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Real World Ecology

Large-Scale and Long-Term Case Studies and Methods

Foreword by Stephen R. Carpenter

Springer

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To our mothers, whose love and support we appreciate.

Foreword

Ecology is not rocket science – it is far more difficult (Hilborn and Ludwig 1993). The most intellectually exciting ecological questions, and the ones most important to sustaining humans on the planet, address the dynamics of large, spatially heterogeneous systems over long periods of time. Moreover, the relevant systems are self-organizing, so simple notions of cause and effect do not apply (Levin 1998). Learning about such systems is among the hardest problems in science, and perhaps the most important problem for sustaining civilization. Ecologists have addressed this challenge by synthesis of information flowing from multiple sources or approaches (Pickett et al. 2007). Some major approaches in ecology are theoretical concepts expressed in models, long-term observations, comparisons across contrasting systems, and experiments (Carpenter 1998). These approaches have complementary strengths and limitations, so findings that are consistent among all of these approaches are likely to be most robust.

Ecosystem data are noisy. There are multiple sources of variability, such as external forcing, endogenous dynamics, and our imperfect observations. Thus it is not surprising that statistics have played a central role in ecological inference. However, with few exceptions the statistical approaches available to ecologists have been imported from other disciplines and were designed for problems that are simpler than the ones that ecologists face routinely. If you need to cut a board and all you have is a hammer, you might try pounding on the board until it breaks. Such a misapplication of force resembles some uses of statistics in ecology. But the metaphor is not quite right. It would be more accurate to say that ecosystem and landscape ecologists need to create and compare multifaceted models for large-scale processes, whereas the readily available tools were designed for testing null models that are usually trivial or irrelevant for this family of ecological questions.

The mismatch between the needs of scientists and the availability of statistical tools is acute in the analysis of ecosystem experiments. Ecosystem experiments have been an important contributor to ecological science for more than 50 years (Likens 1985, Carpenter et al. 1995). While humans have manipulated ecosystems since at least the beginnings of agriculture, if not longer, deliberate experiments for learning about ecosystems are traced to limnology in the 1940s (Likens 1985). The earliest whole-lake manipulations lacked reference systems, and so sometimes it was difficult to determine whether changes in the ecosystems were caused by the manipulations or by other environmental factors. In 1951, Arthur Hasler and his students divided an hour-glass shaped lake with an earthen dam, thereby creating two basins, Paul and Peter lakes. Peter Lake was manipulated, while Paul Lake served as an unmanipulated reference ecosystem (Johnson and Hasler 1954). The use of a reference or "control" ecosystem was a pathbreaking innovation (Likens 1985). It allowed Hasler and his students to separate the effects of the manipulations of Peter Lake from those of the environmental variability that affected both lakes (Stross and Hasler 1960, Stross et al. 1961). As a result of their experiences as students of Hasler, Gene Likens and Waldo Johnson were inspired to create two of the most influential centers of ecosystem experimentation in the world, the Hubbard Brook Ecosystem Study (Likens 2004) and the Experimental Lakes Area (Johnson and Vallentyne 1971).

Most ecosystem experiments involve spatially extensive systems (often observed at several spatial extents) over long time spans. Such experiments pose statistical challenges that cannot be handled by the methods of laboratory science or small agricultural plots (Carpenter 1998). It is not possible to substitute small-scale experiments run for short periods of time, because results of such experiments do not predict dynamics at spatial and temporal scales relevant to ecosystem science or to management (Carpenter 1996, Schindler 1998, Pace 2001). Instead, we must perform our studies at the appropriate scales – possibly at multiple scales. Then, we must learn how to learn from noisy observations of transient, heterogeneous, and non-replicable systems. This is a daunting challenge.

Thus many ecologists have broken free of the constraints of older statistical methods in order to explore new alternatives that seem better-adapted to the world of large-scale ecological change. The method of multiple working hypotheses (Chamberlain 1890) is now explicit in many ecological papers. Multiple hypotheses are expressed as quantitative models and confronted with data (Burnham and Anderson 1998, Hilborn and Mangel 1997). New approaches are explored for long-term monitoring data (Stow et al. 1998). Experiments are designed for critical tests of multiple alternative models to address fundamental questions about ecological dynamics (Dennis et al. 2001, Wootton 2004). Comparisons of multiple models are providing new insights about long-term field observations of big systems (Ives et al. 2008). These are but a few selections from a diverse and rapidly growing literature. This new phase of ecological research is turbulent and subject to rapid intellectual progress. Some of the emerging practices are nonstandard and are themselves objects of inquiry. Some approaches are tried, found wanting, and abandoned. New approaches are introduced frequently. It is an era of creativity, innovation, discarding of mistakes, and selection among alternatives – in a nutshell, a time of rapid evolution by the discipline.

The volume before you presents a sampling of case studies and syntheses from this fertile field of research. The authors and editors aim to improve our tools for ecological inference at scales that are relevant for fundamental understanding, as well as for management of ecosystems and landscapes. The book conveys the excitement and novelty of emerging approaches for learning about large-scale ecological changes.

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Chapter 3
Approaches to Predicting Broad-Scale Regime Shifts Using Changing Pattern-Process Relationships Across Scales

Debra P. C. Peters, Brandon T. Bestelmeyer, Alan K. Knapp, Jeffrey E. Herrick, H. Curtis Monger, and Kris M. Havstad

3.1 Introduction

Shifts from one ecosystem state to another with dramatic consequences for ecosystem organization and dynamics are increasing in frequency and extent as a result of anthropogenic global change (Higgens et al. 2002, Foley et al. 2003, Scheffer and Carpenter 2003). Ecosystem state changes (i.e., regime shifts) have been well-documented for a number of different systems, from lakes (Carpenter 2003) to oceans (Beaugrand 2004), coral reefs (McCook 1999), and grasslands (Rietkerk and van de Koppel 1997). Ecosystem state changes are usually characterized by a shift in dominant species that persists through time. For example, shifts in dominant fish species in lakes can result in significant changes in prey populations (Magnuson et al. 2006), and shifts to woody plant dominance in grasslands result in increased rates of erosion and land degradation (Schlesinger et al. 1990). Ecosystem state changes can also occur with changes in the production of a single species in association with modification of one or more biophysical processes (e.g. Howes et al. 1986). In many cases, ecosystem state changes are "ecological surprises" in that they are observed and confirmed after they occur. These surprises result from our inability to understand the full suite of mechanisms driving and maintaining these shifts. New approaches are needed to improve our understanding and to allow the detection and prediction of impending ecosystem state changes, in particular those that impact the delivery of goods and services to human populations.

Experimental and analytical approaches designed to detect and predict ecosystem state changes must enhance our understanding of cross-scale interactions and elucidate the role of these interactions in determining ecosystem thresholds (the level or magnitude of an ecosystem process that results in a sudden or rapid change in ecosystem state).

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Critical thresholds are often crossed during or following a state change such that a return to the original state is difficult or seemingly impossible (Bestelmeyer 2006). Here, we define thresholds as points in time where a change in an environmental driver results in a discontinuous increase or decrease in the rate of a process and the resultant change in a state variable (Peters et al. 2004a, Groffman et al. 2006). Thresholds can occur either in the environmental driver, the rate of a process or a state variable. Thresholds indicate that a change in a dominant process has occurred and that distinct exogenous drivers or endogenous positive feedbacks are governing rates of change (Scheffer et al. 2001, Peters et al. 2004a). Feedbacks tend to maintain a state, and it is often the change in these feedbacks and the resultant alteration in pattern–process relationships that differentiate a regime shift from a reversible ecosystem change that is not maintained through time (Carpenter 2003, Peters et al. 2007). For example, shifts from grasslands to woodlands can be maintained for hundreds of years by positive feedbacks between woody plants and soil properties. Once critical thresholds in surface soil properties are crossed, soil water availability is modified to promote woody plant growth and limit the establishment of grasses; thus promoting the maintenance of woodlands. These state change dynamics are differentiated from successional dynamics following disturbances that remove the vegetation without major changes to soil properties (e.g., wildfire). Critical thresholds in soil properties do not exist following these disturbances; thus a return to grass dominance through a succession of species is possible.

In some cases, state changes are driven by processes at one spatial or temporal scale interacting with processes at another scale (Carpenter and Turner 2000, Gunderson and Holling 2002, Peters et al. 2007). For example, the Dust Bowl of the 1930s in the US resulted from interactions among broad-scale patterns of extremely low rainfall, landscape-scale patterns in the number and spatial arrangement of abandoned agricultural fields, and fine-scale patterns in plant mortality, which resulted in shifts from vegetated to bare states throughout the Central Great Plains (Peters et al. 2004a). Observations at single or even multiple, independent scales would have been insufficient to predict such cross-scale interactions that ultimately generated the emergent behavior characterized as an ecosystem state change (Michener et al. 2001). Detailed monitoring of vegetation on small plots during the 1930s was insufficient to account for the spatial extent and rate of loss of vegetation being driven by landscape- and broader-scale processes, on a continental-scale (Weaver and Albertson 1940).

Approaches that explicitly account for thresholds and cross-scale interactions are expected to improve our understanding of the mechanisms driving ecosystem state changes and to allow more informed predictions of impending changes (Ludwig et al. 2000, Diffenbaugh et al. 2005, Bestelmeyer et al. 2006b). Alternatively, downscaling the effects of broad-scale drivers on fine-scale patterns can, under some conditions, improve understanding of key ecological processes driving these patterns. Extrapolating information about fine-scale processes to broad scales can be used, under some conditions, for predicting responses through time and space. Previous studies have described hierarchical, multi-scale approaches to improve both understanding and prediction (e.g., Wiens 1989, Stohlgren et al. 1997, Petersen et al. 2003). Our approach considers the interactions and feedbacks in patterns and processes across land areas from an ecosystems perspective that links different kinds of data across spatial and temporal scales. Most studies of cross-scale interactions have documented changing patterns in vegetation through time and across space, and then assumed changing patterns resulted from changing ecological processes (Peters et al. 2004a). However, an approach that combines pattern analyses with experimental manipulation of processes and simulation modeling of rates of ecosystem change under different drivers is needed to tease apart the role of drivers and processes in determining patterns at different scales.

We had three objectives: (1) to describe an experimental approach that would identify changing pattern–process relationships across scales and the dominant processes within a scale that drive and maintain state changes in terrestrial systems; (2) to describe statistical approaches for detecting and predicting state changes; (3) to apply these approaches to broad-scale shifts from grasslands to woody plant dominance in the Chihuahuan Desert, but they are applicable to the United States and globally. Our approach built on existing methods that examined multiple scales hierarchically, and combined observation, manipulation, and simulation modeling (e.g., Wiens 1989, Petersen et al. 2003, Stohlgren et al. 1997). However, our approach included three new components: (1) an explicit focus on stratification of the landscape by variation in drivers, in addition to the more common approach of stratifying by underlying environmental (e.g., soils, landuse) and biotic (vegetation cover, species composition) heterogeneity, (2) experimental manipulations of drivers at multiple scales, and (3) sufficient levels of manipulation to allow thresholds to be detected and examined.

3.2 The Shrinking Grasslands: Woody Plant Encroachment into Perennial Grasslands

Woody plant encroachment is a pervasive problem throughout perennial grasslands globally (Scholes and Archer 1997, Briggs et al. 2005, Knapp et al. 2008). In the United States alone, 220–330 million ha of non-forested land either has changed or is changing from a grassland to a woodland (Houghton et al. 1999, Pacala et al. 2001). The consequences of a grassland to woodland ecosystem state change are consistent among grassland types: local ecosystem properties are modified, including primary production, biodiversity, and rates and patterns of nutrient cycling (Schlesinger et al. 1990, Ricketts et al. 1999, Huenneke et al. 2002, Briggs et al. 2005, Knapp et al. 2008). Regional to global processes are altered, including transport of dust to the atmosphere, redistribution of water to the oceans and groundwater reserves, and feedbacks to weather (Jaffee et al. 2003, McKergow et al. 2005, Pielke et al. 2007).

This state change is occurring in most grassland types located along a precipitation gradient from the xeric desert grasslands in the Southwest to the mesic tallgrass prairie in the central Great Plains and the barrier islands along the Atlantic coast (Archer 1994, Briggs et al. 2005, Young et al. 2007), and along a temperature gradient from warm deserts to alpine meadows and arctic tundra (Marr 1977, Shaver et al. 2001, Epstein et al. 2004). Woody plant encroachment most often involves increases in cover and density of native or non-native shrubs or small trees and loss of perennial grasses. At the dry end of the gradient, the size and density of bare soil patches and concentration of soil resources under sparse woody plants increases to create a landscape that is more arid and desert-like (i.e., desertification). At the wet end of the gradient, woody plant encroachment results in an increase in leaf area of woody plants, but no increase in bare ground (i.e., afforestation; Briggs et al. 2005).

During an ecosystem state change from grassland to woodland, the fundamental unit of change is the individual, either a grass or woody plant. Adjacent grass- and woody plant-dominated communities have a dynamic transition zone or ecotone that consists of individual plants and patches of plants. The location of the ecotone shifts through time and space as ecological driving forces fluctuate to favor either grasses or woody plants (Peters et al. 2006b). Historical evidence of a grassland–woodland transition zone that has shifted repeatedly at large spatial and long temporal scales – a tension zone – comes from the paleorecord in the central United States (Grimm 1983) and in the Chihuahuan Desert based on packrat middens (Van Devender 1990), carbon isotopes (Monger et al. 1998) , and fossil pollen (Hall 2005). However, during an ecosystem state change, environmental drivers reach a threshold in magnitude or rate of change that favors woody plant encroachment, woody plants disperse into the grassland, germinate and become established (Peters et al. 2006d). In many cases, woody plants modify the water, light, and nutrient conditions of their microsites to create a positive feedback that promotes their persistence (Schlesinger et al. 1990, Lett and Knapp 2003, McCarron and Knapp 2003, Lett et al. 2004). Successful individuals, by producing seed or through vegetative reproduction, can increase the density of woody plants throughout the transition zone. A broad-scale state change results when woody plants coalesce into patches that then dominate the cover of the community at the landscape scale (Peters et al. 2006b).

On some soil types (e.g., sandy soils in arid systems), when a threshold density of woody plants is reached, a change from biotic (e.g., competition, dispersal) to abiotic control (i.e., wind erosion) takes place. Upon reaching the threshold, the shift from grassland to woodland occurs rapidly (years to decades) (Peters et al. 2004a). Because encroachment by woody plants often results in changes to surface soil properties, a state change can be documented by a combination of changes in vegetation dominance and soil properties (Bestelmeyer et al. 2006a).

It is the change in soil properties and the positive feedbacks with the vegetation that may determine the irreversibility of the system (Davenport et al. 1998).

Although shifts from grasslands to woodlands occur over a very large and diverse area that includes much of the continental United States, there is a common set of drivers and processes that determine these ecosystem dynamics (Fig. 3.1). The relative importance of specific drivers and processes varies in each case; however, the suite of possibilities that determine changing pattern–process relationships across scales is similar. Drivers, such as climate, provide both the spatial and temporal context for finer-scale dynamics, and can interact with finer-scale drivers to influence state change dynamics across scales (Fig. 3.1). At the grassland regional scale, drivers include climate (precipitation, temperature) and atmospheric properties (e.g., nitrogen deposition, carbon dioxide levels, solar radiation) (Bahre and Shelton 1993, Archer et al. 1995, Polley et al. 2002, Knapp et al. 2008) as well as the regional pool of species and their dispersal attributes (Ricklefs 1987). Multi-year drought is the broad-scale driver most often implicated in desertification, whereas extended wet periods can increase the rate of afforestation in more mesic environments (Humphrey 1958, Grimm 1983, Briggs et al. 2005).

As the spatial scale of resolution decreases to the landscape, additional drivers become important, such as patterns of livestock grazing, fire, land use, soils, and geomorphology, which interact with climate variability at multiple time scales (Lyford et al. 2003, Monger and Bestelmeyer 2006). In general, broad-scale drought (xeric systems) or wet periods (mesic systems) combine with landscape-scale variation in intensity and frequency of livestock grazing (xeric systems) and fire (mesic systems) to promote woody plant expansion (Schlesinger et al. 1990, Briggs et al. 2005). At the fine scale of individual plants, patterns in life history traits (e.g., lifespan, drought and grazing tolerance, water- and nitrogen-use efficiency) influence a plant's ability to respond to micro-site conditions.

Processes follow a similar hierarchy of scales. At the finest scale of individuals, recruitment, competition for resources vertically in the soil profile, and mortality of grasses and woody plants as well as plant-soil feedbacks are important to local dominance (Brown and Archer 1989). As the scale of interest increases to the landscape and region, additional processes become important that redistribute resources and propagules horizontally. Transport vectors (i.e., water, wind, animals, humans, and disturbance) redistribute water, soil, nutrients, and seeds, and act to connect adjacent or non-contiguous spatial units (Ludwig et al. 2005; 2007, Fredrickson et al. 2006, Okin et al. 2006). We define contagious processes as those processes that connect spatial units at the same or different scales via transport vectors (Peters et al. 2008).

Because of the explicit linkages among scales, the importance of contagious processes can only be understood with studies of multiple interacting scales. For example, seeds can be dispersed long distances (tens of kilometers) by birds and other vectors to initiate fine-scale woody plant invasion in non-contiguous areas (Chambers et al. 1999, Lyford et al. 2003). Thus, construction of livestock exclosures, designed to alter local scale processes of herbivory on seedlings, can

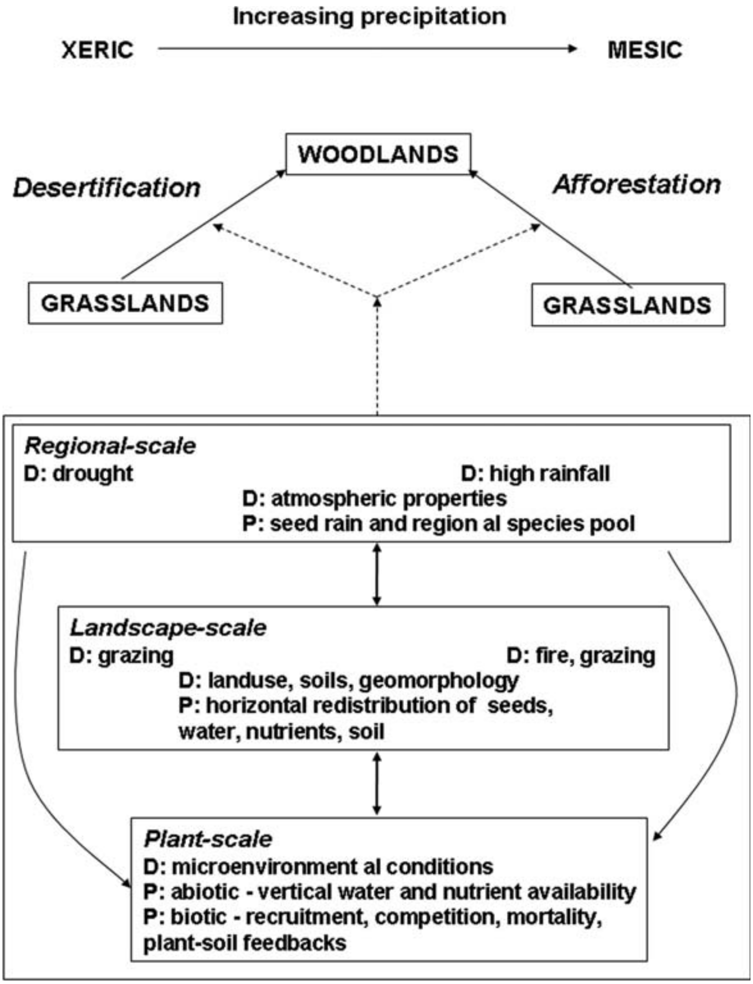

Fig. 3.1 Conceptual diagram of key patterns in drivers and processes associated with grassland to woodland transitions along a precipitation gradient that includes desertification (xeric) and afforestation dynamics (mesic). Pattern–process relationships at three major scales are shown that influence shifts from grasslands to woodlands (*dashed arrows*): regional-, landscape-, and plant-scale. For each scale, patterns in drivers are denoted by D and processes are denoted by P. Dynamics at any given scale are hierarchical and determined by interactions with the next higher and lower scale in the hierarchy. In addition, regional-scale drivers can influence plant-scale dynamics directly. In most cases, similar drivers and processes are important across the precipitation gradient. The exceptions are: (**a**) drought is a key broad-scale driver for desertification whereas afforestation is affected by periods of high rainfall, and (**b**) fire is more important in mesic than xeric areas

be ineffective in delaying or stopping the advancement of woody plants if large numbers of seeds are dispersed by wind and small animals or if seeds were already in the soil seed bank at the time of exclosure construction (Peters et al. 2006a).

3.3 Limits of Current Approaches

In spite of decades-old recognition that scale and spatial heterogeneity are important, there is little systematic understanding of how to design cross-scale studies (Viglizzo et al. 2005, Bestelmeyer et al. in review). Traditional approaches to studying landscapes tend to blend areas of ecologically significant heterogeneity at particular spatial scales and to emphasize randomness within a scale. Fine-scale heterogeneity may be acknowledged, but only certain kinds and scales of heterogeneity are recognized as sufficiently important by the investigator to be sampled. Observer perception that a particular process is important often dictates the scale of interest and the associated sampling design (Wiens 1989). For example, broad climate zones used to examine the effects of drought on grassland to woodland conversion either ignore fine-scale variation in soil properties or stratify by these properties at the landscape or regional scale (Charney et al. 1975, Claussen 1997, Martin and Asner 2005). These designs ignore variation in the distribution of patches within a landscape that may be critical to predicting shifts from grasslands to woodlands (Kéfi et al. 2007, Scanlon et al. 2007).

Within climate zones, random sampling is typically used and heterogeneity is ignored. If heterogeneity is important to understanding ecosystem dynamics, then random sampling can lead to under-sampling of relatively small areas that have a proportionately greater effect on the process of interest. Experimental manipulations, especially those that are intensive and long-term, focus by necessity on relatively few areas and represent selected components of spatial heterogeneity. The results of these focused studies are often over-generalized to the larger suite of conditions that are too costly to explore directly. Furthermore, spatial stratification is most often based on patterns in the environment (e.g., soils, vegetation) and ignores variability in transfer processes that redistribute resources and propagules (Peters et al. 2004b). Contagious processes require a spatially explicit approach that considers spatial heterogeneity and accounts for the transport of material and seeds among spatial units at the same and different scales (Peters et al. 2004b).

Similarly, the temporal scale of studies has often been limited. Studies of state changes have emphasized short-term (year to decade-long) studies of pattern–process relationships performed at different stages of the regime shift. The complete state change is seldom directly observed, but presumably the data collected are related to causes of the shift. Thresholds (especially grassland–woodland transitions) often take a long time to develop (e.g., 30–50 years; Peters et al. 2004a). There are few examples in which ecosystem drivers and processes have been assessed, monitored or evaluated before, during and after reaching a threshold. In most cases, thresholds are observed using analyses of historical data where key processes driving threshold behavior have been inferred (e.g., Peters et al. 2004a). Space for time substitutions have also been used to infer long term dynamics that can not be observed directly, although applicability of space-for-time substitutions has been questioned (Hargrove and Pickering 1992).

3.4 Cross-Scale Approach

Similar challenges in design and analysis of studies exist for grassland–woodland transitions occurring throughout the precipitation and temperature gradients in the US which must be accounted for in any experimental approach (Fig. 3.1). These challenges include: (1) high spatial and temporal heterogeneity in environmental drivers and conditions, and vegetation across a hierarchy of interacting scales, (2) threshold behavior with positive feedbacks that result in a persistent shift in dominance and change in ecosystem state, and (3) the importance of spatial context and connections among spatial units via contagious processes, such as seed dispersal.

We propose that a general design for a cross-scale approach to grassland–woodland transition would include the following steps: (1) identify patterns in broad-scale drivers, (2) determine hierarchical structure of the spatial units, (3) stratify and map the focal region based on these spatial units and environmental gradients, (4) sample and correlate attributes across strata within each spatial scale, (5) perform experimental manipulations of pattern–process relationships within key strata, and (6) use simulation modeling to investigate possible interactions between broad- and fine-scale drivers. Although each step has been conducted in previous studies, either individually or in combination with one or more other steps, the synthesis of all six steps into one approach is novel, in particular for understanding state changes associated with woody plant expansion. With such general approaches, we can explain or evaluate the potential for ecosystem change under a broader array of circumstances than is currently possible. We describe this approach using a case study from the Southwestern US.

3.5 Case Study: State Changes in the Chihuahuan Desert

A multi-scale sampling approach was used to improve understanding and prediction of grassland–woodland transitions in the northern Chihuahuan Desert. Landscapes of southern New Mexico exemplify arid and semiarid regions of the world where perennial grasslands have transitioned to xerophytic, unpalatable shrubs over the past 150 years (Gibbens et al. 2005). In the 1980s and 1990s, most studies of ecosystem state changes focused on the importance of plant-scale processes and the vertical and horizontal redistribution of resources among individual grasses, shrubs, and bare interspaces (Wright and Honea 1986, Schlesinger et al. 1990). The studies revealed that as grasslands degrade and shrubs invade, bare soil patches increase in spatial extent. Wind and water transport soil nutrients from bare areas to shrubs, where they accumulate to form "islands of fertility" maintained by positive plant–soil feedbacks. These plant-scale results were linearly extrapolated to explain state changes at broad scales (Schlesinger et al. 1990). More recently, the importance of spatial processes (e.g., seed dispersal) and redistribution of resources (water, nutrients) within and among patches of plants and larger landscape units have been recognized as influencing spatial and temporal variation in grassland–shrubland transitions (Peters et al. 2006a). Transport vectors (wind, water, animals, humans) act to move materials (seeds, propagules) and nutrients (nitrogen, water) within and among spatial units to result in patterns that can not be explained using a nonspatial, point-based approach.

For example, recent analyses show that redistribution of water from upslope locations to playas during high rainfall events can explain both high and low values of aboveground net primary production (ANPP) that likely depend on timing of the excess water relative to plant growth (Fig. 3.2a; from Peters et al. 2006a). Excess water that precedes the growing season can result in extremely large values of ANPP, whereas large amounts of water during the growing season can result in very small values of ANPP as a result of standing water that kills plants. In another example, spatially explicit, plant-based sampling that accounted for small arroyos where water accumulates and moves downslope was required to locate remnant grass plants in a shrubland (Fig. 3.2b; Peters et al. 2006c). Random sampling or sampling stratified by dominant vegetation characteristics likely would have missed the few plants found on average (0.1 grass/m^2) in this area. Because these grasses can be used as source plants for restoration, the locally, concentrated plants related to heterogeneous redistribution of water are more important to measure than the average value obtained from random sampling.

A recognition of the complexity of landscapes led to the need for a multi-scale approach to understand how changing pattern–process relationships across scales influence the rate and pattern of these transitions. Of particular interest is how plant-scale processes associated with individual grasses and shrubs influence spatial processes, resource redistribution among spatial units, and broad-scale drivers (e.g.., rainfall, temperature) to influence state changes from grasslands to shrublands. We focus on the role of three factors in determining these transitions: (1) spatial variation in environmental drivers (e.g., soil properties, geomorphology, weather), (2) the extent to which resource distribution is modified by patch structure interacting with transport vectors and environmental drivers, and (3) the extent to which changes in patch structure overwhelm within-patch processes (e.g., competition). These factors are examined within the temporal context of known historic legacies and measurements of environmental drivers (Peters et al. 2006a). This approach is designed to test the following hypothesis: as connectivity in bare patches increases, the rate and magnitude of material transfer that connects bare soil patches via wind and water increases. A threshold level of connectivity among bare patches (based on their size and spatial arrangement) is reached where the transfer of

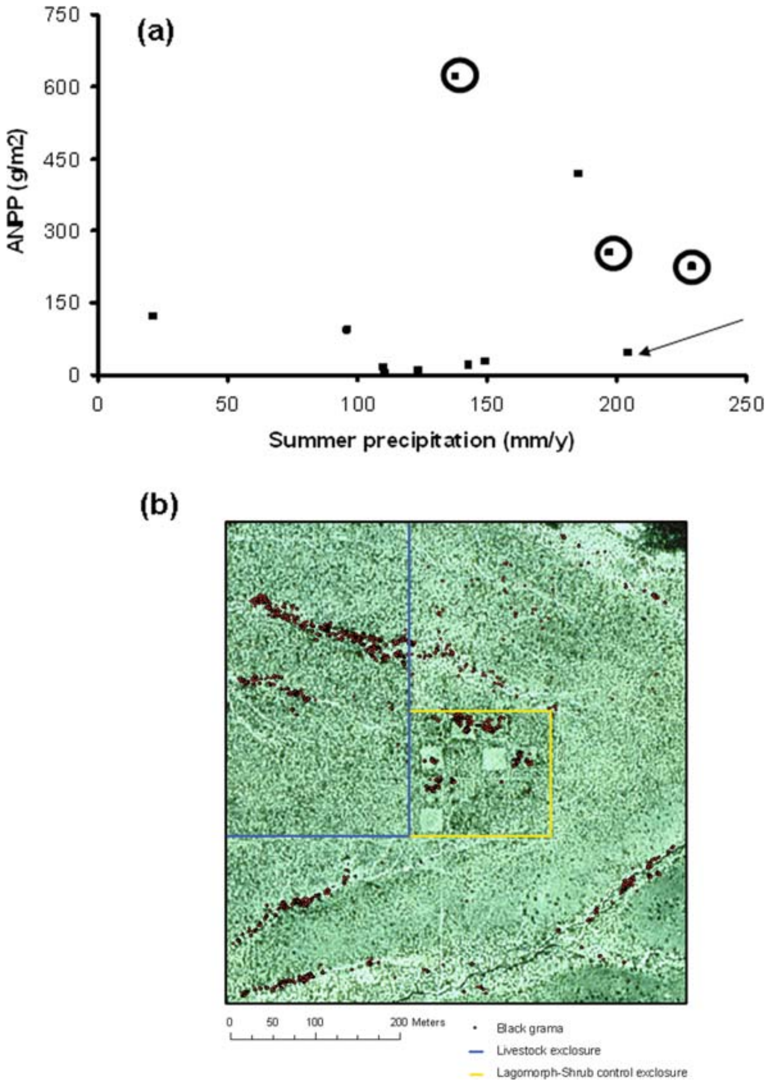

Fig. 3.2 Examples of the importance of transport vectors to landscape-scale dynamics. (**a**) Aboveground net primary production (ANPP) is not always related to rainfall on the site. Redistribution of water during wet years can create flooding events that either lead to higher (*circles*) or lower (*arrow*) than expected values depending on the timing of the excess water relative to plant growth. Redrawn from Peters et al. (2006a) with kind permission from BioScience. (**b**) Low average density (0.1 plant/m^2) of the historically dominant perennial grass, *Bouteloua eriopoda*, is a misleading value when plants are restricted to arroyos that receive additional water during rain events. These remnant plants can provide seed and vegetative propagules for revegetation in systems that are currently dominated by shrubs. Redrawn from Peters et al. (2006c) with kind permission from Rangeland Ecology and Management Journal

materials among patches increases nonlinearly. Because of positive feedbacks between bare ground connectivity and shrub dominance, the spatial extent of shrub dominance also increases nonlinearly, and resource losses from the system are escalated across increasing scales.

A pattern analysis of historical aerial photos and satellite images that started in the 1930s in southern New Mexico, USA provides support for this hypothesis (Peters et al. 2004a). Images show grasslands became dominated by woody plants through time, but the change in area dominated by woody plants increased nonlinearly with three distinct thresholds (Fig. 3.3). These thresholds likely occurred with a change in the dominant process driving shrub invasion and grass loss. The first threshold (T1) occurred at the point in time when transport of woody plant seeds into the area was the dominant process. This introduction phase was followed by a phase where patch expansion through seedling establishment was the dominant process. This shift in dominant process occurred at a second threshold (T2) where the slope of the line is smaller than during the introduction phase. The patch expansion phase lasted until the mid-1980s. At that time, the number and spatial arrangement of bare soil patches accompanying woody plant expansion was sufficient for another shift in dominant process to wind erosion and deposition (Okin et al. 2005). A third threshold (T3) was crossed with this shift in dominant process, and the rate of increase in woody plant-dominated area increased dramatically. A large area became dominated by coppice dunes centered on individual woody plants within 10 years.

Processes associated with these changes in patterns between the 1930s and present were surmised based on previous studies and past experience (e.g., Schlesinger et al. 1990). The connectivity hypothesis of changing pattern–process relationships is now being directly tested at the Jornada Basin Long Term Ecological Research (JER) site located in the northern Chihuahuan Desert of southern New Mexico, USA (32.5° N, 106.8° W, 1188 m a.s.l.) (Fig. 3.4a). The cross-scale approach to test this hypothesis is as follows. The study began in 2007, thus our results are preliminary and limited for Steps 3–5.

3.5.1 Step 1. Identify patterns in broad-scale drivers

We first identified the key broad-scale drivers for our system (wind, water) based on past experience and studies conducted at the JER (Havstad et al. 2006), and then determined the patterns in these drivers that can be used to stratify the landscape in Step 2. Landscape stratification is most often conducted using vegetation, soil, climate or topography. Here, we focus on spatial variability in drivers that influence state change dynamics in arid systems: wind that causes soil movement associated with desertification and water redistribution that influences plant success. In our initial analyses, we used satellite images and aerial photos to qualitatively determine broad-scale spatial

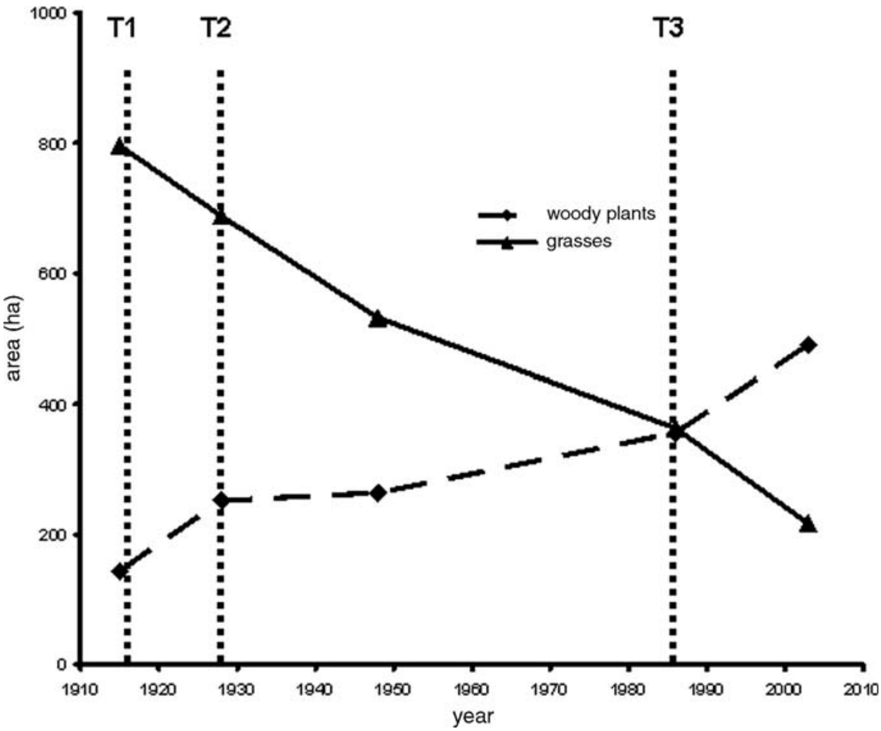

Fig. 3.3 In southern New Mexico, cover of woody plants (mesquite) has increased through time with three thresholds associated with different dominant processes: T1 was associated with the introduction and establishment of woody plants (1912–1928), T2 occurred when patch expansion processes were driving woody plant dynamics (1929–1988), and T3 occurred when wind erosion and deposition overwhelmed biotic processes to become the dominant processes determining woody plant dominance (1989–2004). Redrawn from Peters et al. (2004a)

variability in the effects of wind and water on resource redistribution (Fig. 3.4b). Data collected as part of the research project were used to confirm the quantitative characterizations of patterns in these drivers.

Wind: Patterns in sand deposition follow the prevailing winds from the major source of sand (Rio Grande) to the northeast across the JER (wind arrows; Fig. 3.4b). Sand deposition is less spatially extensive in the southern part of the JER, presumably because the Doña Ana Mountains obstruct wind flow. Thus, initial pattern analyses of sand deposition suggest that the JER can be divided into two general regions based on the effects of strong wind (north and central) and weak wind (south). Because sand deposition is determined by both wind speed and a sand source, long-term measurements of both wind speed and sand movement are needed to create a map of the effects of wind across the JER. These measurements were initiated as part of the multi-scale design.

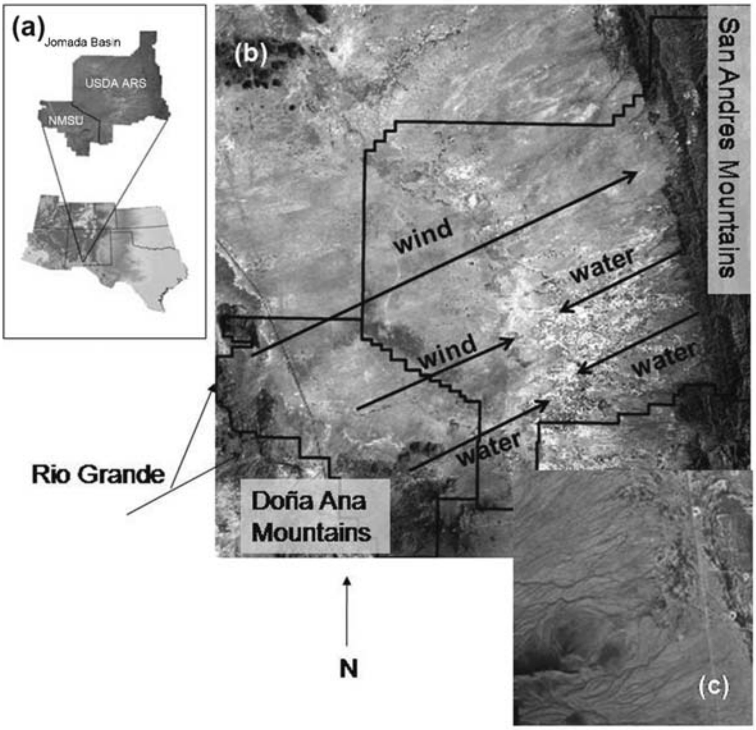

Fig. 3.4 (**a**) Location of the Jornada in southern New Mexico, USA where mean annual precipitation over the past 80 years is 24 cm, and average monthly maximum temperatures range from 13°C in January to 36°C in June. (**b**) Satellite image showing spatial variation in wind redistribution of soil particles, primarily from the southwest to the northeast (*wind arrows*). The southeastern part of the Jornada is blocked from sand movement by the Doña Ana Mountains, but has high redistribution of water from the mountains in the east (San Andres) and west (Doña Ana) to the basin (*water arrows*). (**c**) Redistribution of water from the mountains to lower elevations by arroyos is visible in close up images

Water: The spatial extent of the Jornada Basin is sufficiently large (200,000 ha) that rainfall is spatially variable across the Basin (Wainwright 2006); however, this variation is small (<50 mm/year rainfall; Peters et al. 2006e) relative to the redistribution of water along arroyos visible on high-resolution aerial photos (Fig. 3.4c). In general, the JER can be divided into areas containing arroyos that redistribute rainfall from the San Andres Mountains in the east and the Doña Ana Mountains in the southwest to lower elevations (water arrows; Fig. 3.4b), and relatively flat areas without broad-scale redistribution of rainfall. Stream gauges and small flumes distributed throughout the JER are being used to characterize the amount of water redistribution in these different areas such that a quantitative analysis can be used in the future to differentiate variability in the effects of water.

Wind and water: The resulting qualitative map of broad-scale drivers shows three main areas of the Jornada based on the relative importance of wind and water: (1) high wind, low water, (2) high wind, high water; and (3) low wind, high water (Fig. 3.4b). Interestingly, a transition zone occurs in the central to southern Jornada Basin where these two drivers either act in opposite directions (wind SW to NE; water NE to SW) or water operates from west to east or east to west. These patterns in broad-scale drivers provide an opportunity to evaluate their relative importance through landscape stratification followed by observations, experimental manipulation, and modeling in the steps below.

3.5.2 Step 2. Identify hierarchical levels of spatial units

The next step is to identify hierarchical levels of spatial units and delineate gradients or discrete unit classes (e.g., digital climate, landforms, soils, patch types/ecotones) using existing maps coupled to high-resolution remote sensing and novel analytical approaches, such as the use of object-oriented image classification, to map patterns at user-defined scales (e.g., Laliberte et al. 2007). Fine-grained patch distinctions and gradients that are difficult to detect in imagery at any scale can be complemented by field observations. Identifying hierarchical levels is a step that is often used in multi-scale studies (e.g., Wiens 1989). In our study, we identified four major hierarchical levels of spatial units based on previous research (Fig. 3.5; Peters et al. 2006a): (a) individual plants and associated bare interspaces, (b) patches or groups of plants and interspaces, (c) ecological sites or landscape units, and (d) soil-geomorphic units. The landscape unit (i.e., either a grassland or shrubland) is the spatial scale at which state changes in vegetation are often defined; thus, the landscape unit contained within a larger soil-geomorphic unit was the area of interest in the next step of stratification and mapping.

3.5.3 Step 3. Stratify and map the areas of interest

We used maps of landforms, soils, and vegetation to determine the location of our broadest hierarchical level, the soil-geomorphic unit, of which there are four on the JER (Monger et al. 2006): (1) the *basin floor sand sheet* (SS) on flat (<1% slope) loamy sands dominated by upland grasses and shrubs, primarily honey mesquite, (2) the *piedmont slope (bajada) sand sheet* on loamy sands dominated by honey mesquite, (3) the *piedmont slope (bajada)* (P) on silty and gravelly soils currently dominated by shrubs (creosotebush) with grasses in the understory, and (4) the *transition zone* (TZ) on low-gradient (<1% slope) loamy soils located between the sand sheet and piedmont slope bajada, and often characterized by banded vegetation patterns that commonly occur in arid regions on gently sloping terrain (Tongway et al. 2001) (Fig. 3.6a). Each

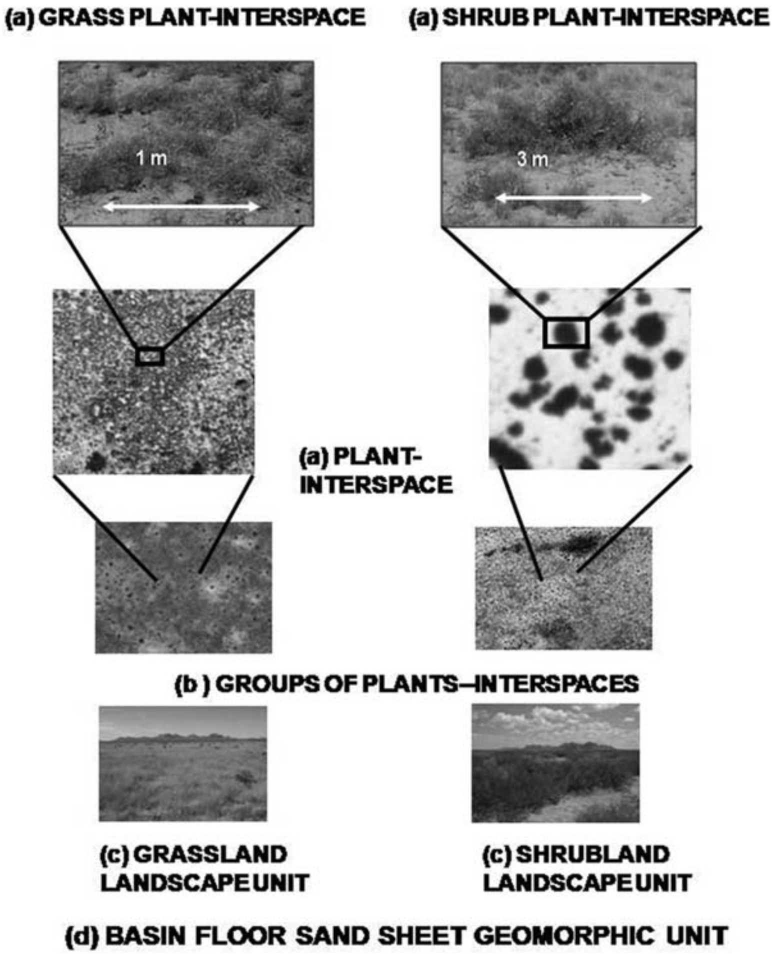

Fig. 3.5 Spatial hierarchy of arid systems includes four major scales: (**d**) the basin floor sand sheet soil-geomorphic unit consists of (**c**) two landscape units (grasslands, shrublands), each of which contains (**b**) patches of plants and bare interspaces; (**a**) each patch consists of individual plants and an associated bare interspace shown on aerial photo and close up photo

geomorphic unit exhibits variation in vegetation and soils across a hierarchy of scales (Fig. 3.5), and contains similar landscape units defined by topography (uplands, slopes, playas) and vegetation (grasslands, shrublands). However, the geomorphic units differ with respect to: (1) the two physical transport vectors (wind, water) at broad scales and all three vectors (including animals) at multiple, finer scales, and (2) feedbacks between spatial variation in patch structure and the other system elements.

Aerial photos were used to document patch structure within each of three of the geomorphic units (SS, TZ, P) and to assess how this patch structure changes

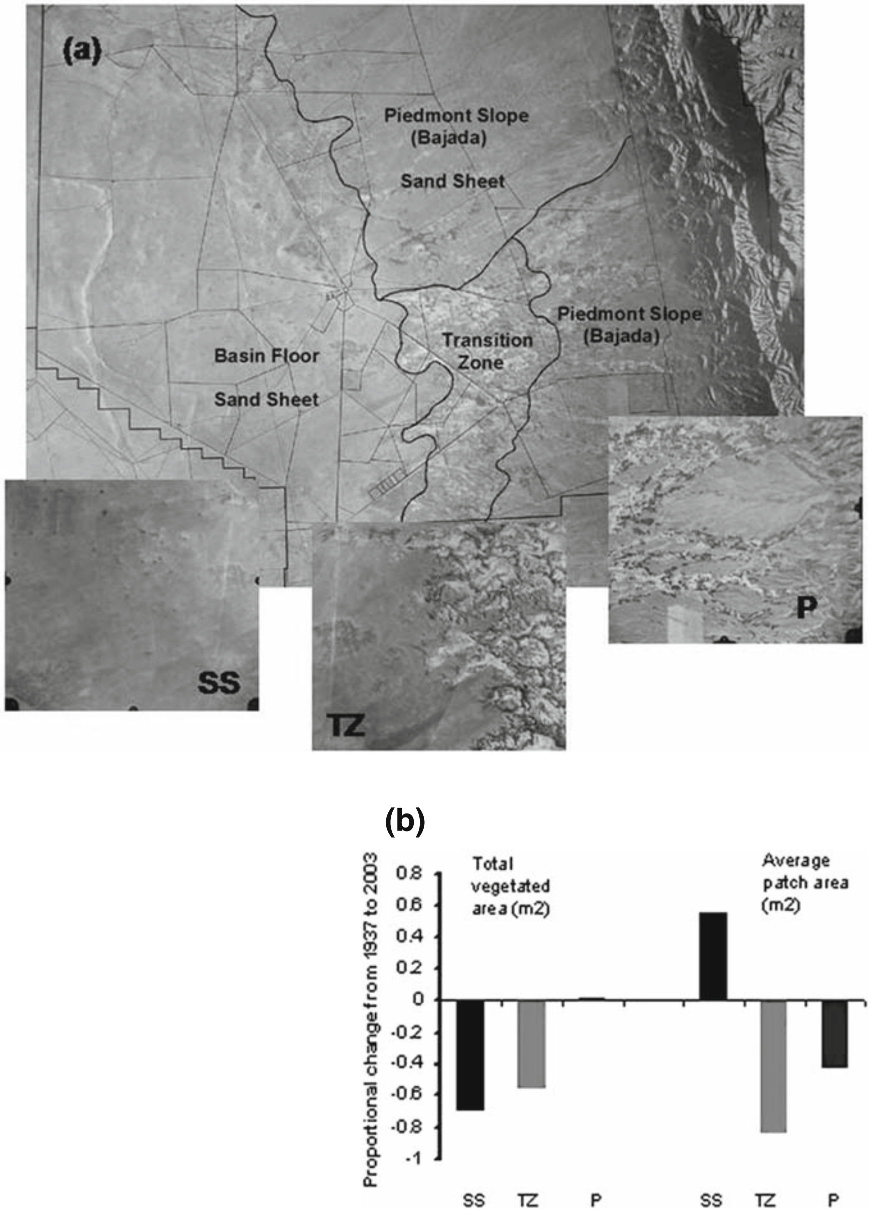

Fig. 3.6 (**a**) Location of four geomorphic units at the Jornada: patterns in soil and vegetation differ based on enlarged images for three of the units. (**b**) Changes in pattern from 1937 to 2003 in randomly selected 500 m × 500 m areas within each of three geomorphic units derived from aerial photos using Erdas Imagine and APACK software. The basin floor sand sheet (SS) decreased in vegetated area, yet increased in average patch size. The transition zone (TZ) decreased in vegetated area and patch size. The piedmont slope (bajada) (P) did not change in vegetated area, yet decreased in patch size. The piedmont slope sand sheet was not analyzed

through time (Fig. 3.6b). In general, different patterns were found through time for each geomorphic unit. Total vegetated cover decreased and average patch area increased for the SS whereas both total cover and patch area decreased for the TZ. The piedmont slope (P) decreased in average patch area with little change in total vegetated cover.

Data were collected to stratify each geomorphic unit into the next smaller level of landscape units. Patterns of vegetation and surface soil features of each landscape unit were quantified using high-resolution aerial imagery from a variety of sources, including unmanned aerial vehicles (UAVs; ground resolution of ca. 5 cm), aircraft images (ca. 25 cm ground resolution), and high- (60–70 cm QuickBird; 1 m IKONOS) and low-resolution (15–30 m resolution ASTER and Landsat) satellite data. Patches of bare ground and vegetation were extracted separately for all imagery and compared to show how landscape metrics for each patch type change with spatial scale. Field measurements were strategically employed to validate image interpretation. Each landscape unit was internally stratified based on levels of connectivity in bare soil patches determined from image analyses and spatial analysis software (Bestelmeyer et al. 2006a), and broad-scale patterns in water and wind vectors was quantified from a sensor network being developed as part of Step 1.

3.5.4 Step 4. Sample and correlate attributes

Field sampling of vegetation and soil was conducted within each landscape unit to document relationships both within and among patches. Sampling across each spatial unit (landscape or patch) in a “snapshot” fashion was used to quantify how patterns and processes underlying transitions vary between spatial units, and to ask how spatial context within the broader-scales affects these relationships. This approach is a relatively simple way to measure cross-scale effects. One example is to ask how erosion rates vary between patch types with 75% grass cover and 25% grass cover, and how this difference, in turn, is affected by the occurrence of these patch types in landscape units containing soils of high versus low erodibility, that, in turn, occur in soil-geomorphic units of high versus low wind speed.

3.5.5 Step 5. Experimental manipulations of drivers

The next step called for conducting experimental manipulations in conditions identified from step 4 as critical to state change dynamics. For example, replicate intensive study sites were selected within each landscape unit to represent a range of broad-scale drivers, in this case, high versus low wind, and a range of connectivity in resource redistribution levels (high to low) at finer scales, as determined from the pattern analyses in Step 3. Manipulations of patch structure were used to either increase or decrease bare ground connectivity. Areas of high bare ground cover were manipulated by adding structures to mimic grass/shrub effects to disrupt connectivity by wind and water transport processes. Areas with low bare ground connectivity were manipulated by removing plants to increase bare ground connectivity and movement of soil by wind. Replicated non-manipulated areas serve as controls. Spatially distributed soil collectors are used within each study site to quantify the scale, direction, and rate of material transport by wind throughout each site through time. Data are collected in adjacent downwind areas to quantify connectivity among replicates and adjacent landscape and geomorphic units. Vegetation (cover, composition, spatial distribution) and soil properties are measured through time.

3.5.6 Step 6. Simulation modeling of responses

Simulation models can be used to investigate possible interactions between broad- and fine-scale drivers using a broader combination of environmental conditions than possible experimentally (e.g., Rastetter et al. 2003, Urban 2005). Model simulations can be conducted by modifying broad- and fine-scale drivers independently and in combination, and multiple regression analyses can be used to determine the relative importance of each driver. Models can also be used to push the system to novel conditions, such as directional changes in climate, and to determine the susceptibility of different patch types to regime shifts (Peters 2002).

Simulation modeling subsequently integrated with results from existing and planned field and greenhouse studies can be used to: (1) identify key processes and interactions driving ecosystem dynamics, (2) develop new testable hypotheses and guide experimental designs, and (3) predict future conditions under alternative management and climatic scenarios. Models of horizontal transport processes (wind, water, animal) are being linked with a vegetation–soil water dynamics model to simulate transfer of materials both within and among spatial units across a range of scales (Fig. 3.7). Modeling experiments will be designed to: (1) identify and assess plant-soil-water-nutrient interactions to determine their importance and the nature of limitations, co-limitations, contingencies, and feedbacks mechanisms, (2) determine the extent to which accounting for cross-scale interactions can improve predictions of ecosystem dynamics across a range of environmental conditions and management scenarios, (3) determine the conditions under which fluxes of water and windborne material between plants and interspaces at fine scales can cascade to impact ecosystem dynamics at broader scales, and (4) the conditions where broad scale drivers begin to overwhelm or constrain fine-scale processes.

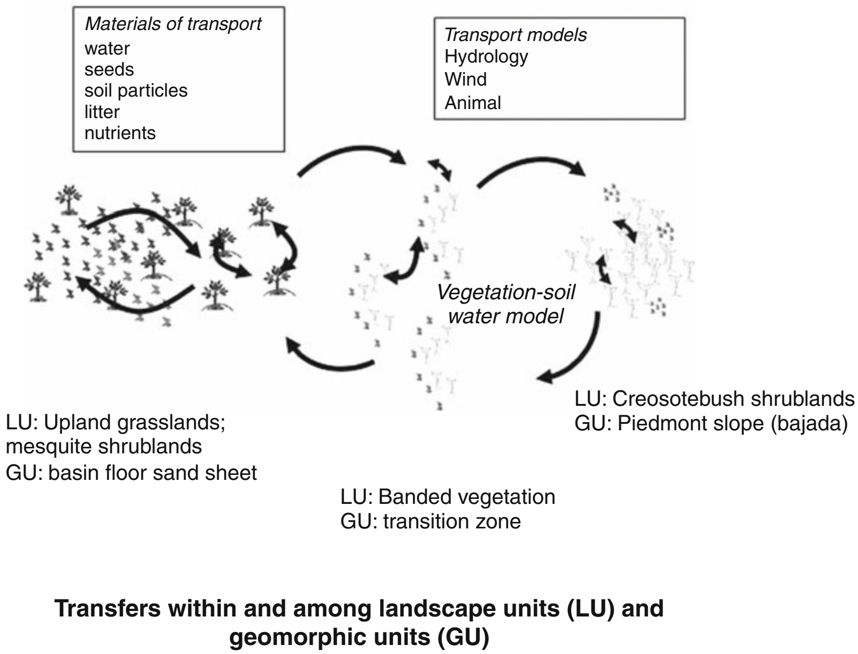

Fig. 3.7 Simulation models of vegetation and soil processes at the scale of individual plants and patches are being linked with transport models of wind, water, and animals to simulate the transfer of materials (water, seeds, soil particles, litter, and nutrients) both within and among landscape units (LU; e.g., upland grasslands) and geomorphic units (GU; e.g., basin floor sand sheet). Specific materials and transport vectors can differ for each landscape unit and geomorphic unit

3.6 Analytical Approaches to Identifying and Predicting Regime Shifts

There is an important role for conventional statistics to analyze data generated from hierarchically structured or spatially structured sampling. The key to such analysis lies in linking inferences gained from broad-scale, pattern-based studies with embedded fine-scale, mechanistic studies to identify transitions. For example, traditional statistics can be used to determine if nonlinearities detected in pattern–process relationships at fine scales (e.g., between grass cover and erosion rate or shrub establishment rate) translate to differences in the occurrence of alternative states at broad spatial and temporal scales. In addition, statistical analyses can be used to determine if the following criteria have been met to identify the presence and type of regime shift (from Scheffer and Carpenter 2003): (1) Is there a discrete step function or intervention in the time series? (2) Does the response variable have a bimodal or multi-modal distribution? (3) Is there a different functional relationship in different regimes? (4) Given different starting conditions, will the system go to different stable states? (5) Does the system shift to an alternative state when perturbed? (6) Does the system have a different trajectory when the forcing function increases compared to when it decreases? (7) Does the second derivative of the time series have peaks that indicate nonlinearities?

There are also a variety of novel statistical approaches to deal with pattern (survey) data gathered at multiple scales that show promise in predicting regime shifts (e.g., Lichstein et al. 2002, Keitt and Urban 2005). Three non-traditional approaches warrant discussion here.

First, quantile regression offers the ability to examine relationships across a range of quantiles of a dataset, especially at the limits of the 'data cloud' that often result when limiting factors (such as soils and climate) structure data (i.e., 5–10% and 90–95%; Cade and Noon 2003). Quantile regression is especially useful when the distribution of a response variable (e.g., grass cover) on environmental gradients in a reference state at a particular scale is obscured by events that cause transitions to alternative states (Bestelmeyer et al. in review). For example, deviations away from an upper limit to the data (defined by sites in a reference state) may be caused by transitions and disjunct clouds of points that represent alternative states.

Second, variability in temporal data may also indicate transitions. Rising variance in time series data of key proximate variables underlying transitions may provide a useful means of predicting transitions (Brock and Carpenter 2006). Increasing variability in grass cover (possibly detected at several scales) or erosion rates with variations in climate may similarly herald an increased risk of a transition to woodland-dominated state (see also Viglizzo et al. 2005 for other approaches).

Third, changes in the size distribution of vegetated or bare soil patches may be warning signs of an impending regime shift in arid systems. Cellular automata modeling suggests that transitions between patch types defined by simple rules can lead to a predictable departure from the power-law behavior of grasslands (Kéfi et al. 2007, Scanlon et al. 2007). Field observations of changing distribution of bare soil patches with increasing soil degradation that leads to transition to woody plant dominance support these theoretical analyses (J.E. Herrick unpublished data).

3.7 Conclusions

State changes from grasslands to woodlands provide the context for development of a multi-scale experimental approach combined with simulation modeling and statistical analyses to examine the key processes influencing these dynamics. This approach is sufficiently general to be applied to other systems where drivers and responses interact across scales, either with or without a state change (e.g., Scheffer et al. 2001, Allen 2007, Willig et al. 2007). In addition, this approach is relevant to broader questions regarding changes in global ecology, such as: how and under what conditions do dynamics and decisions made at fine scales influence dynamics at broader scales and how and under what conditions do broad-scale dynamics overwhelm fine-scale processes to influence landscape patterns? Addressing these questions is becoming increasingly important as ecologists expand the scope and spatial extent of interest beyond individual sites to regions, continents, and the globe (Peters et al. 2008). Existing and emerging networks of sites, such as the Long Term Ecological Research network (www.lternet.edu), the National Ecological Observatory Network (www.neoninc.org), AmeriFlux (public.ornl.gov/ameriflux), and the National Atmospheric Deposition Program (nadp.sws.uiuc.edu), are collecting observational and experimental data primarily at the site scale, yet are charged with addressing broad-scale questions. These networks necessitate a multi-scale approach such as the one described here.

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