Paradigm Integration between Equilibrium and Non-equilibrium Concepts for Evaluating Vegetation Dynamics in Rangeland Ecosystems

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Abstract

There are two major paradigms involved in applied ecological research on rangeland ecosystems: the equilibrium paradigm and non-equilibrium paradigm. The former idea posits that communities will respond in a sequential and predictable manner to the environment and disturbances such as grazing. The latter idea has minimized ecosystem regulation and stability and placed greater emphasis on external factors such as climatic variability and episodic events, implying that ecosystems are less predictable than indicated by the equilibrium concept. Previous literature has suggested that both equilibrium and non-equilibrium paradigms must be incorporated into rangeland management perspectives if the solid science of rangeland ecology is to continue to underpin them. However, the current state-of-the-art in rangeland management appears to be progressing at the extremes of the equilibrium–non-equilibrium continuum. Consequently, there is uncertainty as to whether the current knowledge is the key to successful environmental management of rangeland ecosystems. Here, I have synthesized the extensive debates on rangeland ecology from a rangeland management perspective, and merged the two major paradigms by placing the idea of ecological thresholds at the core of the study framework. The clear implication is that both equilibrium and non-equilibrium paradigms must be incorporated into vegetation management in rangeland ecosystems. Effective vegetation management based on both paradigms can prevent adverse changes in states before ecological thresholds are reached, while maintaining or enhancing the ecological resilience of rangeland ecosystems.

Key words: arid and semi-arid rangelands, ecological theory, ecological threshold, non-equilibrium dynamics, rangeland management

1. Introduction

Predicting the impacts of livestock grazing on natural communities has become a major concern in recent rangeland ecology research, especially where grazing is widespread and its impacts may be in conflict with sustainable use of natural resources and biodiversity conservation (e.g., Milchunas and Lauenroth, 1993; Diaz et al., 2001; Vesk & Westoby, 2001; Pakeman, 2004; Vesk et al., 2004; Diaz et al., 2007). Major advances have been made in revealing the patterns and processes of vegetation changes associated with grazing, generalizing these patterns within a given landscape or region, and reassessing the appropriate paradigm for describing vegetation dynamics.

There are two major paradigms involved in applied ecological research on rangeland ecosystems: the equilibrium and non-equilibrium paradigms. The former idea posits that communities will respond in a sequential and predictable manner to the environment and disturbances such as grazing (Clements, 1936; Dyksterhuis, 1949). The latter idea has minimized ecosystem regulation and stability and placed greater emphasis on external factors such as climatic variability and episodic events, implying that ecosystems are less predictable than indicated by the equilibrium concept (Wiens, 1984; De Angelis & Waterhouse, 1987; Ellis & Swift, 1988; Westoby et al., 1989). Briske et al. (2003) proposed that both equilibrium and non-equilibrium ideas be incorporated into rangeland management perspectives in order that the solid science of rangeland ecology continue to underpin them. However, the current state-of-the-art in rangeland management appears to be progressing at the extremes of the equilibrium-non-equilibrium continuum (Wiens, 1984; Briske et al., 2003). Consequently, there is uncertainty as to whether the current knowledge is the key to successful environmental management of rangeland ecosystems (Briske et al., 2003).
2. Major Paradigms in Rangeland Ecology

2.1 Equilibrium paradigm

The equilibrium paradigm (represented by the “range model” in rangeland ecology: sensu Dyksterhuis, 1949) represents vegetation change along a single axis defined by the successional theory of Clements (1936). It assumes that ecosystems possess the capacity for internal regulation through negative feedback mechanisms, including intense intra- and interspecific competition and plant–animal interactions (De Angelis & Watthouse, 1987). In the range model, vegetation dynamics are considered best characterized as continuous and reversible change (Clements, 1936; Dyksterhuis, 1949). The interpretation of equilibrium vegetation dynamics may therefore be strongly influenced by the degree of managerial involvement imposed within a given system. The main management applications based on the range model are to provide information about “increasers” and “decreasers” (sensu Dyksterhuis, 1949) as a diagnostic tool for rangeland ecosystems (e.g., Diaz et al., 2001; McIntyre & Lavorel, 2001; Vesk & Westoby, 2001; McIntyre et al., 2003; Vesk et al., 2004) and to describe detailed successional pathways within a given site (e.g., Lauenroth & Laycock, 1989; Pakeman et al., 1997; Coffin et al., 1998) (Fig. 1a).

2.2 Non-equilibrium paradigm

Recently, however, some rangeland ecologists have proposed that the understanding of rangeland ecosystems fully based on the equilibrium paradigm may misdirect land management efforts, sometimes leading to degradation of ecosystems (Wiens, 1984; Ellis & Swift, 1988; Walker, 1993). This is due to the equilibrium paradigm’s undervaluing the potential existence of discontinuous and irreversible vegetation dynamics, and the importance of climatic variability and episodic events on ecosystem behavior (Wiens, 1984; Ellis & Swift, 1988). Alternatively, a non-equilibrium paradigm has emerged that minimizes ecosystem regulation and stability and places greater emphasis on discontinuous and irreversible vegetation dynamics. This paradigm implies that ecosystems are less predictable than previously indicated by the equilibrium paradigm and that alternative models are required in order to account for stochastic dynamics (Wiens, 1984; Ellis & Swift, 1988).

Of the models within the non-equilibrium paradigm, the non-equilibrium persistent model has postulated that vegetation dynamics in rangeland ecosystems are driven primarily by periodic and stochastic climatic factors, and that grazing impact plays a relatively small role in determining the biomass or productivity and composition of vegetation (Wiens, 1984; De Angelis & Watthouse, 1987; Ellis & Swift, 1988). Some rangeland ecosystems are reported to be driven by such non-equilibrium dynamics (Fernandez-Gimenez & Allen-Diaz, 1999; Jackson & Bartolome, 2002; Walker & Wilson, 2002; Richardson et al., 2005) and others are not (Fernandez-Gimenez & Allen-Diaz, 1999; Fynn & O’Connor, 2000; Diaz et al., 2001; Walker & Wilson, 2002). However, much of the prevailing rhetoric in rangeland science and management today emphasizes the non-equilibrium nature of most rangelands and the inappropriateness of equilibrium-based models such as the range model as the basis for rangeland management (Briske et al., 2003). The perception that vegetation dynamics is driven entirely by infrequent and unpredictable events reduces the opportunity for observation and experience to be incorporated into management models and decreases incentives for adaptive management (Watson et al., 1996; Fernandez-Gimenez & Allen-Diaz, 1999; Illius & O’Connor, 1999; Walker & Wilson, 2002; Butterolph & Coppock, 2004) (Fig. 1b). Hence, the debate has forced a more comprehensive interpretation of vegetation dynamics along the entirety of the equilibrium–non-equilibrium continuum (Fernandez-Gimenez & Allen-Diaz, 1999; Illius & O’Connor, 1999; Walker & Wilson, 2002; Butterolph & Coppock, 2004). Recent rangeland studies have suggested that a continuum of systems exists rather than a stark dichotomy between equilibrium and non-equilibrium rangelands (Fernandez-Gimenez & Allen-Diaz, 1999; Illius & O’Connor, 1999; Walker & Wilson, 2002; Butterolph & Coppock, 2004).

Another model within the non-equilibrium paradigm is the state-and-transition model that focuses on describing quasi-stable vegetation states, predicting the circumstances that trigger transitions to species-different states, and modelling these changes (Westoby et al., 1989; Laycock, 1991; Bestelmeyer et al., 2003, 2004; Stringham et al., 2003; Briske et al., 2005, 2006, 2008). This model emphasizes the nonlinearity of vegetation responses to grazing and other environmental perturbations (Westoby et al., 1989; Laycock, 1991; Bestelmeyer et al., 2003; Briske et al., 2005). In particular, ecological thresholds (see the next section) have become a focal point in rangeland management through their relationship to state-and-transition models because the identification of thresholds is necessary in order to recognize the various quasi-stable states that can potentially exist at a given ecological site (Briske et al., 2005, 2006, 2008). Previous studies (McIntyre & Lavorel, 2001; Pakeman, 2004; Diaz et al., 2007) suggested that
increased grazing favored a suite of attributes associated with fast regeneration and growth, including annual life cycles and ruderal strategies, whereas decreased grazing favored perennial species, regeneration from a buried seed bank and species that were relatively palatable (Fig. 1). The state-and-transition model assumes that there is an ecological threshold in the shifts between these two quasi-stable states (Westoby et al., 1989; Bestelmeyer et al., 2003; Stringham et al., 2003; Briske et al., 2005, 2006, 2008) and that adverse changes in states beyond the ecological threshold might essentially be irreversible (Scheffer & Carpenter, 2003) (Fig. 1c). However, fewer studies (e.g., Friedel, 1991, 1997; Bestelmeyer et al., 2004) have actually examined whether there is an ecological threshold in such shifts (Fig. 1c). Recognition of nonlinear vegetation dynamics in real ecosystems (Briske et al., 2005; Peters & Havstad, 2006; Peters et al., 2006) will provide a strong incentive for an alternative or substantially modified evaluation procedure that would accommodate a broader spectrum of vegetation dynamics than the classical equilibrium model (Bestelmeyer et al., 2003; Stringham et al., 2003; Briske et al., 2005). This is because continuous and reversible vegetation dynamics prevails within stable vegetation states, whereas discontinuous and irreversible dynamics can occur when ecological thresholds are surpassed and one quasi-stable state replaces another.

3. What is An Ecological Threshold?

An ecological threshold is defined as a point or zone at which relatively rapid change occurs from one ecological condition to another along a gradient in a prevailing disturbance regime (Radford & Bennett, 2004; Radford et al., 2005; Bestelmeyer, 2006; Groffman et al., 2006). Many rangeland studies have reported that the impacts of concentrated grazing on vegetation dynamics generally lead to marked reductions in forage resources, mainly due to shifts in the community composition from dominance by perennial grasses and forbs toward dominance by unpalatable forbs and weedy annuals (e.g., Fernandez-Gimenez & Allen-Diaz, 2001; McIntyre & Lavorel, 2001; Todd, 2006) (Fig. 2). In Mongolian rangeland ecosystems, Sasaki et al. (2008) found strong evidence for the exis-

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**Fig. 1** The illustration of management applications based on three conceptual models in rangeland ecology: (a) range model, (b) non-equilibrium persistent model, (c) state-and-transition model.

**Fig. 2** Severe livestock grazing generally shifts the community composition from dominance by perennial grasses and forbs (dominated by *Allium polyrrhizum*; upper panel) toward dominance by unpalatable forbs and weedy annuals (dominated by *Chenopodium album*; lower panel).
tence of an ecological threshold in such shifts along a grazing gradient across all ecological sites, even though the vegetation types, edaphic conditions, landscape positions and climatic conditions differed among the sites (Fig. 3; Sasaki et al., 2008). This suggests that vegetation responses to grazing in the study areas were essentially nonlinear. Because Sasaki et al. (2008) obtained this evidence from snapshot data, the repeatability of this ecological threshold across several years needs to be examined to account for high rainfall variability in arid and semi-arid regions such as Mongolia.

4. A Study Framework That Allows Integration of Equilibrium and Non-equilibrium Paradigms

Here, I propose a study framework that incorporates both equilibrium and non-equilibrium vegetation dynamics (Westoby et al., 1989; Watson et al., 1996; Bestelmeyer et al., 2003; Briske et al., 2003, 2005) with the understanding that ecosystems need not be classified exclusively as either equilibrium or non-equilibrium from a rangeland management perspective (Fernandez-Gimenez & Allen-Diaz, 1999; Jackson & Bartolome, 2002; Walker & Wilson, 2002; Briske et al., 2003). In this framework, I argue that greater knowledge of the nature and behavior of thresholds in response to the impacts of grazing across observation years (i.e., the existence of an ecological threshold and its repeatability) is essential for sustainable management of rangeland ecosystems. Continuous and reversible vegetation dynamics would prevail within the stable vegetation state before ecological thresholds are reached. In addition, I focus on the responses of functional groups (e.g., perennial grasses, annual forbs) to grazing in relation to the ecological threshold with repeated measurements from the same sites to account for rainfall variability across Mongolian rangeland ecosystems. Consequently, this procedure allows important signs to be extracted that could forewarn of the occurrence of threshold changes in the vegetation state. The study framework should thus allow for generalization of ecological knowledge based on both equilibrium and non-equilibrium paradigms.

5. Applying the Study Framework to Rangeland Management: An Empirical Example in Mongolian Rangeland Ecosystems

Figure 4 shows typical examples of significant and similar responses in functional groups to grazing at each site across observation years (from 2006 to 2008). Repeatability was observed in the ecological threshold along a grazing gradient (Sasaki et al., unpublished manuscript). This provides strong evidence that real accumulated damage by livestock grazing on rangeland ecosystems still remains and can be observed even under fluctuations in rainfall. In general, dominant functional groups at each site drastically decreased prior to the crossing of an ecological threshold. The data from recovery experiments established along the grazing gradients suggested that beyond the ecological threshold the prior the vegetation state cannot recover after short-term livestock exclusion (Sasaki et al., unpublished manuscript). Therefore, the first step in annual management under system uncertainty must be to identify sharp decreases or increases in the cover of these species—definitive signs that the grazing intensity will soon cross the threshold level.
6. Conclusion

I have thus synthesized the extensive debates on rangeland ecology from a rangeland management perspective and merged two major paradigms by placing the idea of ecological thresholds at the core of the study framework. The clear implication is that both equilibrium and non-equilibrium paradigms must be incorporated into vegetation management in rangeland ecosystems. Effective vegetation management based on both paradigms can prevent adverse changes in states before ecological thresholds are reached, while maintaining or enhancing the ecological resilience of rangeland ecosystems.

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Takehiro SASAKI is a Postdoctoral Fellow in the Ecosystem Adaptability Global COE program at Tohoku University. His research mainly focuses on non-linear vegetation dynamics in arid and semi-arid ecosystems, including the patterns and processes of nonlinear vegetation responses to grazing, and the mechanisms of how local extinctions in communities impact ecosystem functioning. For more information, please visit his website: http://homepage3.nifty.com/landscape Ecology/.

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