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State and Transition Models: Response to an ESA Symposium

This article responds to the symposium: Thresholds and non-linear responses in ecosystems: understanding, sustaining, and restoring complex rangelands, which was sponsored by the ESA Rangeland Ecology Section and organized by D. D. Breshears and J. Herrick. Recent discussion of the State and Transition (ST) model and its application to arid and semiarid rangelands indicated significant confusion and misunderstanding about the concept. State and transition models are evolving in their applications (Archer et al. 2001) and enjoying wide use (Bestelmeyer et al. 2001), while they are also being adopted by agencies as the model approach for managing rangelands (Joyce et al. 2001, Stringham et al. 2001).

ST models are simple box-andarrow diagrams in which boxes represent observed or theoretical ecosystem states and arrows represent the observed or theoretical transitions among these states. These models have also been called Forrester diagrams (Haefner 1996), and are commonly used to conceptualize either formal mathematical models or the complex behavior of dynamic systems. They are essentially a means of mapping system behavior in the absence of adequate predictive models. Westoby et al. (1989) were the first to espouse the use of ST models as a specific tool in an ecological context. These models were immediately attractive to rangeland ecologists whose semiarid and arid systems often exhibited nonlinear dynamics and seemed to be beyond basic description using Clementsian climax theory and its derivative, the Range Condition model. With the ST framework, such nonlinear behavior not only could be described at multiple scales, but also led toward the development of testable hypotheses in which transition probabilities could be theorized and/or empirically generated.

We feel that further discussion of the ST approach should occur prior to its widespread, "top-down" implementation by management agencies and the ecological community. Particularly distressing to us were some of the symposium discussions regarding the intent of Westoby et al. (1989). Many questions were asked about ST models during the discussion period that were inadequately posed and/or answered. Three significant questions are:

1) Do ST models offer new theory in lieu of the failure of Clementsian climax theory?

The ST model in Westoby et al. (1989) has been extrapolated into a theory for vegetation change—it is not. Westoby et al. (1989) proposed it as a means of cataloging observed or hypothesized states and transitions in an effort to better understand the interactions between weather and management. As Westoby et al. (1989) state,

We are proposing the state-andtransition formulation because it is a practicable way to organize information for management, not because it follows from theoretical models about dynamics. In consequence, we consider management rather than theoretical criteria should be used in deciding what states to recognize in a given situation.

2) How does the ST model differ from the classical, Clementsian-based Range Condition (RC) model?

The RC model was developed by Dyksterhuis (1949) to guide the management of range systems that followed equilibrium-type community dynamics. In equilibrium-type systems, biotic interactions are assumed to be the dominant forces shaping floristic assemblages—communities (Wiens 1984). These interactions can be plant–plant (competition), plant– animal (herbivory), or both. State and transition models can accommodate

multiple equilibria (alternative stable states) or nonequilibrium (no stable states) dynamics. Nonlinear dynamics occur where the spatiotemporal variability of abiotic forces entrains community change. Phenomena like grazing disturbances are of lesser import in determining the overall community structure because the mechanisms that they influence most, biotic interactions, are swamped by environmental stochasticity. The ST model is well suited for developing testable, quantitative hypotheses about community structure (Allen-Diaz and Bartolome 1998).

3) Is the concept of thresholds fundamental to ST model development?

Thresholds are important conceptually as a means of understanding nonlinear community interactions occurring over spaces and/or periods that are larger than humans typically perceive (Laycock 1991). However, they are not fundamental to the ST concept or its applications. To relegate ST models to such phenomena exclusively is to severely limit their utility in understanding a variety of scales for the same system, e.g., intravs. interannual compositional change. Stringham et al. (2001) call this approach "general," and the approach we espouse "specific." Their rationale for the general approach relies on the concepts of community resistance and resilience. These are equilibrium-based concepts in which communities resist change and recover from disturbances based on some notion of the potential natural vegetation state. They assign community changes that do not cross "thresholds" as mere phase shifts, which are reversible with proper management. Unfortunately, many systems do not exhibit such response to management (Heady et al. 1992, Illius and O'Connor 1999, Oba et al. 2000). Although some communities may display multiple equilibria behavior (i.e., local resistance/resilience), others may fall under the nonequilibrium rubric in which no stable states are observed (Jackson and Bartolome, in press). Furthermore, the ST framework envisioned by Stringham et al. (2001) depends on determination of "fully functioning" ecosystems. We feel that this concept is too nebulous to quantify on any meaningful level, and is subject to the vagaries of observer bias. For example, does a desirable plant community make an ecosystem fully functional? Or are hydrological properties the most important metric? Is nutrient status necessarily invoked in this concept?

State and transition models are analogous to Dyksterhuis's Range Condition (RC) model. They provide a framework for describing, understanding, predicting, and ultimately controlling rangeland ecosystem dynamics, the goals of science and management. State and transition models are an empirical approach toward rationally addressing these goals, as outlined by Begon et al. (1996). The shortcoming of equilibrium-based RC models is that they do not account for contingencies such as long-term drought cycles and interannual precipitation variability, i.e., environmental and management factors vary along a single axis and need to be highly general (Allen-Diaz and Bartolome 1998). Factors like rainfall and grazing intensity could only be considered as additive factors. State and transition models are an important tool for understanding factorial system behavior and can be made as specific as needed, given adequate data.

We are concerned that the adoption of ST models by agencies is being done in a way that will doom it to failure as a management tool and as a means of scientific inquiry. The generality of the ST concept is potentially compromised by linking it exclusively to scales that incorporate vegetation shifts from one life-form type to another, e.g., from grassland to shrubland. This minimizes its utility to the rangeland manager trying to understand important interactions and/or to manage opportunistically within the variability inherent to a grassland. Furthermore, the ST approach is being advertised as explicitly linked to "irreversible" or "difficult to reverse" shifts as the only credible or important transitions. This further limits the scales at which the tool can be employed.

During the ESA symposium discussion, Steven Archer pointed out the importance of utilizing the tool on a site-by-site basis-in a grassroots sort of way. Indeed, this is a fundamental appeal of the approach-it can, and, we argue, should, be used by scientists and managers to catalog change at multiple scales, during multiple periods, to generate data sets that will aid managers in adaptive behavior (this is the opportunistic part of Westoby et al. 1989) and to generate testable hypotheses about community dynamics. Such an approach will provide the reliable information that is needed for effective management. With time, patience, and data, more general theory may be derived from the development of specific and general ST models. To sweep away the worthiness of the specific models because general theory has yet to evolve from them is shortsighted.

Hence, ST models, as we understand them (sensu Westoby et al. 1989), are heuristic, empirical tools that are flexible and general—and hence, powerful. It is imperative, we feel, that a "bottom-up" approach to these models be allowed to develop and evolve within both the scientific and management communities, thereby avoiding the rigidity and dogma that are associated with the preceding theoretical paradigm and associated management blunders.

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"Newcomers" Invade the Field of Invasion Ecology: Question the Field's Future

Rejmánek et al. (2002) recently critiqued a nomenclature scheme for invasion ecology we had proposed (Davis and Thompson 2000). They stated that we tried to change the field's terminology "in response to governmental policy statements," an attempt, they said, that "probably has no precedent." Specifically, they described our effort as an attempt to make the terminology "concordant with the definition in an Executive Order of one country's President." They also stated that we believe "invasion always implies some sort of impact, and all "invasive" taxa are harmful." There is no truth to these statements.

Rejmánek et al. did not cite the original paper (Davis and Thompson 2000), in which we made our nomenclature proposal. In this paper, we did not refer to any executive order or any public policy issue; nor did we address in any way communication between scientists and the general public. Our proposed nomenclature was conceived, written, and justified entirely as a way to improve communication and research *within* the scientific community.

Rejmánek et al. confused our proposed operational definition of the word "invasion" with the phenomenon of new species coming into a region. We developed our proposed nomenclature on the explicit recognition that some new species "have a negligible effect on the new environment, whereas some have a very large impact" (Davis and Thompson 2000). We proposed that usage of the word "invasion" be confined to those circumstances in which the newcomers have a large impact on the community, ecosystem, or economy. Our operational definition, as we presented it, is completely neutral as to whether the impact is deemed helpful or harmful by humans.

We brought up Clinton's Executive Order in a subsequent response on this issue (Davis and Thompson 2001) as an example of the extent to which the nonscientific and scientific communities differ in their use of such words as "invasion" and "invader." (President Clinton's Executive Order on Invasive Species [Order 13112, 3 February 1999] defines invasive species in terms of impact: "invasive species means an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health.") We pointed out in our response that, in addition to its benefits to scientists working within the field (our sole emphasis in the original paper), our proposed nomenclature system also might be helpful in our communication with nonscientists. Even though we never considered the latter possibility in preparing the original paper, it is certainly true that ecological issues are now commonly and directly addressed in national-scale policy discussions, and it would seem to behoove ecologists to reflect on whether the language we use enhances or detracts from our ability to communicate effectively with nonscientists. Others have made this same point in other contexts. For example, in their recent review of the definition and