

Land Management in the American Southwest: A State-and-Transition Approach to Ecosystem Complexity

BRANDON T. BESTELMEYER*
JEFFREY E. HERRICK

USDA-ARS, Jornada Experimental Range
 New Mexico State University
 Las Cruces, New Mexico 88003, USA

JOEL R. BROWN
DAVID A. TRUJILLO

USDA-NRCS, Jornada Experimental Range
 New Mexico State University
 Las Cruces, New Mexico 88003, USA

KRIS M. HAVSTAD

USDA-ARS, Jornada Experimental Range
 New Mexico State University
 Las Cruces, New Mexico 88003, USA

ABSTRACT / State-and-transition models are increasingly being used to guide rangeland management. These models provide a relatively simple, management-oriented way to classify land condition (state) and to describe the factors that might cause a shift to another state (a transition). There are many formulations of state-and-transition models in the literature. The version we endorse does not adhere to any particular

generalities about ecosystem dynamics, but it includes consideration of several kinds of dynamics and management response to them. In contrast to previous uses of state-and-transition models, we propose that models can, at present, be most effectively used to specify and qualitatively compare the relative benefits and potential risks of different management actions (e.g., fire and grazing) and other factors (e.g., invasive species and climate change) on specified areas of land. High spatial and temporal variability and complex interactions preclude the meaningful use of general quantitative models. Forecasts can be made on a case-by-case basis by interpreting qualitative and quantitative indicators, historical data, and spatially structured monitoring data based on conceptual models. We illustrate how science-based conceptual models are created using several rangeland examples that vary in complexity. In doing so, we illustrate the implications of designating plant communities and states in models, accounting for varying scales of pattern in vegetation and soils, interpreting the presence of plant communities on different soils and dealing with our uncertainty about how those communities were assembled and how they will change in the future. We conclude with observations about how models have helped to improve management decision-making.

Ecosystem management and conservation are based on conceptual models that represent our understanding of how and why ecosystems change over time and how different management actions are likely to affect them. These models are rarely explicitly defined by land managers. For grazing-land ecosystems in the United States, state-and-transition models are beginning to be used by managers to organize, communicate, and apply our understanding of these ecosystems. (Westoby and others 1989; USDA NRCS 1997)

Government and academic scientists, federal and state rangeland managers, conservation biologists, and

local ranchers throughout the country are becoming involved in the production of these models in individual efforts and workshops led by the US Natural Resources Conservation Service and other organizations (e.g., the Nature Conservancy). Models are becoming increasingly available on websites and in publications that are targeted to both resource managers and laypersons. Hundreds of models have already been generated in the United States, Australia and other countries with significant areas of rangeland. We expect that thousands of these models will be developed over the next decade, each tailored to a specific set of soil, landscape, and climate conditions and organized around specific (but probably unspecified) assumptions. The conceptual models reflect our current understanding of ecosystem dynamics and are easily modified as knowledge increases. The basic structure of the models and the fact that they are designed to highlight knowledge limitations makes them useful for many

KEY WORDS: Chihuahuan Desert; Community dynamics; Desert grassland; Grazing management; Simulation models; Rangeland; Resilience; Soil maps; Thresholds

Published online May 28, 2004.

*Author to whom correspondence should be addressed, *email:* bbestelm@nmsu.edu

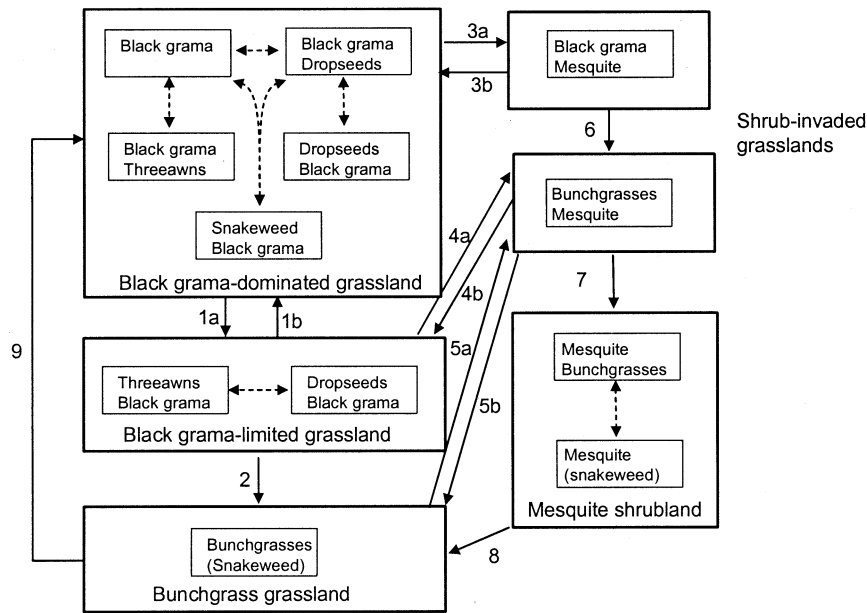


Figure 1. A state-and-transition model for the Sandy ecological site in the southcentral/southwestern Chihuahuan Desert of New Mexico, USA. Smaller boxes are communities identified by dominant perennial species and the large boxes are states. Dashed arrows between communities represent known pathways of change caused by variation in livestock disturbance intensity and frequency or variation in the timing and amount of precipitation. Solid arrows are transitions that are described in the legend below. See the text for a discussion of the distinction between transitions and pathways. Black grama, dropseeds, and threewawns are perennial grasses. Black grama is palatable to cattle for a longer duration than the other species and is comparatively sensitive to grazing pressure. Snakeweed (*Xanthocephalum* Willd. spp.) is a subshrub that tends to proliferate with reductions in grasses or with adequate winter-spring precipitation. Mesquite is a large shrub that tends to invade intact or degraded grasslands, promote the loss of grasses in intershrub spaces, and concentrate resources beneath its canopy. 1a. Grazing in drought periods, moderate soil degradation. 1b. Restoration of soil fertility (if climate not involved). 2. Black grama extinction due to heavy grazing in drought, severe soil degradation. 3a. Introduction of mesquite seeds, reduced grass competition, lack of fire. 3b. Shrub removal, restoration of fuel loads and fire. 4a, 5a. Mesquite invasion. 4b, 5b. Shrub removal, restoration of fuel loads and fire. 6. Black grama extinction due to mesquite competition and grazing. 7. Heavy grazing and grass loss, inter-shrub erosion, soil fertility loss, high soil temperatures, small mammal herbivory. 8. Dune destruction, mesquite removal, soil stabilization, nutrient addition, seeding during wet periods. 9. Reseeding, replanting with restoration of soil fertility.

other ecosystems (Llorens 1995; Herrick and others 2002).

Conceptual state-and-transition models expand upon earlier models of rangelands based solely on succession (Dyksterhuis 1949). In successional models, overgrazing and other catastrophic disturbances could push land away from an historic climax plant community, but it was assumed that the land would always recover when the degrading process was halted. State-and-transition models have been used to revisit these ideas and incorporate the possibility for “nonequilibrium,” “nonlinear,” and “threshold” behavior in rangelands (Westoby and others 1989; Laycock 1991). In other words, altered rangelands might not recover their historical structure for decades (Valone and others 2002), or longer, because of changes in soil water and nutrient availability, often initiated by changes to the structure of the plant community itself. For example, it

has long been recognized that grassland recovery in many shrub-invaded sites in the southwestern United States and northern Mexico is limited by self-reinforcing changes in fire frequency and in the spatial distribution of water and nutrients (Valentine 1970; Wright and Honea 1986; Schlesinger and others 1990). These persistent vegetation and soil changes can be represented in a diagram with two or more boxes with arrows between them (Figure 1). The shift from a self-perpetuating grassland toward a shrubland or bare-ground dominated state has been referred to as crossing a “threshold” (Freidel 1991). In this way, a shift between states implies that an intensive, expensive management practice would be required to restore historical ecosystem structure (Freidel 1991; Bestelmeyer and others 2003). Relatively reversible changes [e.g., those due to short-term climate fluctuations (Jackson and Bartolome 2002)] in which species establishment and mor-

tality rates fluctuate over time can be included in each large box (state). This distinction allows state-and-transition models to represent both nonequilibrium and multi equilibrium dynamics (Briske and others 2003) and help focus management on predicting and avoiding undesirable transitions and identifying opportunities to promote desirable ones.

In the creation of specific models, participants are able to reconsider generalizations about the nature and causes of ecosystem dynamics (Harwell and Gentile 2003). Our efforts at synthesis in southwestern US rangelands indicate that vegetation occurring on different soil types and in different climatic regions exhibit vastly different kinds of change—sometimes successional, sometimes not. The different kinds of response are probably due to both differences within and between species and their varying interactions with soil properties and climate (MacGregor and O'Connor 2002). Perhaps most important, the fundamental notion of a “climax” plant community, featured in both early succession models and many state-and-transition models, is revealed to be at odds with our current understanding of these ecosystems. Climate regimes and soils change over decades (Nielson 1986) and centuries (McAuliffe and Van Devender 1998) and vegetation changes with it, despite our management. The slow, dispersal- and evolution-driven march of relatively recent invaders, such as cheatgrass [*Bromus tectorum* (Novak and Mack 2001)] or older ones such as creosotebush [*Larrea tridentata* (Hunter and others 2001)] generates change irrespective of climate, soils, or management. Species themselves are dynamic entities because they disperse, adapt and evolve. We create state-and-transition models to pull together these different processes and theories to understand ecosystem complexity and our contributions to it. To avoid repeating the errors that initiated interest in state-and-transition models in the first place, models must be flexible and unencumbered by adherence to any one concept of ecosystem function and dynamics.

In our experience, state-and-transition models have become much more than a recasting of ecosystem dynamics using box-and-arrow diagrams or precursors to simulation models. They induce model builders and model interpreters to think broadly and critically about the nature of biological communities, the role of scale, and the interactions among factors structuring soils and vegetation. They also help focus attention on the costs and potential benefits of applying different management actions to different parts of the landscape. The models create an opportunity to integrate the different kinds of dynamic process that we currently recognize and to consider the importance of different

processes in different parts of landscapes and regions. In this article, we discuss (1) our approach to the structure and theoretical basis of the models in contrast to related approaches, (2) provide examples to illustrate how models can represent systems governed by varying processes and with different degrees of (recognized) complexity, and (3) explain how information in the models is being applied.

A Conceptual, Hands-on Approach to State-and-Transition Models

One goal in state-and-transition modeling is to focus the attention of managers on issues and processes that have been inadequately considered in the past. These interrelated issues include (1) variation in vegetation and surface soil properties within groups of similar soil series [i.e., the ecological site as defined by the Natural Resources Conservation Service] (Bestelmeyer and others 2003)] and within a soil series, (2) differences in vegetation as a function of combined differences in climate, land use history, and subtle inherent soil differences, (3) distinguishing current human impacts from climate effects and the legacies of historical impacts, and (4) differences in the apparent resistance and resilience of similar parcels of land, even when managed similarly. We explore these topics in producing conceptual state-and-transition models in order to provide managers with (1) an accounting of the multiple, scale-dependent causes and patterns of vegetation change and spatial turnover, (2) a review of scientific results that suggest potentially important vegetation and soil processes at a site, and (3) indicators that provide evidence that these processes are operating at a site.

Unlike other formulations of state-and-transition models, our approach is not quantitative. Distributional landscape models [e.g., Markov or semi-Markov models (Baker 1989, Scanlan 1994) Vegetation Dynamics Development Tool (Buekema and Kurz 2000)] or even more sophisticated spatially dependent transition models (Soares-Filho and others, 2001) that have proven useful for some forest and savanna systems have limited utility for land managers in southwestern US rangelands for at least three reasons.

First, and most important, conceptualizing transitions among states as a probabilistic disturbance and deterministic recovery process acting at fixed scales does not reflect our current ecological understanding of semiarid rangelands. Our conceptual models are designed to alert managers to processes and their interactions (such as grazing or drought disturbance, grass mortality, bare-ground expansion, soil microbial

biomass depletion, and erosion) that, if sustained, will gradually or rapidly (and deterministically) produce transitions with long or infinite recovery times (Ludwig and Tongway 1997, Ludwig and Tongway 2000; Davenport and others 1998; Northup and others 1999; Wilcox and others 2003). These processes are coupled across spatial scales and time, exhibit feedbacks with one another, are buffered or accelerated by the weather, and exhibit nonlinear rates of change (Okin and others 2001; Scheffer and others 2001). This type of transition is not discrete and the probability that a transition will “go to completion” on a parcel of land of a given size depends on time, the weather, and local and landscape effects on the rates of interacting processes. Static or even “multiple-scenario” transition probabilities derived from expert guesswork or retrospective empirical analyses are unlikely to capture these processes (see Underwood 1995).

Second, it is widely believed that many, if not most, transitions in semiarid rangelands are determined by interactions of land use with the weather (Herbel and others 1972; Neilson 1986; Fynn and O’Connor 2000; Van Auken 2000; Okin and others 2001). For example, the reduced establishment and increased mortality of perennial grasses that could initiate many transitions is believed to result from sequences of drought years and grazing and trampling by cattle (Wright and Van Dyne 1976). The establishment of a dominant Chihuahuan Desert grass, black grama [*Bouteloua eriopoda* (Torr.) Torr.] might occur only when dry winters are followed by one or more wet summers (Neilson 1986). In addition, instances of catastrophic soil degradation, gully formation, erosion, and sand burial of grasses might occur when high-intensity rainfall events or severe windstorms strike low-cover grasslands (Schumm 1977; Gibbens in press). Such sequences of climatic events are presently inestimable at subregional scales for a variety of reasons (e.g., Pielke and Avissar 1990). Thus, even if we develop mechanistic models of the transition process (e.g., Rastetter and others 2003), they might still be incapable of providing useful site specific forecasts of the consequences of land-use strategies.

Finally, landscape models (*sensu* Baker 1989) are usually focused on generalizations about (Rupp and others 2002) or hypothetical scenarios of (Hemstrom and others 2002) broad-scale changes that are logical consequences of assumed local probabilities of change. Such an approach emphasizes the triggers of change, rather than the underlying factors predisposing a site to change (Stafford Smith 1996). Our models, on the other hand, seek to aid managers in *manipulating* local probabilities across landscapes. Given the presence of threshold behavior and irreversible degradation in eco-

systems, any nonzero transition probability will eventually lead to a stable landscape composed of degraded states. Indeed, this appears to be happening in some desert grasslands (Gibbens and others, unpublished data). In order to arrest this process, managers must be able to detect the processes predisposing particular sites to undesirable transitions and to minimize transition probabilities, rather than play a game of ‘degradation roulette’ implied by Markov models.

Consequently, the conceptual state-and-transition models discussed in this article employ empirical and mechanistic simulation modeling results and, where these are unavailable, expert opinion and observations to describe the conditions under which sites become susceptible to different kinds of transition [e.g., the loss of resilience (Scheffer and others 2001)]. The description of transition processes include indicators of risk and change, and indicator patterns are connected to processes using experiments and monitoring studies (Pyke and others 2002). The models guide the on-the-ground interpretation of patterns in vegetation and surface soil properties that are used to form hypotheses or conclusions (where monitoring is not employed) about the future condition of vegetation and soils on specific parcels of land (Underwood 1995). The philosophy underlying this approach holds that useful forecasts of ecosystem states must focus on the underlying resilience of ecosystems and account for unique local characteristics and landscape/temporal context.

Theoretical Basis and Structure of State-and-Transition Models

As Jackson and others (2002) pointed out, “the state and transition model” is not a theory of vegetation dynamics (see also Rodriguez Iglesias and Kothman 1997). Model structures, however, are certainly, influenced by theory. Our approach recognizes the utility of nonequilibrium and equilibrium theories of vegetation dynamics (*sensu* Illius and O’Connor 1999; Sullivan and Rohde 2002; see also Briske and others 2003), although we emphasize shifts among variable—but bounded—equilibria because of their management significance. Persistent shifts in plant species composition and ecosystem processes are a major concern in many southwestern U.S. ecosystems over the last two centuries (Bahre and Shelton 1993, Allen and others 2002, Gibbens and others, unpublished data).

Although such discontinuous changes have been referred to as “nonequilibrium” with respect to plant community structure (Jackson and others 2002; Briske and others 2003), previous authors have used this term to indicate that livestock populations are not in equi-

librium with forage resources because of frequent drought disturbance and subsequent livestock mortality (Ellis and Swift 1986; Sullivan and Rohde 1999). In this latter conceptualization, livestock do not have significant effects on vegetation in nonequilibrium systems because their populations are seldom large or persistent enough at a point in space to cause plant mortality (but see Illius and O'Connor 2000). Although this might be true in some ecosystems featuring a relatively high annual rainfall, deep mollic (organic matter-rich) surface soils, grazing-tolerant plants, or unrestricted livestock movements, this might not be true for many ecosystems in the American Southwest (and elsewhere).

There is a considerable body of evidence that livestock grazing directly and indirectly contributed to persistent degradation in southwestern US rangelands by selective herbivory on grazing-intolerant grasses, disturbance and exposure of erosion-sensitive soils, dispersal of competitive shrubs' seeds, and fire suppression (Brown and Archer 1999; Allen and others 2002; Herrick and others 2002). The control of movement patterns and supplementation of livestock with fences, food, and water in the United States may be an important cause of departures from nonequilibrium predictions because such management maintains a tight coupling of livestock to forage production at small scales despite drought/recovery cycles (Ellis and Swift 1986). Thus, attempts to "equilibrate" inherently nonequilibrium environments by manipulating biotic interactions and their scales (Wiens 1984; DeAngelis and Waterhouse 1987) might contribute to persistent degradation.

Consequently, model structures must describe dynamics associated with equilibrium and nonequilibrium theoretical constructs in order to be effective. For example, communities occurring together within a state fluctuate from one to the other due to stochastic disturbances and succession, but such shifts by themselves are not believed to determine long-term community trajectories such as through changes to critical soil properties [e.g., infiltration rates, organic matter (Davengport and others, 1998)] or priority competitive effects (Brown and Archer 1987). Such fluctuations could however, affect the vulnerability of a site to transitions among equilibria. These dynamics reflect both equilibrium (succession and the persistence of a state) and nonequilibrium (abiotic variability) processes.

In our models, states reflect distinct rules that define different equilibria. States are distinguished by persistent differences in plant community composition, production, and the status of relatively dynamic (Herrick and others 2002) or use-dependent (Grossman and others 2001) soil properties. States often reflect

changes in the nature and direction of positive feedback relationships (Van de Koppel and others 1997). Nonequilibrium forces, such as drought or disturbance, might catalyze transitions among feedback-determined equilibria in circumstances where resilience is compromised. Thus, our concept of states also blends equilibrium and nonequilibrium theory.

In creating and applying models, then, a fundamental question is "How should we designate the communities and states in state-and-transition models?" The answer to this question determines the form an individual state-and-transition model takes, the theory underlying the model, and how states and communities are recognized on the land. Once a community (and state) has been recognized, how do we interpret its presence on a particular soil, within a particular region? How do we deal with our uncertainty about how that community came to be, and what it will become in the future? In the sections that follow, we define our approach to these questions. Rather than tackling each question separately in a general way, we illustrate how we integrate the answers to these questions by discussing how we have constructed state-and-transition models of varying nature and complexity. Although the examples are specific to rangeland ecosystems, the issues are relevant to nearly all ecosystems in which persistent transitions occur.

Components of State-and-Transition Models

Currently, state-and-transition models used by US federal agencies are categorized according to the *ecological sites* of the Natural Resources Conservation Service. These "sites" are edaphic functional groups that differ in important properties, such as texture, chemistry, erodibility, or restrictive horizons (Dyksterhuis 1949). Because soil genesis depends on climate, parent material, and landscape position (Jenny 1941), ecological sites can also often be distinguished as distinct geomorphic units occurring in an area with similar climate.

For each model, plant communities were used as the basic units. Although some authors advocate quantitative, multivariate (e.g., TWINSpan) community delineations (Allen-Diaz and Bartolome 1998; Jackson and Bartolome 2002), we have found it more useful to employ flexible definitions based on dominant, keystone, or valuable species (Figure 1). This allows us to focus on species that are important to managers and that we hypothesize are important to ecosystem functioning. Thus, the specification of communities is embedded in the hypothetical and theoretical framework of each model.

Communities that are grouped together within states are hypothesized to replace one another along traditional succession–retrogression pathways (Figure 1). For example, within a state, heavy grazing could result in dominance by unpalatable grass species, but reduced grazing intensity will initiate relatively rapid recovery of palatable species (Figure 1: dashed arrows in the “Black grama-dominated grassland” box). Short-term fluctuations in climate could have similar effects by favoring different species in different years. Thus, facilitating practices (grazing management) can be used to promote a particular community type within a state (Bestelmeyer and others 2003). Highly resilient community types, such as those featuring highly fertile soils and an evolutionary history of grazing (e.g., mid-western US tall-grass prairie), might have only one state.

In less resilient communities, recovery within management time frames might be achieved only through relatively intensive practices, if recovery is possible at all, once dominant species are driven extinct, highly competitive exotics invade, soil is degraded, hydrology altered, or climate is changed. We denoted these kinds of change as transitions to a new state (Figure 1; arrows 1a, 2, 3a, 4a, 5a, 6, and 7). Intensive practices vary widely in their costs and include seeding, the removal of competitive species, or the addition of soil amendments. Persistent or directional changes in climate that underlie important changes in plant communities are unlikely to be reversed even with intensive practices.

Generation of state-and-transition models requires that continuous variables (plant community composition, soil properties, and time) be used to define discrete states, communities within states, and transitions. This is a useful simplification for communicating ecological dynamics (Westoby and others 1989). The distinction between “shifts among communities” and “transitions among states” is used to communicate the operation of different ecological processes and the need for external inputs to create changes between some pairs of communities (Stringham and others 2003). In reality, some transitions might be reversed to some degree over sufficiently long time periods, but only a few of the species comprising a historic or desired community might recover. Consequently, state-and-transition model development requires that assumptions about time frames, community identity, and inputs be clearly defined (Dale 2003). The time frame in our models is generally a management time frame (at least several decades; but see Stringham and others 2003). Communities are generally identified using dominant or otherwise important plant species. “External inputs” usually include addition of nutrients and

organic matter or the use of machinery or herbicides to modify plant community composition or soil structure. External inputs do not include changes in grazing management and other factors that do not require a significant addition of resources and energy.

Case Studies

The following four case studies from rangelands in southern New Mexico, USA illustrate how we have applied these concepts to systems that vary widely in their complexity. These models are described in greater detail at www.nm.nrcs.usda.gov/technical/fotg/section-2/ESD.html.

A Six-State Model: The Importance of Black Grama on Sandy Loams

The state-and-transition model for sandy loam soils [e.g., a coarse-loamy Petronodic Haplocalcid; nomenclature follows Soil Survey Staff (1999)] in the 20–25 cm precipitation zone of southcentral/southwest New Mexico emphasizes the importance and vulnerability of black grama and the tendency of honey mesquite (*Prosopis glandulosa* Torr) to invade grasslands and exacerbate grass loss and subsequent erosion (Figure 1). In historical, highly productive grasslands on these soils, black grama was often highly dominant (black grama-dominated state) and its caespitose, bushy growth form is relatively effective in retarding soil erosion compared with many other grasses native to the region (Paulsen and Ares 1962). Black grama is particularly vulnerable to persistent loss because it is highly favored as winter forage by cattle. In addition, black grama’s dominant mode of local colonization is via stolons, and stolon establishment is vulnerable to trampling and drought (Nelson 1934, Wright and Van Dyne 1976). Decreases in black grama are associated with increases in the relative abundances of bunchgrasses such as dropseeds (*Sporobolus* R. Br. spp.) and threeawns (*Aristida* L. spp.), which are less able to stabilize sandy soils. Consequently reductions of black grama have ecosystem-level effects.

Because establishment by seed is limited in black grama (Jackson 1928), recolonization following extensive mortality is severely limited. Furthermore, the persistent absence of black grama might affect soil fertility such that it is difficult for black grama to reestablish, possibly owing to the loss of soil organic matter or microbial associates (e.g., Bever and others 1997; Barrow, personal communication). Because of the importance of losing black grama and the difficulty in naturally reestablishing this grass following its reduction, we

defined a “black grama-limited” state. This state appears to be stable—black grama persists in patches but does not expand with release from grazing. Strategies to promote a transition back to a black grama-dominated state are currently unknown, but might require amendments to soil organic matter (Figures arrow 1b). If complete loss of black grama occurs (leaving bunchgrasses as the sole dominants), then recovery by seed or stolon might be impossible without additions of propagules. This additional effort required to recover black grama is used to define the “bunchgrass” state.

A series of states were created to capture the consequences of mesquite invasion and possible responses to it. Mesquite might invade either a black grama-dominated or bunchgrass-dominated system due to a reduction of fire frequencies, reduced competition by grasses due to overgrazing, or reduced native herbivore pressure on shrubs [see references in Bestelmeyer and others (2003)]. The importance or veracity of these various explanations is unknown. Once mesquite has been established, competitive effects could result in further reductions of grasses. Fire management and/or physical removal are required to halt the proliferation of the shrub. The capacity to remove shrubs and recover grasses defines the “shrub-invaded state.”

If mesquite persists in the system, its superior tolerance of periodic drought and low nutrient levels leads to proliferation at the expense of grasses. This might be compounded by competition-mediated reduction of grasses. As grasses decline, erosion accelerates, leading to increased redistribution of nutrients from under grass canopies and the relatively small grass interspaces to mesquite plants (Schlesinger and others 1990). Once bare patches expand beyond 50 cm in diameter, wind erosion rates increase dramatically (L Herrick, unpublished data). Grass reestablishment is difficult in the eroded interspaces and mesquite removal alone often does not result in the recovery of grasses. Grass recovery likely requires nutrient amendments or physical redistribution of nutrients associated with shrubs. This requirement defines the “mesquite shrubland state.”

This model is particularly complex (i.e., has many states and transitions) because of the importance of black grama in maintaining fertility and production in sandy soils, black grama’s vulnerability to different types of stress or disturbance, the difficulty in reestablishing black grama once it has declined, and the tendency of mesquite to invade and contribute to local grass extinction. We contrast this situation with more simple scenarios and models that follows.

A Four-State Model: Black Grama as a Subordinate and Soil Heterogeneity on Loams

On slightly finer-textured soils (e.g., a fine-loamy Typic Haplargid) within the same climatic zone, black grama declines in dominance and other perennial grasses become important, including tobosa (*Pleuraphis mutica* Buckl.) and burrograss (*Scleropogon brevifolius* Phil.; Figure 2). Grazing tends to favor these latter species because they are less often palatable to cattle throughout the year than is black grama. Historically, black grama could have been more dominant on these soils than it is observed to be today, but black grama appears to perform less well on many loamy soils than on sandy ones (c.f. Herbel and others 1972). On loams and silt loams, substantial grass cover by the bushy, sod-forming tobosa persists even after black grama is lost. Thus, herbaceous production and retention of resources within loamy soils is less dependent on black grama than within sandier soils. Given the somewhat diminished importance of black grama in maintaining function on these soils, an equivalent to the “black grama-limited state” was omitted, resulting in fewer states.

The loss of black grama alongside increases in bunchgrasses and especially burrograss is related to increasing bare ground and increased erosion and rain-drop crusting of the soil surface. The transition to the “burrograss–tobosa–threeawn state” captures this change. As in the sandy-loam model, shrub invasion causes both competition-mediated, and possibly allelopathy-mediated, reductions in grasses via compounds present in creosotebush [*Larrea tridentata* (DC) Cov.] and tarbush [*Flourensia cernua* D.C. (Dayan and Tellez 1999; Whitford and others 2001)]. Shrub dominance with the loss of grasses is associated with erosion, soil truncation and exposure of impermeable horizons, and/or soil-surface sealing (depending on the soil) and thus constitutes a distinct state. These states parallel those found in the sandy-loam model, although with different shrub species and distinct changes to soil properties.

In this model, several communities within the “burrograss–tobosa–threeawn” state and the shrub-invaded/shrub-dominated states are not connected by dashed arrows. This indicates that there is no temporal successional relationship among these communities. Instead, these different communities represent soil-determined variants. This phenomenon is especially pronounced in loamy soils, because soils placed in this category exhibit a range of properties that create important differences for plants in the southern New Mexico region. Silt loam soils tend to favor burrograss,

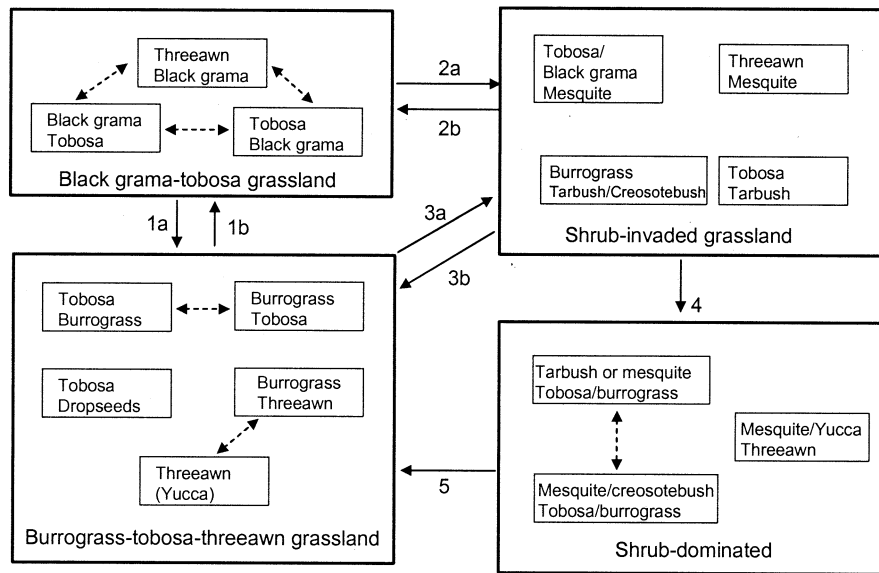


Figure 2. A state-and-transition model for the Loamy ecological site in the southcentral/southwestern Chihuahuan Desert of New Mexico, USA. Black grama, tobosa, burrograss, and threawns are perennial grasses. Black grama is palatable to cattle for a longer duration than the other species and is comparatively sensitive to grazing pressure. Tobosa and burrograss tend to become dominant with high grazing pressure on finer soils (e.g., loam and silt loam), whereas threawns become dominant on coarser soils (fine-sandy loams). These soil-based differences are represented by small boxes without arrows. Mesquite tends to invade on coarser soils, whereas tarbush and creosotebush invade on finer soils and calcareous soils that are currently circumscribed within this ecological site. Yucca [*Yucca elata* (Engelm.) Engelm.] is a stem succulent that could become subdominant as grass density declines. 1a. Heavy grazing, black grama extinction, soil fertility loss/sealing, localized erosion and sand loss. 1b. Soil stabilization or modification, seeding. 2a. Shrub invasion to bare patches and/or lack of fire. 2b. Shrub removal, seeding. 3a. Shrub invasion to bare patches. 3b. Shrub removal, with grass recovery. 4. Persistent heavy grazing, competition from shrubs, interspace erosion and soil truncation. 5. Shrub removal with soil addition, seeding.

creosotebush, and tarbush, whereas loams with higher sand content favor threawns and mesquite. Nonetheless, the characteristics of these communities and their behavior with respect to management are similar, so they were included within the same model and state. Subsequent revisions to the ecological site categorizations could split these communities into different models that exhibit similar structures. For the time being, the high number of communities within the loamy states is a consequence of soil heterogeneity within an overly broad ecological site. This adds a distinct layer of complexity to models.

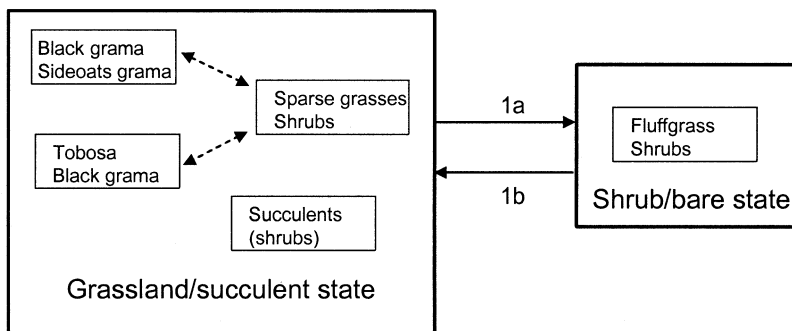
A case study of patterns at a loamy site in Dona Ana County, south-central New Mexico illustrates the importance of subtle differences in soil heterogeneity for the interpretation of plant communities in state-and-transition models (Bestelmeyer and others, in press). On relatively level land in a single pasture and soil map unit (Berino-Doña Ana association), we observed a sharp, spatial transition between the black grama-tobosa grassland state and the shrub-dominated state (Figure 3). Very often, such a contrast would be asso-

ciated with differing management—the shrub-dominated state would be interpreted as having received heavier stocking rates at some point in the past than the grassland state.

In this case, however, the contrast does not occur in different pastures or ranches, nor is there evidence that a fence line ever existed at the transition boundary. The contrast was not associated with systematic differences in soil texture, either. Instead, we found higher amounts of calcium carbonate in the surface soil of the shrub-dominated state than in the soil of the grassland state. Although this difference could be related to erosion that exposed carbonate-rich horizons in the shrubland, carbonate-rich surface horizons were present in only one of the soil series associated with the soil map unit (Doña Ana series). The nature of the boundary is thus likely to be a consequence of differing parent material or ages of the soils. Calcium carbonate or related factors, in turn, might have affected the initial composition of grasses, the vulnerability of grasses to grazing pressure or drought, and/or the propensity of shrubs to invade. This example highlights our limited



Figure 3. A sharp ecotone in a Loamy ecological site in south-central New Mexico, about 25 km east of Las Cruces, Doña Ana County, New Mexico, USA. On the left side of the ecotone, the vegetation is dominated by tarbush, mesquite, and creosotebush with few grasses. The right side of the ecotone is dominated by tobosa with some black grama and scattered mesquite. The shift from shrub to grass dominance corresponds with a decrease in calcium carbonate amounts in the surface soils (0–20 cm) but not with a change in soil texture in the surface soils. See the text.



1a. Heavy grazing, erosion, and loss of soil fertility
1b. Soil accumulation or addition

Figure 4. A state-and-transition model for the Hills ecological site in the south-central/southwestern Chihuahuan Desert of New Mexico, USA. Both black grama and the perennial grass sideoats grama [*Bouteloua curtipendula*, (Michx.) A. Gray.] are palatable to livestock throughout much of the year compared with threeawns and especially snakeweed. Succulents, including sotol and yuccas, often dominate on south-facing slopes. 1a. Heavy grazing, erosion, and loss of soil fertility 1b. Soil accumulation or addition

understanding of important sources of heterogeneity. Uncovering the roles of these factors, even on a case-by-case basis if need be, is a critical step in interpreting rangeland patterns using state-and-transition models.

A Two-State Model for an Inherently Resistant and Resilient Ecological Site (Hills)

The complexity of the models described earlier contrasts sharply with that of the model of the hills ecological site (Figure 4). This site is composed of soils that are rocky and shallow (less than ~60 cm) to igneous or sedimentary rocks and that often exhibit relatively steep slopes (e.g., a clayey Lithic Haplargid). Consequently, aspect is an important determinant of plant

community (and soil) variation. Succulents such as banana yucca (*Yucca bacata* Torr.) and sotol (*Dasyliirion wheeleri* S. Wats.) can be especially abundant on dry, south-facing slopes with relatively thin soils and little grass. On more level areas and on north-facing slopes, grasses are often abundant. In fact, productive grasslands are often preserved on hills soils in the midst of degraded vegetation on surrounding sandy and loamy soils.

In many cases, the shallow soils and exposed rocks appear to simultaneously retard local expansion and competition from woody plants and buffer grasses from environmental stress. The shallow soils might not permit deep-rooting shrubs to capitalize on their capacity

to exploit relatively stable sources of moisture. At the same time, shallow, rocky soils could perch water within the rooting depth of grasses and laterally concentrate moisture inputs from sheet flow to pockets of soil where grasses root (e.g., Cerda 2001). In addition, the crowns and lower leaves of grasses growing adjacent to rocks are protected from overgrazing because cattle are unable to reach these plant parts (e.g., Milchunas and Noy-Mier 2002). Thus, protected plants are able to respond to favorable conditions via growth and reproduction more quickly than are heavily grazed individuals and are likely to serve as sources for local recolonization.

Because of these factors, severe reductions of grass cover are less likely than on other soils and recovery is often rapid with proper grazing management and/or increased precipitation for several consecutive summer seasons. In some cases, and on especially thin soils, erosion during periods of low grass cover could lead to a transition after which recovery by perennial midgrasses is very slow or absent. In this case, short, sparse perennials such as fluffgrass [*Dasyochloa pulchella* (HBK) Hitchc] predominate. Shrubs and succulents are believed to be an historical component of this system and increases in them are not associated with this transition. Because shrub invasion, encroachment, and associated processes do not usually occur, the state- and-transition model for this system is relatively simple.

Another Two-State Model: No Woody Invaders on Higher-Elevation Clay Loams

The clay loam upland model (Figure 5) is distinct from the previous models in that this ecological site occurs in a different climatic zone. Whereas the other models apply to soils found within areas receiving 20–25 cm of annual rainfall at an elevation of 1220–1524 m, the clay loam upland model applies to slightly wetter soils (30–35 cm/year) and higher elevations (1432–1828 m) on the Otero Mesa of southern New Mexico and northwest Texas (e.g., a fine-loamy Ustic Haplocambid). Like the two-state, hills model described earlier, the clay loam upland model is relatively simple. The soils composing this site, however, exhibit similar textural properties to the loamy site for which we created a relatively complex (four state) model.

Why is the clay loam model so simple? Unlike silt and clay loam soils at lower elevations, such soils in the context of Otero Mesa harbor few shrubs and are not subject to local shrub invasion. This might be due to the limited tolerance of shrubs such as creosotebush, mesquite, and tarbush to the cooler winter temperature at this site or to other factors. Furthermore, encroaching woody species characteristic of higher elevations,

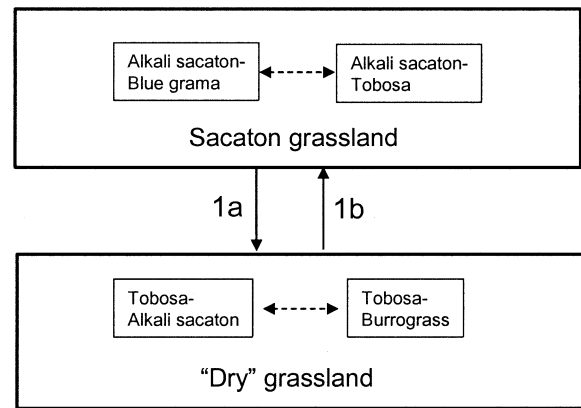


Figure 5. A state-and-transition model for the Clay Loam Uplands ecological site on the Otero Mesa of southcentral New Mexico and northwest Texas, USA. Blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Steud. Hitchcock] and alkali sacaton [*Sporobolus airoides* (Torr.) Torr.] are both perennial grasses. Alkali sacaton seems to require a greater duration of soil moisture than tobosa or burrograss. 1a. Gullyng, diversion of run-on water, grass loss, soil-surface sealing. 1b. Repair gullies, use water spreaders.

such as one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.] and ponderosa pine [*Pinus ponderosa* Laws. (Miller 1999)] are likewise rarely present at these elevations. The clay loam soils in Otero Mesa seem to represent an environmental domain in which woody encroachment is unimportant. Regional climate change could push the clay loam upland outside of this domain and increase the complexity of the model.

Improved Decision-Making Using State-and-Transition Models

In each of the above four case studies, we used a qualitative analysis of existing knowledge and data to create general hypotheses regarding the patterns of, and causes and constraints to, ecosystem change. These general ideas serve as a basis from which “local working models” can be refined. Refinements incorporate local, spatially explicit information, including soil and climate maps, remote-sensed vegetation maps, digital terrain models, land-use histories, and maps of past and current roads, livestock trails, and water points. The potential effects of spatial context on local dynamics (such as when upslope degradation affects downslope sites) can be considered in this way. Because the processes determining ecosystem change are spatially structured and scale/context dependent (Soares-Filho and others 2001), state-and-transition models must be

spatially arrayed to be useful (Stafford Smith 1996; Ludwig and Tongway 2000).

By arraying the map layers and hypothetical impacts and vulnerabilities in a geographic information system, state-and-transition models are used to guide the formation of management hypotheses (Bowman 1995; Havens and Aumen 2000) in which we specify the likely costs and consequences of a management action (or inaction) across specified areas of land. Local measurements and reference values highlighted in state-and-transition models, such as plant species dominance, bare patch size, soil aggregate stability, or evidence of soil deflation (Pyke and others 2002), are used to apply and test hypotheses. Hypotheses are tested empirically via monitoring of ecosystem attributes in carefully selected locations after the application of management guidelines [see Ludwig and others, 2000) for an excellent example].

How are the model-based hypotheses useful to managers? First, they call attention to the idea that some ecological sites within a landscape are both more resistant and resilient than others. In general, prevention of degradation should focus on the less resistant (more sensitive) ecological sites, whereas recovery efforts should be directed toward more resilient sites. For example, in an area dominated by the Hills (Figure 4) and Sandy (Figure 1) ecological sites, degradation prevention should be focused on the Sandy site because it is more sensitive to degradation. In the absence of information about resilience organized by state-and-transition models, inexperienced managers might direct their limited resources to degraded-looking Hills grasslands, which are least likely to experience persistent degradation.

A similar analysis can be applied within areas of similar soils. Within the Sandy ecological site, the models suggest that the probability of preventing the loss of a black grama-dominated grassland state is often quite high and the cost low, when compared with the probability and cost of recovering a black-grama grassland from a mesquite shrubland. This information provides agencies such as the Bureau of Land Management (that are charged with monitoring and setting management guidelines for millions of hectares of public land in the western United States) with a justification for "triage" in stratifying assessment areas and pursuing controversial management changes that may be challenged in court (Bureau of Land Management 2001; BLM range staff, personal communications). The information in state-and-transition models formally acknowledges key ecological phenomena [e.g., thresholds (Roe and Van Eeten 2001)] that have important policy implications but were seldom considered in the past.

Perhaps the most important use of state-and-transition models is to communicate the notion of threshold phenomena in a simple way to land users. Even knowledgeable ranchers faced with financial losses during a drought year might be compelled to play 'degradation roulette' by grazing drought-stressed grass plants with the hope that better years lay ahead (BLM range staff, personal communications). Periodic multiyear drought, such as currently faces the southwestern United States (J. Betancourt, personal communication) could be critical periods in which the risk of transition is elevated. Although local variations; nonlinearities, and insufficient data preclude useful estimates of transition probabilities, the results and ideas in state-and-transition models call attention to the heightened risk of degradation. The improved perception of risk may better frame the art of rangeland management.

Conclusions

We feel that state-and-transition models should not make definitive statements about the likelihood of site responses to various factors. To do so would be to misrepresent the data we have as well as our understanding of ecosystem complexity in the southwestern United States. Instead, our state-and-transition models define the breadth of possible ecosystem dynamics as we currently understand them, organized by climate and soils. The models are then used as broad starting points for the specification of management hypotheses and interpretations based on refined local models. The development of local models from state-and-transition models calls upon scientists and managers to use their experience and the reasoning and examples in models to evaluate local data make predictions based on these data, and initiate tests of management hypotheses (Underwood 1995). Because model predictions are unlikely to be general even within a zone of similar climate and soil type, state-and-transition models are tools to aid the process of induction rather than deduction. In this way, state-and-transition models support a "method of case-studies" by helping managers confront the limited facts about particular situations and make sense of them (Shrader-Frechette and McCoy 1993).

Acknowledgments

We thank the many individuals who contributed data and ideas that are represented in this article, especially Jim Powell, formerly of NRCS, George Chavez of the NRCS, Bob Alexander, and Phil Smith of the BLM. S. Bestelmeyer, V. Dale, D. Pyke, E. Roe, T. Stringham, B. Wilcox, and an anonymous reviewer provided valuable comments on the article.

Literature Cited

- Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of Southwestern ponderosa pine ecosystems: A broad perspective. *Ecological Applications* 12:1418–1433.
- Allen-Diaz, B., and J. W. Bartolome. 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. *Ecological Applications* 8:795–804.
- Bahre, C. J., and M. L. Shelton. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography* 20:489–504.
- Baker, W. L. 1989. A review of models of landscape change. *Landscape Ecology* 2:111–133.
- Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, G. Chavez, R. Alexander, and J. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.
- Bestelmeyer, B. T., Brown, J. R., Herrick, J. E., Havstad, K. M., 2003. What does an ecological threshold look like? pp. 688–690, C.N. Allsop, A.R. Palmer, S.J. Milton (eds.) in Proceedings of the VIIth International Rangeland Congress, Durban, South Africa.
- Beukema, S. J., and W. A. Kurz. 2000. Vegetation dynamics development tool. User's guide. Version 4.0. ESSA Technologies Ltd, Vancouver, Canada.
- Bever, J. D., K. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology* 85:561–573.
- Bowman, D. 1995. Down in the forest something stirred.. *New Scientist* 148:54.
- Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2003. Vegetation dynamics on rangelands: A critique of current paradigms. *Journal of Applied Ecology* 40:601–614.
- Brown, J. R., and S. Archer. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. *Vegetatio* 73:73–80.
- Brown, J. R., and S. Archer. 1999. Shrub invasion of grassland: Recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80:2385–2396.
- Bureau of Land Management 2001. H-4180-1 Rangeland health standards, BLM Manual, release 4-107. Bureau of Land Management, Washington, DC.
- Cerdà, A 2001. Effects of rock fragment cover on soil infiltration, interrill runoff and erosion. *European Journal of Soil Science* 52:59–68.
- Dale, V. H. 2003. Opportunities for using ecological models for resource management. Pages 3–22 in V. H. Dale (ed.), Ecological modeling for natural resource management. Springer-Verlag, New York.
- Davenport, D. W., D. D. Breshears, B. P. Wilcox, and C. D. Allen. 1998. Viewpoint: Sustainability of pinon-juniper ecosystems—A unifying perspective of soil erosion thresholds. *Journal of Range Management* 51:231–240.
- Dayan, F. E., and M. R. Tellez. 1999. Phytotoxicity of tarbush (*Flourensia cernua* DC) leaf extracts. *Allelopathy Journal* 6:1–12.
- DeAngelis, D. L., and J. C. Waterhouse. 1987. Equilibrium models and nonequilibrium concepts in ecological models. *Ecological Monographs* 57:1–21.
- Dyksterhuis, E. J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2:104–115.
- Ellis, J. E., and D. M. Swift. 1986. Stability of African pastoral systems: Alternative paradigms and implications for development. *Journal of Range Management* 41:450–459.
- Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: A viewpoint. *Journal of Range Management* 44:422–426.
- Fynn, R. W. S., and T. G. O'Connor. 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semiarid savanna, South Africa. *Journal of Applied Ecology* 37:491–507.
- Gibbens, R. P. . Long-term vegetation trends in the Jornada Basin: The 1950's drought in historical perspective. in J. L. Betancourt, and H. F. Diaz. (eds.), The 1950's drought in the American Southwest: Hydrological, ecological, and socioeconomic impacts. University of Arizona Press, Tucson, Arizona.
- Grossman, R. B., D. S. Harms, C. A. Seybold, L. A. Pytlík, and J. E. Herrick. 2001. Coupling use-dependent and use-invariant data for soil quality evaluation. *Journal of Soil and Water Conservation* 56:63–68.
- Harwell, M. A., and J. H. Gentile. 2003. Overcoming barriers to the use of models in environmental decision making. Pages 3–22 in V. H. Dale (ed.), Ecological modeling for natural resource management. Springer-Verlag, New York.
- Havens, K. E., and N. G. Aumen. 2000. Hypothesis-driven experimental research is necessary for natural resource management. *Environmental Management* 25:1–7.
- Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, U.S.A. *Conservation Biology* 16:1243–1255.
- Herbel, C. H., F. N. Ares, and R. H. Wright. 1972. Drought effects on a semidesert grassland range. *Ecology* 53:1084–1093.
- Herrick, J. E., J. R. Brown, A. Tugel, P. L. Shaver, and K. M. Havstad. 2002. Application of soil quality to monitoring and management: Paradigms from rangeland ecology. *Agronomy Journal* 94:3–11.
- Illius, A. W., and T. G. O'Connor. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* 9:798–813.
- Illius, A. W., and T. G. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* 89:283–294.
- Jackson, C. V. 1928. Seed germination in certain New Mexico range grasses. *Botanical Gazette* 86:270–294.
- Jackson, R. D., and J. W. Bartolome. 2002. A state-and-transition approach to understanding nonequilibrium plant community dynamics in California grasslands. *Plant Ecology* 162:49–65.

- Jackson, R. D., J. W. Bartolome, and B. Allen-Diaz. 2002. State-and-transition models: response to an ESA symposium. *Bulletin of the Ecological Society of America* 83:194–196.
- Jenny, H. 1941. Factors of soil formation. McGraw-Hill, New York.
- Hunter, K. L., J. L. Betancourt, B. R. Riddle, T. R. Van Devender, K. L. Cole, and W. G. Spaulding. 2001. Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology and Biogeography* 10:521–533.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands a viewpoint. *Journal of Range Management* 44:427–433.
- Llorens, E. M. 1995. Viewpoint: the state-and-transition model applied to the herbaceous layer of Argentina Calden forest. *Journal of Range Management* 48:442–447.
- Ludwig, J. A., and D. J. Tongway. 1997. A landscape approach to rangeland ecology. Pages 1–12 in J. Ludwig, D. Tongway, D. Freudenberger, J. Noble, and K. Hodgkinson. (eds.), *Landscape ecology, function and management: Principles from Australia's rangelands*. CSIRO Publishing, Collingwood, Australia.
- Ludwig, J. A., and D. J. Tongway. 2000. Viewing rangelands as landscape systems. Pages 39–52 in O. Arnalds, and S. Archer. (eds.), *Rangeland desertification*. Kluwer Academic, Dordrecht, The Netherlands.
- Ludwig, J. A., G. N. Bastin, R. W. Eager, R. Karfs, P. Ketner, and G. Pearce. 2000. Monitoring Australian rangeland sites using landscape function indicators and ground- and remote-based techniques. *Environmental Monitoring and Assessment* 64:167–178.
- MacGregor, S. D., and T. G. O'Connor. 2002. Patch dieback of *Colophospermum mopane* in a dysfunctional semi and African savanna. *Austral Ecology* 27:385–395.
- McAuliffe, J. R., and T. R. Van Devender. 1998. A 22,000-year record of vegetation change in the north-central Sonoran Desert. *Palaeogeography, Palaeoclimatology, and Palaeoecology* 141:253–275.
- Miller, M. E. 1999. Use of historic aerial photography to study vegetation change in the Negrito Creek watershed, southwestern Mew Mexico. *The Southwestern Naturalist* 44:121–137.
- Neilson, R. P. 1986. High resolution climatic analysis and southwest biogeography. *Science* 232:27–34.
- Nelson, E. W. 1934. The influence of precipitation and grazing upon black grama grass range. Technical Bulletin No. 409. US Department of Agriculture, Washington DC.
- Northup, B. K., J. R. Brown, and J. A. Holt. 1999. Grazing impacts on the spatial distribution of soil microbial biomass around tussock grasses in a tropical grassland. *Applied Soil Ecology* XXX:1–12.
- Novak, S. J., and R. N. Mack. 2001. Tracing plant introduction and spread: Genetic evidence from *Bromus tectorum* (Cheatgrass). *BioScience* 51:114–122.
- Milchunas, D. G., and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99:113–130.
- Okin, G. S., B. Murray, and W. H. Schlesinger. 2001. Degradation of sandy arid shrubland environments: Observations, process modeling, and management implications. *Journal of Arid Environments* 47:123–144.
- Paulsen, H. A., Jr., and F. N. Ares. 1962. Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the Southwest. Technical Bulletin 1270. US Department of Agriculture, Washington DC.
- Pielke, R. A., and R. Avissar. 1990. Influence of landscape structure on local and regional climate. *Landscape Ecology* 4:133–155.
- Pyke, D. A., J. E. Herrick, P. Shaver, and M. Pellant. 2002. Rangeland health attributes and indicators for qualitative assessment. *Journal of Range Management* 55:584–597.
- Rastetter, E. B., J. D. Aber, D. P. C. Peters, D. S. Ojima, and I. C. Burke. 2003. Using mechanistic models to scale ecological processes in space and time. *BioScience* 53:68–76.
- Ricklefs, R. E. 1990. Ecology, 3rd ed. W. H. Freeman, New York.
- Rodriguez Iglesias, R. M., and M. M. Kothman. 1997. Structure and causes of vegetation change in state and transition model applications. *Journal of Range Management* 50:399–408.
- Roe, E., and M. Van Eeten. 2001. Threshold-based resource management: A framework for comprehensive ecosystem management. *Environmental Management* 27:195–214.
- Rupp, T. S., A. M. Starfield, F. S. Chapin III, and P. Duffy. 2002. Modeling the impact of black spruce on the fire regime of Alaskan boreal forest. *Climate Change* 55:213–233.
- Scanlan, J. C. 1994. State and transition models for rangelands. 5. The use of state and transition models for predicting vegetation change in rangelands. *Tropical Grasslands* 28:229–240.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247:1043–1048.
- Schumm, S. A. 1977. The fluvial system. John Wiley & Sons, New York.
- Shrader-Frechette, K., and E. D. McCoy. 1993. Method in ecology: Strategies for conservation. Cambridge University Press, Cambridge.
- Soares-Filho, B. S., R. M. Assuncao, and A. E. Pantuzzo. 2001. Modeling the spatial transition probabilities of landscape dynamics in an Amazonian colonization frontier. *Bioscience* 51:1059–1067.
- Soil Survey Staff 1999. Soil taxonomy. A basic system of soil classification for making and interpreting soil surveys, 2nd ed. US Department of Agriculture Natural Resources Conservation Service, Agriculture Handbook No. 436, Washington, DC.
- Stafford Smith, M. 1996. Management of rangelands: Paradigms at their limits. Pages 325–356 in J. Hodgson, and A. W. Illius. (eds.), *The ecology and management of grazing*. CAB International, Wallingford, UK.
- Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: An ecological process approach. *Journal of Range Management* 56:106–113.

- Sullivan, S., and R. Rohde. 2002. On non-equilibrium in arid and semiarid grazing systems. *Journal of Biogeography* 29:1595–1618.
- Underwood, A. J. 1995. Ecological research and (and research into) environmental management. *Ecological Applications* 5:232–247.
- USDA Natural Resources Conservation Service (NRCS) 1997. National range and pasture handbook. US Department of Agriculture, Washington, DC.
- Valentine, K. A. 1970. Influence of grazing intensity on improvement of deteriorated black grama range. Bulletin No. 553. New Mexico State University, Agricultural Experiment Station, Las Cruces, New Mexico.
- Valone, T. J., M. Meyer, J. H. Brown, and R. M. Chew. 2002. Timescale of perennial grass recovery in desertified and 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* 31:197–215.
- Van de Koppel, J., M. Reiterkerk, and F. J. Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution* 12:352–356.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.
- Whitford, W. G., R. Nielson, and A. de Soyza. 2001. Establishment and effects of establishment of creosotebush, *Larrea tridentata*, on a Chihuahuan Desert watershed. *Journal of Arid Environments* 47:1–10.
- Wiens, J. A. 1984. On understanding a non-equilibrium world: Myth and reality in community patterns and processes. Pages 439–457 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle. (eds.), *Ecological communities: Conceptual issues and evidence*. Princeton University Press, Princeton, New Jersey.
- Wilcox, B. P., D. D. Breshears, and C. D. Allen. 2003. Ecohydrology of a resource-conserving semiarid woodland: Effects of scale and disturbance. *Ecological Monographs* 73:223–239.
- Wright, R. A., and J. H. Honea. 1986. Aspects of desertification in southern New Mexico, USA: soil properties of a mesquite duneland and a former grassland. *Journal of Arid Environments* 11:139–145.
- Wright, R. G., and G. M. Van Dyne. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *The Southwestern Naturalist* 21:259–274.