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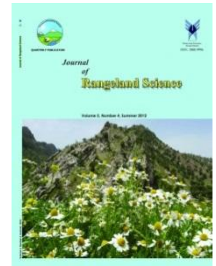

Letter to the Editor

Development of State-and-Transition Models (STM): Integrating Ecosystem Function, Structure and Energy to STM

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Abstract. The main objective of an ecosystem sustainable management is to preserve its capacity to respond and adapt to current disturbances and/or future changes, and maintain the provision of environmental goods and services. Two very important properties linked to this objective are the ecosystem resilience and resistance to disturbance factors. The objective of this paper is to recommend conceptual modifications to the integration of key ecological concepts such as dynamic equilibrium, resistance and resilience to the 'State and Transition Model' (STM) in order to apply them in a more feasible way for rangeland management. Ecological resilience describes the amount of change or disruption required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures. STMs integrated to concepts of structure, function and energy provides greater opportunities to incorporate adaptive management, more accurate forecasts and a better and easier comparison between rangeland ecosystem types than traditional STMs. We propose to enhance the STM considering four principal axes (ecosystem functions and/or processes, natural disturbances and/or negative management activities, required energy to return to the previous state, and structural ecosystem changes and transition time) also simultaneously, to compare the "robust" ecosystem to "fragile" ecosystem. The recommended modifications enable STMs to identify a broader range of variables to anticipate and identify conditions which determine state resilience to better inform ecosystem managers of risk and restoration options.

Key words: STMs, Ecosystem function, Energy, Structure and disturbances.

Introduction

State-and-Transition Models (STMs) describe states, thresholds and management conditions leading to the formation of alternative states (state transitions). Although such models were first formalized for rangeland management (Westoby, 1989; Noy-Meir, 1995), STMs (and similar conceptual models) have become a common means to synthesize information about state transitions in a variety of terrestrial ecosystems (Archer, 1989; Milton *et al.*, 1994; Bestelmeyer *et al.*, 2004; Chartier & Rostagno, 2006; Hobbs & Suding, 2009; Zweig & Kitchens, 2009). In south-western Australia, for example, land managers use STMs to assist with the restoration of Jarrah forest in areas mined for bauxite (Grant, 2006). In the United States, federal land management and assistance agencies have formally adopted STMs as a means to set management benchmarks and recommend practices to achieve desired conditions in rangelands and forests. One of the most challenging issues of rangeland ecology is to build models and tools to enable sustainable management of natural resources. In the 20th century, rangeland management was mainly based on the range model (continuous and reversible vegetation dynamics) (Dyksterhuis, 1949). However, in early 1980s evidence showing that the range model was not applicable to all rangelands began to be accumulated (Westoby, 1980). The concept and the succession model have suffered criticism and constant revisions. The main points having been under constant analysis are the state of equilibrium and linear succession (Tansley, 1939; Egler, 1954; Allen-Diaz & Bartolom´e, 1998; Fern´andez-Gimenez & Allen-Diaz, 1999; Briske *et al.*, 2003, 2005, 2008; Hein, 2006). In this sense, emphasis was focused on building models that represented multidirectional vegetation dynamics, sometimes irreversible, to ease the identification of key processes and factors of good functioning and management for the system under study (Naveh & Lieberman, 1994). The State and Transition Model (STM) (Westoby *et al.*, 1989) was proposed as an alternative and flexible tool. According to this model, for a determined system, there are different alternatives of vegetation states with different transitions between them. The transition into a different state is triggered by a natural event (e.g. abundant rain or extreme drought) by a disturbance and/or management action (e.g. grazing, fire) or by the interaction of any of these factors. Transitions may occur in different directions and generally, may not be linear, occurring by different pathways. There are negative transitions of rangeland degradation (e.g. structure changes, decreasing forage species and productivity) and positive transitions of ecosystem recovery. Negative transitions have higher occurrence probability than positive transitions, and often are irreversible (Westoby *et al.*, 1989). This conceptual model has had very important consequences for rangeland management because there may be a broad variety of vegetation states characterized by a particular dynamics in the same site. The STM includes concepts with different degrees of consensus about its basic definitions and empirical relevance for ecosystem management, such as: states, equilibrium and non-equilibrium, thresholds, ecosystem resilience and resistance (Briske *et al.*, 2003, 2005, 2006, 2008; Stringham *et al.*, 2003; Bestelmeyer *et al.*, 2004, 2009). Our main objectives are to enhance the STM and to increase its explanation power, encompassing the complexity of dynamic ecosystems. Therefore, in this review we propose a set of structural, functional and environmental variables to evaluate rangelands upon which we enhance the STM allowing us to define and/or to quantify the states and transitions of an ecosystem more precisely. Considering this approach we include the dynamic equilibrium concept to approach the steady state definition. Finally, we integrate ecosystem resistance and resilience to the STM and compare rangeland ecosystems‘ types.

Development of State-and-Transition Models

State-and-transition models were presented as a framework to accommodate a broader spectrum of vegetation dynamics on the basis of managerial, rather than ecological criteria (Westoby *et al.,* 1989). These models were initially designed for application on rangelands characterized by discontinuous and nonreversible vegetation dynamics, but they were not intended to replace the range model or suggest that continuous and reversible vegetation change did not occur. The original interpretation indicated that this framework was to be constructed on the basis of 1) potential alternative vegetation states on a site, 2) potential transitions between vegetation states, and 3) recognition of opportunities to achieve favorable transitions and hazards to avoid unfavorable transitions between vegetation states (Westoby *et al.*, 1989). Even though the expressed goal of state-and-transition models was to provide a framework for vegetation management, considerable ecological knowledge and experience is required to define the ecosystem properties associated with these categories of information (Bestelmeyer *et al.*, 2004). The original state-and-transition framework did not specify the use of an ecological reference point (Westoby *et al*., 1989). However, the historic plant community, as defined in the traditional range model, has been adopted as an ecological reference within state-and-transition models developed by the Natural Resource Conservations Service (NRCS) in the United States (USDA, 1997). The desired plant community (SRM Task Group, 1995) represents an alternative reference point for use in these models that is based on management as well as ecological criteria. State-and-transition models can account for a broader spectrum of vegetation dynamics than the range model because they can represent vegetation change along several axes including fire regimes, soil erosion, weather variability, and management prescriptions, in addition to the secondary succession–grazing axis associated with the range model. The succession–grazing axis can track vegetation dynamics within a grassland state, but it cannot accommodate the existence of vegetation transitions to alternative stable states. For example, fire suppression has contributed to vegetation transitions (e.g., fire threshold) from a grassland to a woodland state on many rangelands located in both mesic and semiarid environments (Fuhlendorf *et al.*, 2001). In contrast, weather variation is assumed to contribute to vegetation dynamics within states, rather than between states, for all but the most severe events (Bestelmeyer *et al.,* 2004). State-and-transition models can incorporate reversible and directional vegetation change as described by the range model (Westoby *et al.*, 1989; Bestelymer *et al.*, 2003; Briske *et al.*, 2003). This interpretation is also evidenced by the development of state-and-transition models that closely parallel the traditional range model in grassland regions or where the only substantial modification is the addition of a stable woody plant community (e.g. climatic climax). Recognition that state-and-transition models can incorporate the range model serves to unify further the development of vegetation evaluation procedures for rangeland application. The variables of fire, weather, and grazing may interact to produce unique patterns of vegetation dynamics. The livestock grazing–fire interaction is the most widely recognized and understood interaction contributing to woody plant encroachment. Livestock grazing interacts with fire to reduce fuel loads, reduce herbaceous competition with woody seedlings, and enhance woody plant seed dispersal (Archer, 1994). Consequently, grazing can influence the rate at which the fire threshold is surpassed (Fuhlendorf *et al.*, 1996), but it does not directly define the threshold in the absence of fire (Brown and Archer, 1989, 1999). The removal of grazing would not be expected to reverse the process of woodland conversion without reinstatement of the fire regime (West and Yorks, 2002). In some cases, thresholds may not even be reversed when the prior disturbance regime is reinstated based on the occurrence of reinforcing feedbacks within ecosystems (Scheffer *et al.*, 2001). It is important to recognize that the greatest utility of state-and- transition models originates from the expression of vegetation dynamics along multiple axes, rather than from the development of new ecological information or processes describing the function of rangeland ecosystems. These models provide a framework to catalog information for a greater number of plant communities and vegetation transitions than does the range model, but they do not inherently provide greater insight into the ecological processes associated with this broader spectrum of vegetation dynamics (Archer and Stokes, 2000). Their major advantage is that they accommodate the occurrence of the multiple stable state concept (May, 1977), whereas the range model does not. Development of effective ecological site descriptions is a critical feature of state-and-transition models because the descriptions provide the interpretive information associated with these models. These descriptions explicitly define the various vegetation states, transitions, and thresholds that may occur on a site in response to natural and management events (Stringham *et al.*, 2003).

Function, energy, disturbances and structure axes to enhance the STM

Lópeza *et al*. (2011) proposed two principal axes over which the STM can be optimized: the x axis determined by structural ecosystem changes (vegetation and soil) and the y axis determined by ecosystem functions and/or processes (Fig. 1). These axes determine what we will call the Structural–Functional State and Transition Model (SFSTM). The adoption of these axes is based on the assumption that a disturbance such as overgrazing negatively affects the ecosystem composition, structure, productivity and functioning (Soriano & Movia, 1986; Paruelo *et al.*, 1992; Noy-Meir, 1995; Fern´and ez-Gimenez & Allen-Diaz, 1999; Hein, 2006). High grazing pressures produce loss of plant cover, litter, organic matter and surface soil layer (owing to erosion) drastically change the ecosystem structure. These changes result in a potential loss of soil water storage, water loss by superficial run-off and deep percolation, and great changes in the matter and energy interchange with the environment (Soriano & Movia, 1986; Whitford, 2002; Yong-Zhong *et al.*, 2005; Chartier & Rostagno, 2006). As a consequence, water-use efficiency of an ecosystem decreases under high grazing pressure (Hein, 2006); the micro-environmental conditions also become more unstable and extreme, producing a loss of safe sites for seedling germination and implantation (Snyman, 2004). Thus, each alternative state of an ecosystem has different characteristics of structure function feedback (Bestelmeyer *et al.*, 2009).

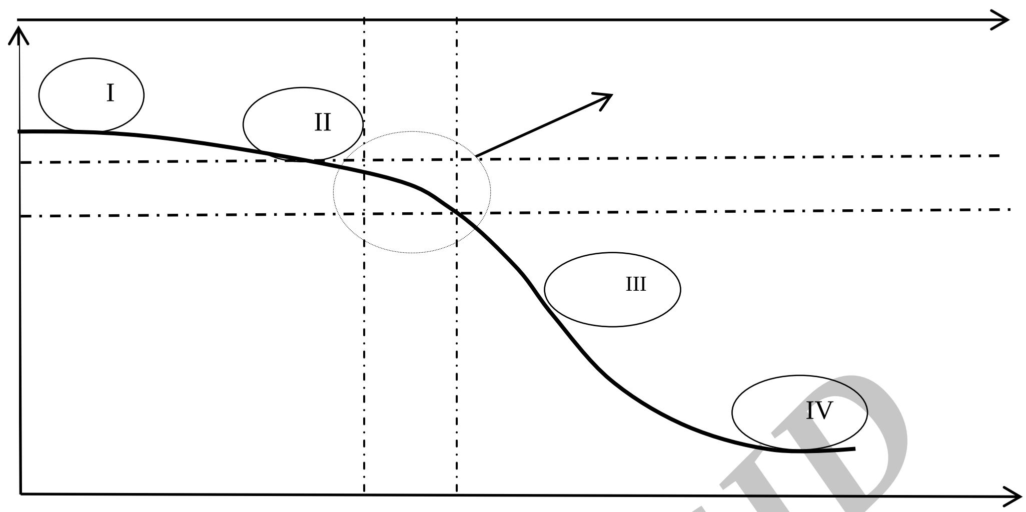

Fig. 1. Schematic representation of the stability of different states in dynamic equilibrium of grass-shrub steppe of *Poa ligularis* and *M. spinosum*, based on: Structural–Functional State and Transition Model (López *et al.*, 2011).

To further improve the model, we recommend four axes over which the STM can be optimized. Axis (X): ecosystem structural changes (physiognomy, relative species composition and growth forms, diversity, vegetation spatial distribution, soil characteristics and the percentage of bare soil) and transition time from a state to another state. Axis (Y): ecosystem functions and/or processes (Stability, Infiltration and Nutrient Cycling). Upper-axis: natural disturbances and/or negative management activities (e.g. climatic events or fire, grazing, farming, burning, etc.). Right-axis: Energy to return to the previous state. It represents the amount of energy that is needed to get back into better condition and also simultaneously, compares the "robust" ecosystem to "fragile" ecosystem (Fig. 2). The ecosystem functions (Y axis) are the ecological processes that maintain the functioning and resilience of the ecosystem (Gunderson & Holling, 2002). The ecosystem functioning is mainly determined by the amount of water and nutrients retained which is measured by LFA indices (Stability, Infiltration and Nutrient Cycling). The loss of ecosystem functions occurs when the amount and the spatial distribution of soil cover has been modified enough to accelerate water, nutrients and soil run-off through the landscape (Briske *et al.*, 2006). Transitions between states are often triggered by multiple disturbances including natural events (e.g. climatic events or fire) and/or negative management actions (grazing, farming, burning, etc.) (Stringham *et al.*, 2003). Although a disturbance simultaneously affects not only the structure, but also the ecosystem functioning, factors such as grazing act directly on the vegetation structure (above-ground biomass consumption). Energy to return to the previous state (Right-axis) represents the amount of energy that is needed to get back into better condition. This energy can be given to ecosystem through positive management activities.

The structure of an ecosystem (X axis, Fig. 2) is defined mainly by physiognomy, relative species composition and growth forms, diversity, vegetation spatial distribution, soil characteristics (depth, organic matter, structure and fertility) and the percentage of bare soil (Briske *et al.*, 2006). This degradation process substantially affects fundamental ecosystem functions. For comparison between two types rangeland ecosystems was used from sigmoid curve that is designed (Tongwy and Hindlly (2000)). In ecosystem function terms, two functional states can be defined, with the inflection point defining the boundary between them. Robust landscape types will have a sigmoid curve characterized by a high upper asymptote a shallow slope and a high lower asymptote (Fig. 2. A). Fragile landscapes would be characterized by a moderate to high upper asymptote, a steep slope and a lower asymptote (Fig. 2. B) (Tongwy and Hindlly, 2000).

Integration of the main concepts to the STM

To integrate the above exposed concepts we propose to interpret the STM based on axes. State I is the most ecosystem function state II is the less ecosystem function then top left corner refers to the less degraded states whereas in the bottom right are the most degraded states. Conversely, in the most ecosystem function the less energy is required to return to the previous state. In other words, required energy to return to the less degraded state is increased as much as ecosystem function is decreased. When natural disturbances and/or negative management activities are strong enough to alter the dynamic equilibrium of a state, a change of greater magnitude than the state amplitude is produced, triggering a negative transition. These changes are persistent in time and are reflected in a 'transition' from one state towards another state in dynamic equilibrium. The transition likelihood depends on the disturbance applied to the system and on the moment at which the state is found within the dynamic equilibrium (López *et al*., 2013). If an ecosystem is disturbed (e.g. overgrazing and/or extreme drought) and a negative transition is produced, we hypothesize that more degraded states would have less state amplitude. Although the decrease in state amplitude is associated with a reduction of functions and processes that can be performed by the ecosystem, we believe this reduction occurs because of a trigger. Triggers are included natural disturbances and human-induced disturbances. Environmental disturbances, such as extraordinary drought (Briske *et al*., 2008) differ from human-induced disturbances such as domestic grazing because the former occur in relatively short periods of time (weeks to months) and the latter maintain their intensity through time (years). The environmental triggers are extraordinary events that would negatively affect the ecosystem structure and functions, directly (fire: burning the vegetation) or indirectly (drought: decreasing the growing space), modifying the dynamic equilibrium of a state. Thus, the probability of a negative transition would increase. A disturbance drove significant changes at vegetation and soil levels causing significant losses in functions and/or processes (increase in the rate of loss of functions and/or processes) which compromise the rangeland sustainability. With the increasing frequency and severity of disturbances and reduction of functions and structure, required energy to return to the less degraded state is increased. Wasted energy of ecosystem can be returned through positive management activities (e.g. Grazing Capacity, species cultivate etc.). A restoration action can also involve an increase in the growing space (fertilization, watering) or enhancements at a structural level (artificial re-vegetation). Everything will depend not only on intrinsic ecosystem factors (community type, species and topography), but also on extrinsic factors (grazing or disturbance type) (López *et al.*, 2011). These factors together are changing the ecosystem from a state to another state. It is important to define these possible states (e.g. between state I and II, Fig. 2) in order to determine how far the rangeland is from crossing the threshold. As energy threshold is regarded as coincident function threshold, this will provide decision-makers of rangeland management with a fundamental tool. At this range, positive transitions become more unlikely and stochastic factors, such as favorable climate events (series of wet years) (Westoby *et al.*, 1989; Briske *et al.*, 2008) or active restoration actions, gain importance as triggers of positive transitions (Friedel, 1991). This type of event produces an increase in the growing space available for a community; therefore, in the state functional and/or structural amplitude, increasing the probability of a positive transition (Westoby *et al.*, 1989) (Fig. 2). Secondly, we propose to compare rangeland ecosystems as for, above concepts. In this model, a robust rangeland ecosystem is compared to a fragile ecosystem. Above concepts are different for the two type ecosystems. In a robust ecosystem, function curve and energy curve have shallow slope and a high lower asymptote, wider threshold range and more transition time from a state to other state than a fragile ecosystem. Thus management activities are different for two type ecosystems.

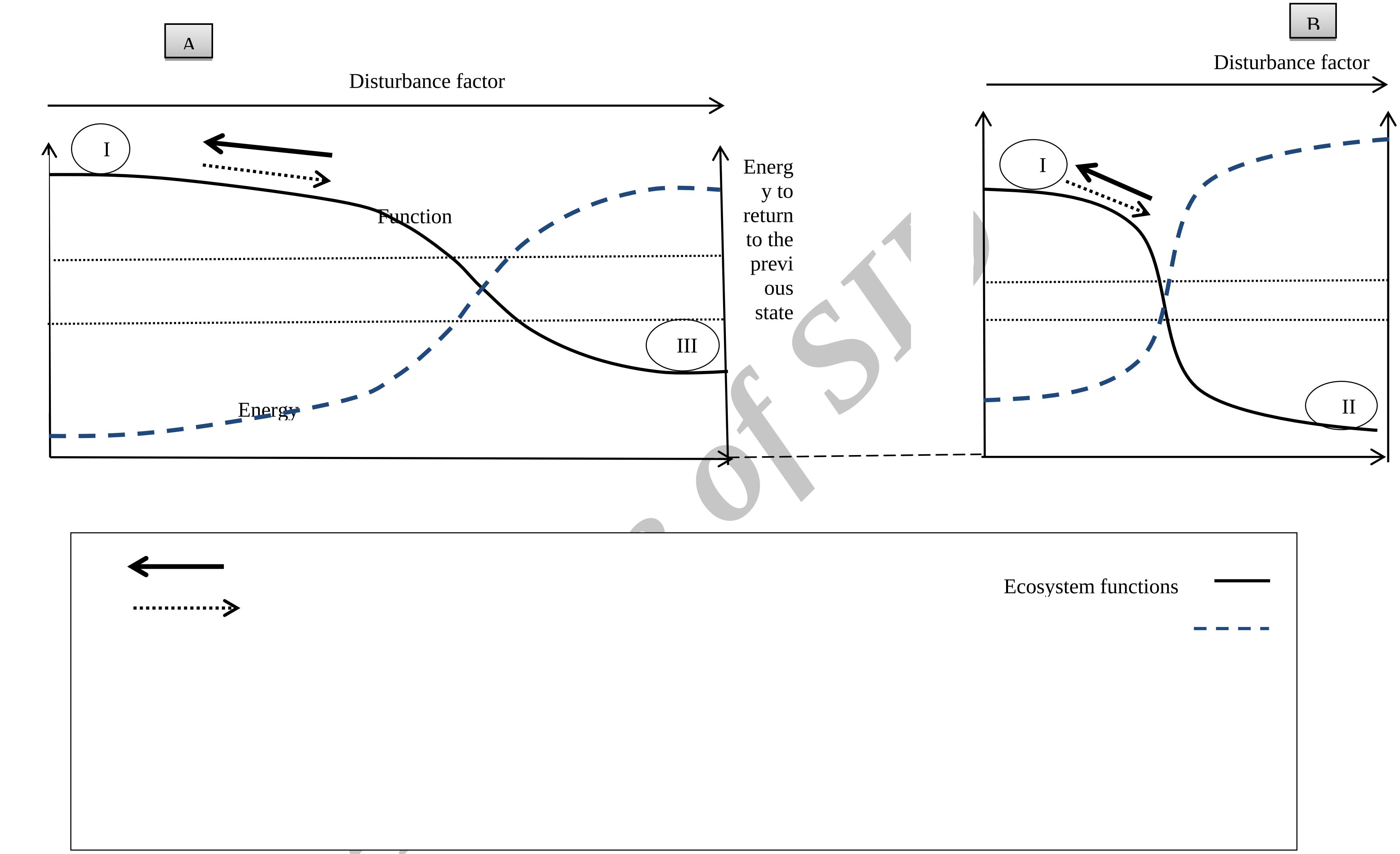

Fig. 2. Integrating function, structure and energy transfer with STM and compare the “robust” ecosystem (A) to “fragile” ecosystem (B)

Conclusions

State-and-transition models organize the combined understanding of scientists and managers to explain ecosystem dynamics across variable rangeland landscapes. It is important to recognize that this framework is not a blanket replacement of an outdated succession-retrogression model, but a complement to it that accounts for the existence of multiple equilibria, as well as the return to equilibrium following perturbations. Furthermore, the contrast between communities and states can be used to distinguish the need for facilitating and accelerating management practices. The results of a broad range of studies and personal experiences can be summarized within this framework and the resulting views can be continually updated as new observations and ideas emerge (Bradshaw and Borchers, 2000). The graph structure of state-and-transition models influences the potential amplification, synchronization, and constraints on state changes independently of from the ecological dynamics within the individual states. The model developed here is more realistic than the static models that are more commonly developed. Use of the state-and-transition framework in this way also enabled us to utilize multiple state variables rather than be forced to use a univariate state value (e.g. vegetation condition scores) as a measure of condition. The ability to predict and manage transitions in many ecosystems would be improved by these STMs. Nonetheless, our review points to a set of approaches for including information on structural and functional processes in the interpretation of states change and design of management actions. These STMs would be of greater use for assessment, monitoring and forecasting than traditional STMs because they better enable natural resource professionals to recognize transition mechanisms and identify where, when and under what circumstances undesirable transitions or opportunities to promote desirable transitions are most likely to occur. We suggest that incorporation of more explicit resilience-based concepts within the STM framework accomplishes one important objective; the recommended modifications enable STMs to identify a broader range of variables to anticipate and identify conditions that determine state resilience to better inform ecosystem managers of risk and restoration options.

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