are groups of patch mosaics that are interconnected, but distinct soil-defined units or "ecological sites" (McAuliffe, 1994; Natural Resources Conservation Service, 1997). The fifth and final scale for our purposes is a geomorphic component that consists of a number of interacting landscape units. These areas are often defined by parent material and landscape position. Common geomorphic components in the Basin and Range physiographic province of the south-western United States include mountain fronts, alluvial fans and piedmont slopes, and basin floors composed of alluvial, fluvial, or lacustrine sediments. Thus, arid and semi-arid landscapes consist of a mosaic of interacting plants, patches, patch mosaics, landscape units, and geomorphic components.

2.2. Key elements that connect spatial units

Connectivity among spatial units is an important determinant of system dynamics. Five key elements interact to connect scales. These elements influence the redistribution of resources through time and across space and affect variation in vegetation patterns and dynamics (Fig. 1). In many cases, connectivity among spatial units determines the relative importance of each of the five key elements in affecting threshold behavior and cross scale interactions: (1) historical legacies, (2) spatial context and patterns in ecological variables (i.e., dynamic template), (3) transport processes, (4) resource redistribution between areas of high and low resources, and

(5) feedbacks among plants, animals, and soils. Climate and disturbance interact with these key elements to influence spatial and temporal variation in ecological patterns and dynamics.

Historical legacies include natural and human impacts with long-lasting imprints on ecosystem patterns and dynamics (Foster et al., 2003; Knapp and Soulé, 1998). Legacies, such as historic disturbances, have important effects on transport of materials through their influence on the dynamic template. For example, disturbances can impact dynamic surface soil properties and cause them to be more easily eroded by water or wind (Johansen et al., 2001; Whicker et al., 2002). Legacy effects have most often been attributed to human activities, land use, and drought within the past century (e.g., Herbel et al., 1972; Rango et al., 2002). However, historic human activity, such as use of mesquite by the Jornada Mogollan in 850–1400 AD, undoubtedly also plays an important role in more recent ecosystem dynamics (York and Dick-Peddie, 1969). Recent studies suggest that mesquite expansion may have occurred in the early 1900s even in the absence of widespread livestock grazing because of changing human activities (Fredrickson et al., 2006). Interactions between human activity and mesquite expansion are complex and likely variable through time and across space as settlement patterns changed between indigenous people and those of European descent (Fredrickson et al., 2006).

Dynamic template refers to the location and characteristics of a study area relative to its surroundings. These characteristics include variables with a very slow rate of change (e.g., geomorphology, parent material, and topography) as well as variables with relatively fast rates of change that can be influenced by other system properties through feedback mechanisms (e.g., soil organic matter, vegetative cover and composition, and distribution of spatial units in the hierarchy). The dynamic template influences patterns in water and nutrient availability and consequently affects distribution patterns and dynamics of plants, animals, and microbes (Monger and Bestelmeyer, 2006). This template occurs across a range of spatial scales from fine scale patterns between plants and their associated interspaces to broad scale geomorphic provinces (Monger and Bestelmeyer, 2006). The history of research at the Jornada has reinforced our understanding that vegetation dynamics are spatially explicit (Peters et al., in press (a)). Recent studies at the Jornada illustrate the importance of the dynamic template regarding spatial variation in shrub invasion and grass recovery. The very slow recovery of black grama in a livestock exclosure following repeated shrub removal is likely related to the low density of black grama plants within the exclosure and in the surrounding area (Peters et al., unpublished data). Even in the absence of competing shrubs, we do not anticipate grass recovery until water and nutrients are sufficient, and seeds from adjacent areas disperse into the local area of the exclosure (Havstad et al., 1999).

Transport processes in arid and semi-arid systems include fluvial (water), aeolian (wind), and animal components. The materials redistributed horizontally and vertically as a result of these transport processes are water, soil particles, nutrients, and plant material (i.e., seeds, litter).

Vertical movement of water in the soil profile is influenced by competing mechanisms, such as bare soil evaporation and transpiration of competing plants.

Erosion and deposition by water occurs across multiple spatial and temporal scales (Parsons et al., 2003; Rango et al., 2006; Schlesinger and Jones, 1984; Wainwright et al., 2002), and has important effects on variability in vegetation dynamics and soil properties (Wondzell et al., 1996). Many of the early remediation attempts at the Jornada involved the redistribution and concentration of water, which affected variation in vegetation dynamics (Rango et al., 2002). Although many of these treatments were deemed unsuccessful initially, their effects on current vegetation patterns can be observed in aerial photographs and documented by ground measurements (Rango et al., 2006).

Redistribution of soil particles, nutrients, and seeds by wind also has important effects on variation in vegetation patterns and dynamics. Redistribution of soil particles and nutrients by wind is particularly important for sandy soils; other soils often have physical and biotic crusts to protect them from erosion (Okin and Gillette, 2001). Controls on and consequences of aeolian processes occur across a range of spatial scales, from plants to patches and regions, and influence variation in soil and vegetation dynamics (Okin et al., 2006).

Small and large animals are effective agents of seed dispersal (in particular for mesquite) and for the redistribution of soil resources. Seed dispersal by livestock is often considered a key process promoting shrub invasion into perennial grasslands over the past 150 years in southern New Mexico (Buffington and Herbel, 1965). However, mesquite invasion and expansion likely occurred prior to this time as a result of complex human–environment interactions that changed through time (Fredrickson et al., 2006). Indigenous peoples often used mesquite in their diet; thus, mesquite during this time period may have been limited in its spatial distribution to localized parts of the landscape (York and Dick-Peddie, 1969). These localized areas may have become foci and seed sources for mesquite expansion upon arrival of Europeans and subsequent reduction in selection pressures on this species (Fredrickson et al., 2006). Thus, current spatial patterns of mesquite may be a consequence of historic transport processes that have fundamentally changed through time.

Resource redistribution between areas of high and low resources occurs across a range of scales. Effects of *feedbacks* among plants, animals, soil, and water on resource redistribution have been well-documented across a range of spatial and temporal scales for arid and semi-arid systems (e.g., Fredrickson et al., 2006; Okin et al., 2006; Rango et al., 2006; van de Koppel et al., 2002). At the plant-interspace scale, the concentration of resources beneath individual shrubs results in a positive feedback to shrub survival and formation of islands of fertility (Schlesinger et al., 1990). Similarly, concentration of water under plant canopies can result in ‘‘islands of hydrologically enhanced productivity’’ (Rango et al., 2006). High infiltration rates under shrub canopies result from protection from raindrop impact and reduced compaction (Schlesinger et al., 1999; Wainwright et al., 1999, 2000). Water and nutrients are also concentrated by stemflow and throughfall, resulting in increased plant available water. At a patch scale, the distinctive ‘‘striped’’ patterns in vegetation on shallow slopes result from the accumulation of water beneath herbaceous plants with feedbacks to plant establishment and growth

(HilleRisLambers et al., 2001; Ludwig et al., 2005). Similarly, beads or small patches of plants on bajadas with subtle reductions in elevation can increase shrub growth and promote infiltration with feedbacks to the herbaceous vegetation (Peters et al., 2004b). Interactions between small or large animals and vegetation often result in feedbacks to the animals or plants across a range of scales (Brown and Morgan Ernest, 2002; Walker et al., 1981). At a broad scale, land–atmosphere interactions following desertification and widespread woody plant expansion can result in decreased rainfall and higher albedo with consequences for subsequent broad scale shifts between grasses and woody plants (Claussen et al., 1999).

Threshold behavior has also been investigated in arid and semi-arid systems and has consequences for variation in woody plant invasion (Archer, 1994; Breshears et al., 2004; Davenport et al., 1998). Cross scale interactions associated with threshold behavior were recently shown for mesquite invasion into black grama dominated grasslands at the Jornada (Peters et al., 2004a). Three thresholds were identified based on the prevalence of different dominant processes: (1) recruitment and growth of mesquite shrubs within a patch, (2) spread of shrubs among patches, and (3) expansion of mesquite dunefields associated with wind erosion. The nonlinear propagation of mesquite through time from fine to broad spatial scales suggests the importance of cross scale interactions that cannot be predicted based on individual scale studies. Similarly, the reduction in perennial grass cover over a 140 year period (1858–1998) exhibited nonlinear dynamics and threshold behavior (Gibbens et al., 2005; Peters and Gibbens, in press).

3. Forecasting and applications to management

Forecasting spatial and temporal variation in future dynamics of arid and semi-arid systems has often been challenging (Gao and Reynolds, 2003). Landscape scale approaches based on our framework and that combine quantitative tools, such as simulation models, spatial databases, and remotely sensed images, have provided a range of forecasts that depend, at least in part, on the climatic conditions and management regimes imposed (Peters and Herrick, 2001). We have also used simulation models to predict the sites expected to be most sensitive to experimental manipulations (Peters et al., in press b). However, new simulation models and integrated experiments are needed that explicitly account for nonlinear dynamics generated from feedback mechanisms and threshold behavior. These models and experiments need to include both horizontal and vertical redistribution of resources as affected by multiple, potentially interacting transport processes (wind, water, animals) and account for historical legacies and landscape context.

Successful management of these systems requires a consideration of these nonlinear processes and interactions. Information from plot-level, process-based experiments has often been used to make management decisions at the landscape scale. Our framework suggests that historic legacies and landscape context that influence transport processes across scales can also be important, and need to be considered in management decisions. In addition, a classification system of vegetation transition patterns integrated with a repeat photography database can be used to determine different monitoring strategies based on an explicit consideration of spatial scale (Bestelmeyer et al., 2006). Integrated frameworks for organizing, synthesizing, and applying our science-based approach are being developed to address multi-objective needs of assessment, monitoring, and management systems (Herrick et al., 2006). In addition, extrapolation of information across scales, in particular from fine scales used for experimentation to broader scales most useful to management, requires an objective approach to determining the key processes involved (Peters et al., 2004c). Improved forecasts and management decisions will arise from the incorporation of a landscape linkages approach to dealing with complex systems that exhibit nonlinear dynamics.

4. Conclusions and global applications

We discussed a new conceptual framework for understanding, forecasting, and managing spatial variation in vegetation patterns and dynamics associated with the conversion of grasslands to shrublands. Our framework expands upon existing frameworks by focusing on resource redistribution (e.g., Schlesinger et al., 1990), yet includes four additional key elements (historical legacies, dynamic template and spatial context, transport processes, and feedback mechanisms) that interact to create complex patterns and nonlinear dynamics and threshold behaviors across a range of spatial and temporal scales. Our approach has applications to the approximately 40% of the land's surface and one-fifth of the world's human population that live in arid and semi-arid regions. In addition, our approach has application to combating desertification, including its current manifestations, such as the invasion by exotic species or noxious weeds that is occurring in many ecosystems globally (Peters et al., 2004d). Technologies and strategies for restoration or remediation of degraded landscapes is one of our most immediate research challenges, and this conceptual framework provides an ecological basis for this experimentation that is missing from previous work. Our framework also has relevance to other types of systems where spatial and temporal nonlinearities are important (Peters et al., 2004a).

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