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States, transitions, and thresholds: Further refinement for rangeland applications

T.K. Stringham, W.C. Krueger, and P.L. Shaver

INTRODUCTION

Applied ecology disciplines, such as range management, are necessarily organized around a response model based on theoretical supposition. Thus, the litmus test for an ecological process model is its ability to predict the consequences of natural disturbances and/or management activities with acceptable precision over timescales relevant to management. Traditional theories of plant succession leading to a single climax community have been found to be inadequate for understanding the complex successional pathways of semi-arid and arid rangeland ecosystems considering timescales important for making management adjustments (West 1979, Westoby 1980, Anderson 1986, Foran et al. 1986, Tausch et al. 1993). After 50 years of applying the quantitative climax model of Dyksterhuis (1949) to rangeland management its predictive capabilities have come under scrutiny. The inability of the model to incorporate multiple pathways of change has led some ecologists to abandon the model completely (Wilson 1984, Smith 1988). The recognition of this inadequacy has generated a search for an alternative theory that more correctly reflects the observed dynamics of rangeland ecosystems. As many scientists were questioning the validity of the climax model, Westoby et al. (1989) developed a foundational discussion and conceptual model based on non-equilibrium ecology. Numerous scientists have utilized these concepts as a basis for the development of conceptual models of vegetation dynamics which incorporate multiple successional pathways, multiple steady states, thresholds of change, and discontinuous and irreversible transitions (Archer 1989, Friedel 1991, Laycock 1991, Fuhlendorf et al. 1996, Stringham 1996, Rietkerk and Van de Koppel 1997, Davenport et al. 1998, Oliva et al. 1998, Petraitis and Latham 1999, Plant et al. 1999, West 1999, West and Young 2000, Stringham et al. *In press*). However, the ecological interpretation of Westoby's model has varied due to a lack of universally accepted definitions of the key concepts. The lack of consistency in definitions has led to confusion and criticism indicating the need for further development and refinement of the theory and associated models (Iglesias and Kothmann 1997).

The USDA Natural Resources Conservation Service (NRCS) adopted the use of state-and-transition vegetation dynamics in describing rangeland ecological sites. The attempt to use this concept illustrated the inconsistency in the definitions and concepts. NRCS recognizes the need for consistency in the application of the concepts (USDA 1997). In order for management to utilize the non-equilibrium ecological model the definitions of model objects must be succinctly stated and validated.

BACKGROUND

Westoby et al. (1989) was the first to apply the use of state-and-transition terminology to non-equilibrium theory for the purpose of producing a management focused model that describes vegetation dynamics in a non-linear framework as an alternative to the linear continuum process incorporated in the quantitative climax model. The authors defined a state as an alternative, persistent vegetation community that is not simply reversible in the linear successional framework. We interpret Westoby's transitions as pathways between states with the characteristic of the transition being either transient or persisting. Transitions between states are often triggered by multiple disturbances including natural events (e.g., climatic events or fire) and/or management actions (grazing, farming, burning, etc.). Transitions may occur quickly, as in the case of catastrophic events like fire or flood or slowly over an extended period of time as in the case of a gradual shift in weather patterns or repeated stresses like frequent fire. Regardless of the rate of change the system does not stabilize until the transition is complete.

Quantitative approaches to ecological thresholds have been presented by May (1977), Wissel (1984) and Rietkerk and van de Koppel (1997). Archer (1989) introduced the qualitative concept of a transitional threshold. He modeled the expansion of a woodland community into a grassland domain using a transitional threshold as the boundary between the respective grassland and shrub domains. Whisenant (1999) proposed a stepwise model of degradation, similar to Archer's, which incorporates two transition thresholds, the first being controlled by biotic interactions and the second by abiotic limitations. The concept of a transitional threshold as used by both Archer and Whisenant is similar to the persistent transition as the successional processes shift from grass controlled to shrub controlled, however, in Whisenant's (1999) model the focus is on ecological processes not vegetative groups. Friedel (1991) focused on the concept of thresholds of environmental change **between** domains of relative stability. She defined a threshold as a boundary in space and time between two domains or states, which is not reversible on a practical time scale without substantial inputs of energy. As defined, Friedel s thresholds mirror Westoby et al. s (1989) definition of persistent or irreversible transitions. However, the use of thresholds in current state-and-transition models has not been consistent nor clear on whether thresholds exist between all states or only a subset of states.

Conceptual models, based on these ideas, have incorporated states and transitions but not always thresholds. As a result, there have been both a broad interpretation of states, more or less separated by thresholds, and a narrow interpretation of states that approximate seral stages or phases of vegetation development. Broadly applied, states are climate/soil/vegetation domains that encompass a large amount of variation in species composition. Specifically a grassland state would include many seral stages of the overall grassland community. These seral stages are within the amplitude of natural variability characteristic of the state and represent responses to disturbances that do not force a threshold breach. Westoby et al. (1989), Archer (1989), and Archer and Smeins (1991) provided examples of this broad definition of state where domination of successional processes determine the boundary of the state (e.g. grass controlled succession versus shrub controlled succession). Figure 1, derived from the Society for Range Management, Task Group on Unity in Concepts and Terminology (1995) depicts the broad application of states with multiple vegetative stages diagrammed within one state. Whisenant (1999) de-emphasized the species component of the ecosystem within his model, focusing instead on the functional integrity and transition limitations of the site for determining state boundaries. In the broad definition of state the natural variability characteristic of plant communities within a site is the result of, and contributes to, the current functional integrity of the site's primary ecological processes.

The narrower interpretation of state allows for far less variation in plant community composition. States are typically depicted as seral stages or phases of vegetation development. In the narrow application of the model a state change does not necessarily represent a movement across a threshold as envisioned by Friedel (1991). Figure 2 is a representation of the specific application as adapted from West (1999). Boxes represent states and arrows indicate the transitions between states. Note that many of the transitions are reversible, however, the threshold indicates a persistent transition. Other examples of specific applications of states are presented by Weixelman et al. (1997), Oliva et al. (1998), Allen-Diaz and Bartolome (1998), West (1999), and West and Young (2000). The specific approach to state-and-transition modeling may be the reason for statements that such models are structurally similar to traditional linear climax-seral stage models. The significant difference being the description of communities as discrete entities as opposed to the continuum concept of the quantitative climax model (Iglesias and Kothmann 1997).

ECOLOGICAL RESISTANCE AND RESILIENCE

The concept of stability as defined by the resistance and resilience of plant communities have been discussed in the literature for sometime and offer important insights for state-and-transition models (Margalef 1969, Verhoff and Smith 1971, Holling 1973, May 1977, Noy-Meir and Walker 1986). Resistance is defined as the ability of the system to remain the same while external conditions change whereas resilience is the ability of the system to recover after it has changed. Thus, fully functioning ecosystems are both resistant to change and resilient or able to self recover from external disturbances, thereby maintaining stability while allowing for fluctuating combinations of plant species over time. States, by definition are relatively stable (Westoby et al. 1989), therefore it follows that a state change is only possible when a threshold is crossed. Accepting this concept points out the confusion that is apparent in the current attempts to produce state-and-transition models. The specific or narrow approach has produced models, which depict state changes occurring without having crossed a threshold. Often such changes are diagrammed as reversible and perhaps occur without the input of management resources (Figure 2). Rather than consider these vegetation dynamics as state changes it is more consistent with ecological thought to consider them as phase shifts or plant community dynamics within a state. Therefore, within a state there exists the potential for a large variation in species composition, which is merely a reflection of plant community dynamics. A state change, on the other hand, requires a shift across a boundary or threshold, defined by a change in the integrity of the site's primary ecological processes, resulting in a different potential set of plant communities.

RANGELAND ECOLOGICAL PROCESSES

Ecological processes functioning within a normal range of variation will support a suite of specific plant communities. The important primary processes are (1) hydrology (the capture, storage, and redistribution of precipitation); (2) energy capture (conversion of sunlight to plant and animal matter); and (3) nutrient cycling (the cycle of nutrients through the physical and biotic components of the environment (Pellant et al. 2000, Whisenant 1999). Pellant et al. (2000) defines the functioning of an ecosystem by "the degree to which the integrity of the soil, vegetation, water, and air, as well as the ecological processes of the rangeland ecosystem, are balanced and sustained". Integrity is defined as the "maintenance of the functional attributes characteristic of a locale, including normal variability" (Pellant et al. 2000). Degradation of an ecosystem occurs when the integrity of the system is damaged or lost. Maintenance of a functional site or repair of a damaged site requires management focused on soil stability, nutrient cycling, and the capture, storage and safe release of precipitation. Vegetation goals should be based on the concept of vegetation as a tool for maintaining or repairing damaged ecological processes rather than predefined species groups. Monitoring of species groups may be a mechanism for evaluating or detecting change in the site's ecological processes.

CLARIFICATION OF THE CONCEPTS AND DEFINITIONS

Spatial Scale

Ecosystems are difficult to define or delimit in space and time. Hierarchy theory, as applied to ecological systems, suggests several levels of organization exist, i.e., organisms, populations, communities, ecosystems, landscapes (Archer and Smeins 1991). Each level of organization encompasses one or more of the primary ecological processes that are operating at specific spatial and temporal scales. Although landscape scale management may be the goal, our current understanding of organization function declines with increasing spatial and temporal scale.

The ecological site concept has long been utilized as an organization level that provides an appropriate spatial scale for inventory, evaluation, and management of rangelands. Organisms, populations, and communities exist within this spatial scale and interact with one another through the flow of water and energy, and the cycling of nutrients. An ecological site has evolved a kind of characteristic plant community such as cool season shrub-grass or warm season grassland. Within an ecological site numerous expressions of the various developmental stages of the characteristic plant community can occur. The concept and definition of an ecological site fits the large-scale interpretation of the state-and-transition model. We define the ecological site as the minimum scale for definition of a state.

Temporal Scale

The definition of threshold as presented by Friedel (1991) indicates that once a threshold has been breached return to the previous state is precluded within a time frame relevant to management, without substantial inputs of energy. Ecological management models should focus on the time required to repair damaged ecological processes not on a time scale predicated by management. Careful consideration of the threshold concept negates the need for including management timescales in the definition of ecological thresholds as these thresholds represent a permanent change in the function of the state. Thus, restating the threshold definition, independent of management timescales, results in the conclusion that once a threshold has been violated return to the prior state is precluded without substantial inputs of energy. Therefore, under the current climatic conditions and without substantial inputs of energy, state changes are permanent. The temporal scale is defined by the permanence of the current climate regime.

State

A state is a recognizable, resistant and resilient complex of two components, the soil base and the vegetation structure. The vegetation and soil components are necessarily connected through integrated ecological processes that interact to produce a sustained equilibrium that is expressed by a specific suite of vegetative communities.

Soil Base and Vegetation Structure

The base of any rangeland ecosystem is the soil resource that has developed through time from a specific parent material, climate, landscape position, and interaction with soil and terrestrial biota. These factors are the primary determinants of the ecological site's capability. The integrity of the soil resource, as reflected by site hydrology and nutrient cycling, is directly connected to the composition and energy capture process of the above-ground vegetative component. The interaction between the soil resource and the associated vegetative community determines the functional status of the state's ecological processes.

- Soil Base: a component that results from the interaction of climate, abiotic soil characteristics, soil biota and topography that determines the hydrologic characteristic and biotic potential of the system.
- Vegetation Structure: a component resulting from above ground communities of living organisms, whose vital attributes (Noble and Slatyer 1980) competitively capture and utilize the system's available energy, water, nutrients, and space.

The interaction between the structural attributes of soil and the vegetative communities, through the processes of energy capture, hydrology and nutrient cycling defines the resilience and resistance of the state.

Resilience and Resistance

The stability of a state is defined above in terms of resilience and resistance. Resilience focuses on how far a system can be displaced from equilibrium before return to equilibrium is precluded. The emphasis is placed on the persistence of relationships as they affect the systems ability to adapt to change (Walker et al. 1981), therefore, resilience relates to the functioning of the system's ecological processes. Resistance indicates the ability of a system to remain at or near its equilibrium condition by maintaining control of its ecological processes. Thus, the strength of this control determines a system's inherent resistance to change. Consequently, under an existing climate, stability of a state is a function of the combination of its inherent resilience and resistance.

Thresholds and Transitions

Thresholds are points in space and time at which one or more of the primary ecological processes responsible for maintaining the sustained equilibrium of the state degrades beyond the point of self-repair. These processes must be actively restored before the return to the previous state is possible. In the absence of active restoration a new state, which supports a different suite of plant communities and a new threshold, is formed

- Thresholds: boundary in space and time between any and all states, or along irreversible transitions, such that one or more of the primary ecological processes has been irreversibly changed and must be actively restored before return to a previous state is possible.

Transitions are trajectories of change that are precipitated by natural events and/or management actions which degrade the integrity of one or more of the states primary ecological processes. Transitions are often composed of two separate properties that are defined by the state threshold. The first property is reversibility and it occurs within the state. The second property is irreversibility and it occurs once a threshold has been breached. Transitions are vectors of system change that will lead to a new state without management intervention. The primary difference between the reversible and irreversible property of a transition is the degree of action required to reverse the trajectory direction.

- Transition: a trajectory of system change triggered by natural events, management actions, or both that will not come to rest until a new equilibrium is established.
    - Reversible Property of the Transition: trajectory of change that occurs within a state and indicates the system is moving toward a threshold. Reversal requires management action. Maintenance of the state requires vegetation management practices such as prescribed grazing and prescribed burning for vegetation maintenance. Facilitating practices such as fencing and water development may be needed in the application of the vegetation management practices (USDA 1997).
    - Irreversible Property of the Transition: trajectory of change that occurs after a threshold has been breached. Arrest or reversal of degradation will not occur without significant inputs of management resources and energy. Restoration requires application of accelerating practices such as brush management, erosion control and seeding (USDA 1997).

MODEL STRUCTURE

The conceptual model, illustrating the above definitions, is represented in Figures 3 and 4. The model accommodates both the quantitative climax approach and the narrow application of the non-equilibrium approach to states and transitions (Figure 5). States are diagrammed as the large boxes and are bordered by thresholds. Thresholds are the boundaries of any and all states. For a state change to occur a threshold must be breached. The small boxes within the state are referred to as plant community phases or seral stages and are joined by community pathways that flow in both directions. Transitions are reserved for a trajectory of change with the dashed line inside the state indicating the portion of the transition that is reversible with minimal input from management. Figure 4 illustrates the process of a state change. Once the threshold is crossed the state has lost control of its primary ecological processes and will transition to a new equilibrium with a different ecological capability. The entire trajectory from a vegetation phase in State 1, across the threshold to the formation of State 2 is considered a transition and represents a degradation of ecological capability. The portion of the transition contained within the boundary of State 1 is reversible with minimal input from management, however, once the trajectory crosses the threshold it is not reversible without active restoration including substantial energy input. Additional thresholds may occur while the system is in transition, changing the direction of the trajectory away from State 2 towards State 3 (Figure 4). State-and-transition modeling efforts indicate the first threshold is forced by a change in the biotic component of the system whereas additional thresholds would involve changes in the soil resource (Westoby et al. 1989, Milton et al. 1994, and Whisenant 1999).

Plant community phase changes within states, in addition to transitions of change, thresholds and multiple stable states are illustrated in Figure 5. The management and natural mechanisms responsible for community phase shifts and transition initiation must be defined in terms of ecological processes and included in the model description. For example, prolonged drought or overgrazing leads to a reduction in the perennial herbaceous understory. The decrease in perennial understory leads to a decrease in total energy capture and nutrient cycling. In addition, the plant community's ability to protect the soil from raindrop impact and potential soil erosion declines. The mechanism (or mechanisms) of disturbance have led to a change in the three primary ecological processes and a phase shift as diagrammed by community phase pathway P1 (Figure 5). In the case of prolonged drought return to the late seral sagebrush steppe phase would gradually occur with a return to a normal or above normal precipitation period (P2). Increased available moisture leads to an increase in biomass of the herbaceous understory that translates into an increase in energy capture, nutrient cycling and an improvement in soil protection and site hydrology. The degradation mechanism of overgrazing would need to be addressed through grazing management with the goal of ecological process improvement. Continued overgrazing would further decrease the vigor of the native herbaceous understory and further impact the community's ability to maintain control of the primary ecological processes. As the vigor of the native herbaceous community declines, the site is opened up for invasion by annual species. The transition from State 1 towards State 2 has begun and will continue without the application of prescribed grazing along with facilitating practices (T1a). At the point in time where annuals dominate the herbaceous understory and fire frequency intensifies, the state has crossed a threshold and is transitioning to a new state (T1b). During this transition phase the plant community may still retain a minor component of sagebrush; however, this is not representative of a stable state and with increased fire frequency the brush will be eliminated and the new equilibrium state formed. The new state is defined as a *Bromus tectorum* (cheatgrass) and/or *Taeniatherum asperum* (medusahead) dominated community with a fire frequency interval of 2 to 3 years. Energy capture has declined and the time period for energy capture has been reduced. Nutrient cycling in both the vertical and horizontal plane has decreased with the shift to a shallow rooted, primarily monoculture community. The hydrology of the site will be impacted through a reduction in the amount of organic material being added to the soil and an increase in the potential for damage to soil surface structure from raindrop impact. Return to State 1 may be impossible even with the use of accelerated management practices. In some cases, accelerated practices may be used to create State 3.

Although many scientists have recognized the short-comings of the quantitative climax model developed by Dyksterhuis (1949) there are ecosystems, generally of more mesic climates, where the linear model is appropriate. It is important to realize that any modeling approach is a best-fit solution, not a perfect-fit solution. Therefore, the retrogression-succession continuum can be modeled within the states to depict the situation where plant community phases do respond linearly. However, it is also possible for linear response mechanisms to be pushed past an ecological threshold, resulting in a state change.

CONCLUSIONS

Definitions and model concepts as discussed in this paper are being adopted by the USDA Natural Resources Conservation Service as the standard for describing vegetation dynamics in rangeland ecological site descriptions. State-and-transition models hold great potential to aid in understanding rangeland ecosystems' response to natural and/or management-induced disturbances by providing a framework for organizing understanding of potential ecosystem dynamics. Many state-and-transition model applications are available in the literature, although the scale of interpretation of the concepts has varied. We have attempted to review and clarify a large amount of information into a proposed conceptual model of state/transition/threshold relationships that are determined by the resilience and resistance of the systems' primary ecological processes. Most of the components presented are not new; however, the proposed model attempts to clarify the definitions and concepts and to link them together into a process-based model for management and research. The management and natural mechanisms responsible for community phase shifts and transition initiation must be included in the model description. The description of these mechanisms should contain information on their impact on the primary ecological processes and the resulting change in the biotic community and system function. Further research is needed to identify indicators of change for ecological processes that will allow management to intervene prior to a threshold change. Once a threshold has been crossed, the focus of management should be on restoration of the damaged ecological processes, not on reestablishing a specific plant community. Although this conceptual model suggests that the ecological site is the minimum scale associated with a state, understanding ecological processes at the landscape scale should be the target. This model contains the flexibility to accommodate landscape level dynamics; however, further research is needed to clarify the ecological relationships occurring at that scale. This effort is not viewed as completed, but rather as another step in the process to further develop understanding of rangeland ecosystems.

Figure 1. Broad application of the state-and-transition concepts. Derived from the Society for Range Management, Task Group on Unity in Concepts and Terminology (1995). The plane labeled SCT (site conservation threshold) represents a change from one ecological site to another and may also be considered a threshold between two states. The individual boxes or ovals represent plant communities or seral stages that exist within one state.

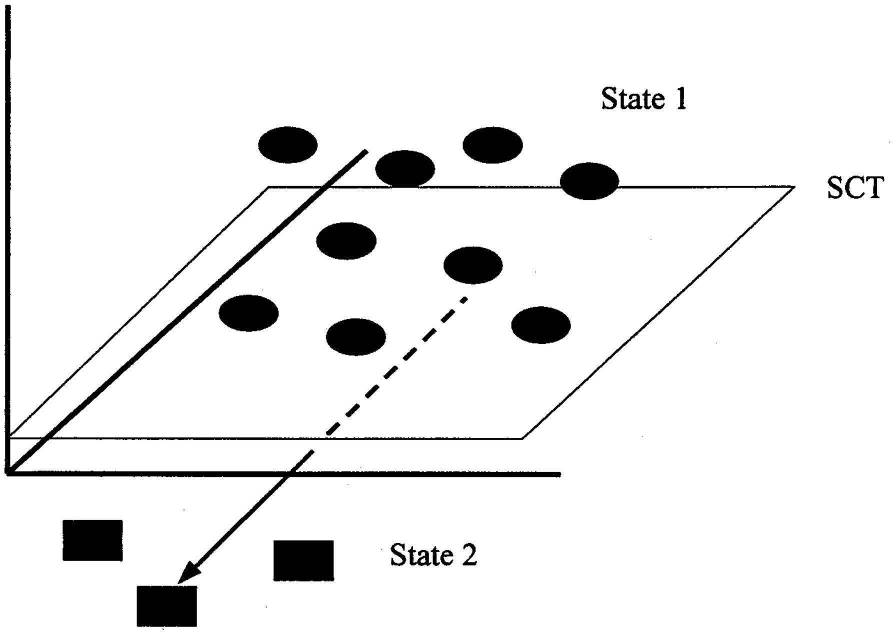


Figure 2. Specific, or narrow, application of states with each state (box) representing one phase or seral stage of vegetation development. Transitions between states are indicated by arrows and the dashed line represents a threshold. The dashed transitional line signifies the requirement of substantial energy input to move the state back across the threshold. Modified from West (1999) and West and Young (2000).

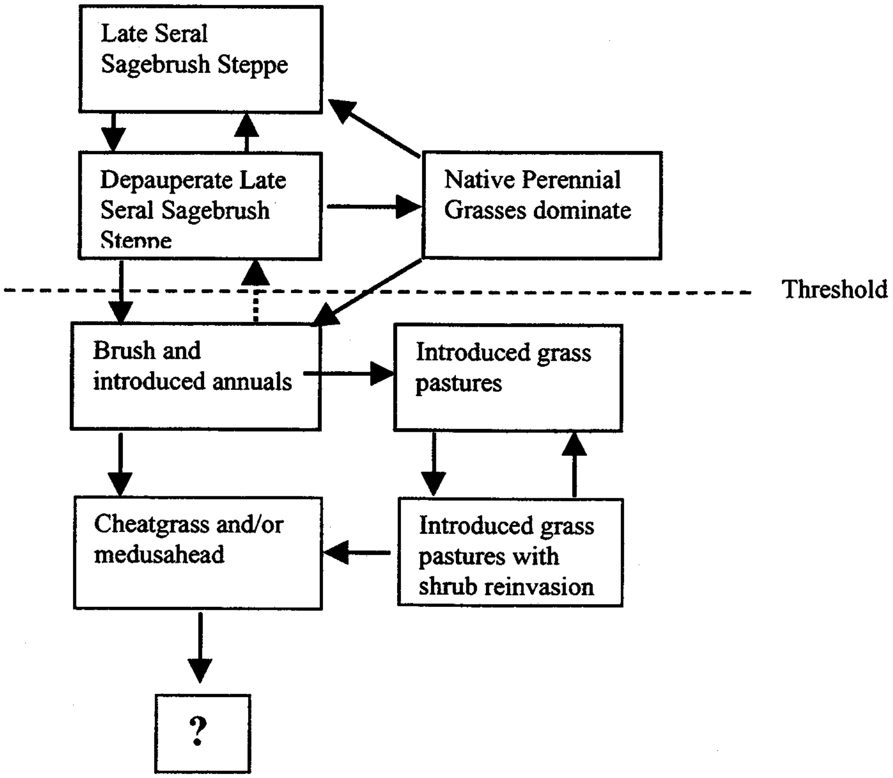


Figure 3. Conceptual model depicting the objects of one state. Note the linear response, retrogression-succession model may be modeled within the state (i.e., a to b to c and vice-versa).

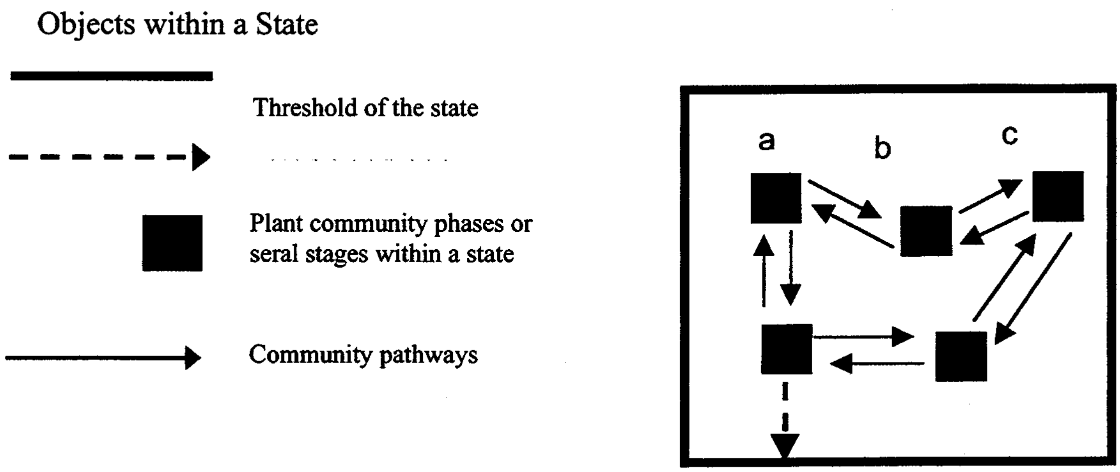


Figure 4. Conceptual state-and-transition model incorporating the concepts of community pathways between plant community phases within states, reversible transitions, multiple thresholds, irreversible transitions, multiple pathways of change, and multiple steady states.

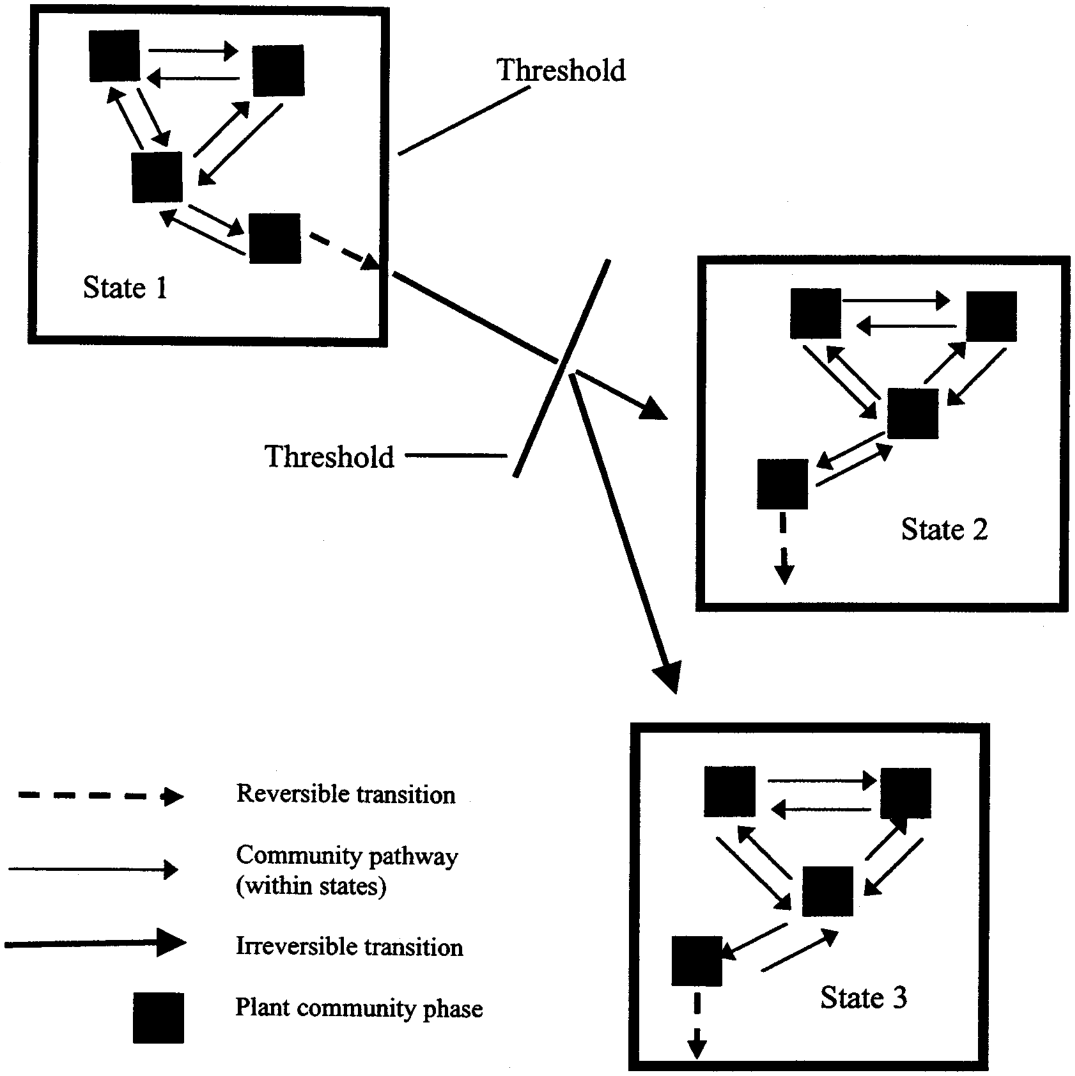
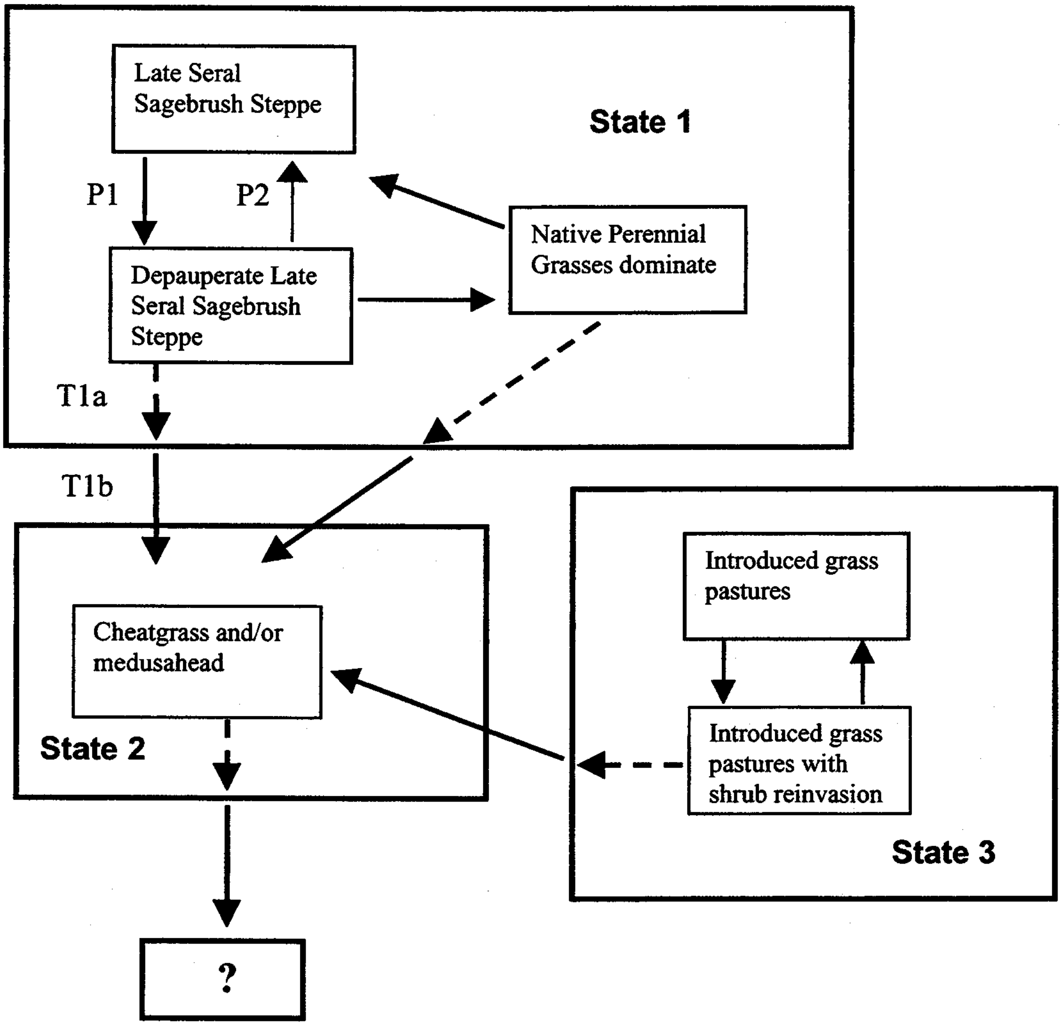


Figure 5. Modification of the West (1999) and West and Young (2000) specific sagebrush steppe model (see Figure 2) to illustrate the broad concept of state with plant community phases and community pathways (i.e., P1 and P2) within states. T1a and T1b signify the reversible and irreversible properties of the transition between State 1 and State 2. For additional discussion of the mechanisms leading to community phase shifts see West (1999) and West and Young (2000).



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