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ESSAY REVIEW

Vegetation dynamics on rangelands: a critique of the current paradigms

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Summary

1. Rangeland ecologists have been debating the validity of two current paradigms for the evaluation of vegetation dynamics on rangelands. This debate frequently contrasts the conventional model of continuous and reversible vegetation dynamics (range model) with a more contemporary model that can accommodate discontinuous and non-reversible vegetation change (state-and-transition model).

2. The range and the state-and-transition models are conceptually related to the equilibrium and non-equilibrium paradigms within ecology, respectively. The methodological dichotomy that has developed between the range and the state-and-transition models has fostered the perception that these two ecological paradigms are mutually exclusive. We challenge this perception and contend that both methodologies and their corresponding paradigms are non-exclusive.

3. Equilibrium and non-equilibrium ecosystems are not distinguished on the basis of unique processes or functions, but rather by the evaluation of system dynamics at various temporal and spatial scales. Consequently, ecosystems may express both equilibrium and non-equilibrium dynamics. This confirms early interpretations that ecosystems are distributed along a continuum from equilibrium to non-equilibrium states.

4. Although both equilibrium and non-equilibrium dynamics occur in numerous ecosystems, the empirical evidence is frequently confounded by (i) uncertainty regarding the appropriate evidence necessary to distinguish between paradigms; (ii) disproportionate responses among vegetation attributes to climate and grazing; (iii) comparisons among systems with varying degrees of managerial involvement; and (iv) the evaluation of vegetation dynamics at various spatial and temporal scales.

5. *Synthesis and applications.* This critique supports the conclusion that a paradigm shift has not taken place in rangeland ecology, but rather, the debate has forced a more comprehensive interpretation of vegetation dynamics along the entirety of the equilibrium–non-equilibrium continuum. Therefore, the rangeland debate should be redirected from the dichotomy between paradigms to one of paradigm integration.

Key-words: equilibrium systems, event-driven dynamics, non-equilibrium systems, paradigm shift, range condition, rangeland ecology, state-and-transition model, thresholds.

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Introduction

Rangeland ecologists have been reassessing the appropriate paradigm to interpret and manage vegetation dynamics on rangelands. This reassessment has contrasted the conventional model of continuous and reversible vegetation dynamics (range model) with a more contemporary model that can accommodate discontinuous and non-reversible vegetation dynamics (state-and-transition model). The origins of the rangeland paradigm debate can be traced directly to dissatisfaction with the Clementsian-based procedure for range condition and trend analysis (range model;

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sensu Dyksterhuis 1949). The range model has long been a standard procedure for evaluating vegetation dynamics on rangelands, particularly in North America. This model is generally depicted to show that grazing intensity proportionally counteracts secondary succession, in a continuous, directional manner, to modify species composition variously (Westoby, Walker & Noy-Meir 1989; Walker 1993a). Community composition defines range condition on the basis of its relative position along a successional gradient, with the composition of a presumed pre-settlement climax community representing excellent range condition (Dyksterhuis 1949).

The range model has received substantial criticism, contending that it is an ineffective, over-simplification of vegetation dynamics on many rangelands (Laycock 1989; Smith 1989; Westoby, Walker & Noy-Meir 1989) and that its application may contribute to mismanagement and degradation of some rangeland ecosystems (Ellis & Swift 1988; Mentis *et al.* 1989; Walker 1993a). State-and-transition models were specifically developed to overcome the limitations associated with the range model for evaluation of vegetation dynamics in variable rangeland environments (Westoby, Walker & Noy-Meir 1989).

Emphasis on the range and state-and-transition models has largely overshadowed the fact that the rangeland debate is underpinned by a broader ecological re-evaluation of the appropriate paradigm to interpret ecosystem behaviour in response to disturbance (DeAngelis & Waterhouse 1987; Wu & Loucks 1995; Paine 2002). The re-evaluation of ecological paradigms is relevant to the rangeland debate because the range and state-and-transition models are conceptually related to the equilibrium and non-equilibrium paradigms, respectively. The re-evaluation of ecological paradigms has focused on the contention that the equilibrium paradigm has over-emphasized internal ecosystem regulation and stability, which has minimized the importance of climatic variability and episodic events on ecosystem behaviour (Wiens 1984; Ellis & Swift 1988; Wu & Loucks 1995). In contrast, the non-equilibrium paradigm has minimized ecosystem regulation and stability and placed greater emphasis on external disturbances as drivers of ecosystem behaviour. The latter paradigm implies that ecosystems are less predictable than previously indicated by the equilibrium paradigm and that alternative models are required to account for this variability (Wiens 1984; Ellis & Swift 1988; Wu & Loucks 1995). Paradigm re-evaluation on rangelands is defined by two interrelated ecological questions. Do ecosystems possess single or multiple equilibrium points in response to various disturbance regimes? Are vegetation dynamics around these equilibrium points characterized by continuous and reversible or by discontinuous and non-reversible change?

The influential contributions of Ellis & Swift (1988) and Westoby, Walker & Noy-Meir (1989) had a synergistic effect on the rangeland debate by identifying the limitations of the equilibrium paradigm and providing a vegetation methodology for adopting the non-equilibrium paradigm, respectively. However, ecological paradigm re-evaluation was not explicitly linked with the assessment of methodologies for vegetation evaluation on rangelands. Although methodologies for vegetation evaluation are of fundamental importance to rangeland ecology, we argue that a disconnection between vegetation methodologies and ecological theory has contributed to the rangeland debate by fostering the perception that the two methodologies and their corresponding ecological paradigms are mutually exclusive. We challenge this perception and contend that both the methodologies and their corresponding paradigms are non-exclusive.

We have addressed five major topics in this synthesis with the intent to clarify and redirect the rangeland debate to promote progress in this important challenge confronting rangeland ecology. First, we interpret the rangeland debate within the broader context of the equilibrium and non-equilibrium paradigms. Secondly, we evaluate the status of the three non-equilibrium models developed to accommodate discontinuous vegetation dynamics. Thirdly, we explore ecological variables and processes that can influence the interpretation and application of the equilibrium and non-equilibrium paradigms. Fourthly, we assess the theoretical and empirical evidence for equilibrium and non-equilibrium vegetation dynamics on rangelands. Finally, we present an alternative interpretation of the relationship between these two paradigms. A solution to this debate has important implications for the science of rangeland ecology, natural resource conservation and management, and policy development on rangelands throughout the world (Ellis & Swift 1988; Mentis *et al.* 1989; Walker 1993a).

Paradigm crisis

Paradigms play a critical role in science by establishing a model of nature that is used to identify problems and interpret results (Kuhn 1996). Therefore, paradigms strongly influence the legitimacy of both the problems and solutions proposed. Consequently, a major shift of paradigms promotes an alternative interpretation of nature (Kuhn 1996). Resistance to an impending paradigm shift ensures that science is not too easily distracted and that the adoption of a new paradigm will represent a substantial scientific advancement.

The rangeland debate possesses several elements of a paradigm crisis according to the criteria of Kuhn (1996; Mentis *et al.* 1989). The equilibrium paradigm and the associated range model have encountered (i) mounting dissatisfaction, (ii) a growing number of anomalies, (iii) development of an alternative paradigm represented by the state-and-transition model and (iv) the polarization of groups championing their respective paradigm. Kuhn (1996) describes science as progressing by periods of

Table 1. Attributes of equilibrium and non-equilibrium systems are based on varying degrees of internal regulation and the corresponding response of system behaviour to external disturbances. Modified from Ellis & Swift (1988) with permission of the Society for Range Management

	Equilibrium systems ⟵⟶	Non-equilibrium systems
Abiotic patterns	Relatively constant	Stochastic/variable
Plant–herbivore interactions	Tight coupling	Weak coupling
	Biotic regulation	Abiotic drivers
Population patterns	Density dependence	Density independence
	Populations track carrying capacity	Dynamic carrying capacity limits population tracking
Community/ecosystem characteristics	Competitive structuring of communities	Competition not expressed
	Internal regulation	External drivers

normal science punctuated by non-cumulative breaks in tradition, i.e. scientific revolutions. This interpretation of scientific advancement raises the question, 'does the rangeland debate represent a sufficient break in traditional science to represent a paradigm crisis?' It is yet to be determined whether a paradigm crisis exists or whether a paradigm shift has occurred in rangeland ecology (Mentis *et al.* 1989; Brown 1994; Cowling 2000).

PARADIGM COMPARISON

The equilibrium and non-equilibrium paradigms establish the ecological basis for the rangeland debate. The equilibrium paradigm has been in existence since the beginning of scientific inquiry, while the non-equilibrium paradigm is of more recent origin (Egerton 1973; Wu & Loucks 1995). The two paradigms represent unique interpretations of ecosystem behaviour in response to disturbance. However, paradigm reassessment has been largely theoretical and has produced generalized interpretations at the extremes of the equilibrium–non-equilibrium continuum (Wiens 1984; Paine 2002). Unfortunately, these generalizations are difficult to evaluate or apply in specific ecosystems (Walker & Wilson 2002).

Rangeland ecology has emphasized vegetation dynamics as the primary variable to assess ecosystem behaviour within the context of these two paradigms. Therefore, we have opted to emphasize exclusively the dynamics of species compositional shifts in this synthesis, even though it does not encompass all of the processes associated with equilibrium–non-equilibrium dynamics (Wiens 1984; Ellis & Swift 1988). Illius & O'Connor (1999) have developed a thorough interpretation of this paradigm debate from the perspective of plant–herbivore interactions within rangeland landscapes.

EQUILIBRIUM PARADIGM

The equilibrium paradigm and its associated metaphor, 'the balance of nature', are founded on the assumption that ecosystems possess the capacity for internal regulation through negative feedback mechanisms, including intense intra- and interspecific

competition and plant–animal interactions (O'Neill *et al.* 1986; Wu & Loucks 1995) (Table 1). However, life-history attributes of the component populations (O'Neill 2001), water–vegetation–herbivore interactions (Van de Koppel *et al.* 2002) and climate–ecosystem coupling (Higgins, Mastrandrea & Schneider 2002) may also contribute directly to ecosystem behaviour. The capacity for internal regulation is assumed to contribute to the predictable and directional response of equilibrium vegetation dynamics because succession must pass through similar stages to a single equilibrium point (Pickett & Ostfeld 1995). Therefore, equilibrium systems are assumed to return to their pre-disturbance state (i.e. homeostasis) or to their pre-disturbance trajectory (i.e. homeorhesis) when disturbance has ceased (O'Neill *et al.* 1986; Wu & Loucks 1995).

The range model is based on the equilibrium paradigm and it emphasizes the importance of plant competition and plant–herbivore interactions on ecosystem behaviour. This interpretation of equilibrium refers to a high degree of internal system organization and regulation (Chesson & Case 1986). Within the context of this paradigm, grazing represents a biotic process that internally regulates system behaviour by imposing negative feedbacks on vegetation processes, rather than a disturbance that externally influences system behaviour (e.g. fire or climatic variability). Misinterpretation of the function of grazing in the equilibrium paradigm has contributed considerable confusion to the rangeland controversy.

Ecologists began to criticize the equilibrium paradigm early in the 20th century for several reasons, including (i) limited evidence to support the occurrence of equilibrium systems, (ii) inability to account for the dynamic behaviour of various ecological systems and (iii) the implication that historical events play only a minor role in ecosystem dynamics (O'Neill *et al.* 1986; Wu & Loucks 1995; O'Neill 2001). However, it was not until the 1970s that the theoretical basis for vegetation dynamics deviated from the equilibrium paradigm, when several prominent ecologists promoted the existence of multiple steady or equilibrium states (Holling 1973; Hurd & Wolf 1974; Sutherland 1974; Noy-Meir 1975; May 1977). Disturbances were assumed to force one stable community across a threshold to a

subsequent stable community on the same site. However, the validity of the multiple steady-state concept has been questioned on the basis of various conceptual and experimental issues (Rodriguez Iglesias & Kothmann 1997; Petraitis & Latham 1999; Walker & Wilson 2002).

NON-EQUILIBRIUM PARADIGM

The non-equilibrium paradigm and its associated metaphor, 'the flux of nature' (Pickett, Parker & Fiedler 1992; Pickett & Ostfeld 1995), are founded on the assumption that ecosystems possess a limited capacity for internal regulation (Ellis & Swift 1988; Wu & Loucks 1995). This implies that the behaviour of non-equilibrium systems is more vulnerable to external disturbances, compared with those of equilibrium systems (Table 1). Consequently, the behaviour of non-equilibrium systems is characterized as more dynamic and less predictable than equilibrium systems (Hurd & Wolf 1974; Pickett, Parker & Fiedler 1992; Pickett & Ostfeld 1995). The non-equilibrium paradigm emphasizes 'event-driven' vegetation dynamics, which implies that the greatest potential for vegetation change is associated with the occurrence of periodic and often stochastic climatic events (Westoby, Walker & Noy-Meir 1989; Walker 1993a; Watson, Westoby & Holm 1997a). However, the non-equilibrium paradigm does not imply that ecosystem behaviour is unconstrained by functional, historical or evolutionary limits (Pickett, Parker & Fiedler 1992).

Development of non-equilibrium models

Three non-equilibrium models have been developed to accommodate the occurrence of stochastic and discontinuous vegetation dynamics described in the non-equilibrium paradigm (Fernandez-Gimenez & Allen-Diaz 1999) (Fig. 1a–d).

THRESHOLD MODEL

Thresholds represent boundaries that separate multiple equilibrium states in time and space, and their existence determines that a system is non-equilibrial (Holling 1973; May 1977). The ball and cup analogy has frequently been used to illustrate the threshold model (Hurd & Wolf 1974; Noy-Meir 1975) (Fig. 2). A stable state is assumed to persist until the disturbance regime is modified sufficiently to cross a threshold to an alternative stable state. The concept was later applied to rangelands to identify stable vegetation states that were non-reversible in managerial time frames (Friedel 1991) and to support the absence of vegetation change following the removal of grazing (i.e. suspended stages) (Laycock 1991). Thresholds are often distinguished on the basis of (i) changes in community physiognomy, plant growth form or life-history strategy and (ii) positive or negative changes in soil properties that alter site
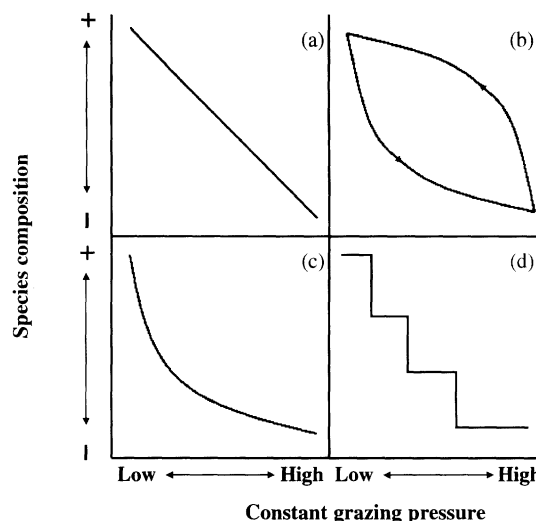
Fig. 1. Hypothetical relationships between species composition and grazing intensity. (a) Linear relationship associated with the range succession model; (b) hysteresis effect in response to priority competition from the most abundant species; (c) monotonic effect produced by selective grazing; (d) stair-step response to discrete events and thresholds. Reprinted from Walker (1993b) with permission of the International Grassland Society.
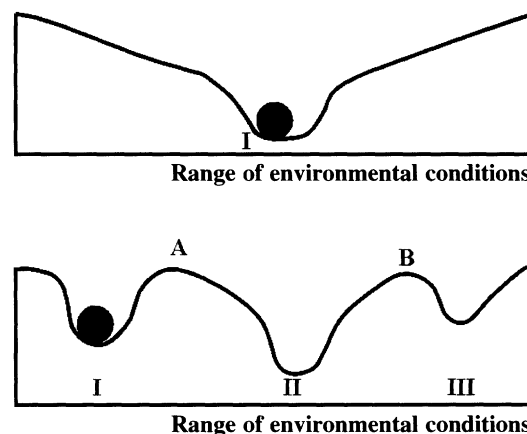

Fig. 2. Ball and cup analogy used to illustrate the presence of thresholds (letters) between multiple stable vegetation states (numerals). The depth of the cup indicates the degree of system stability and the magnitude of disturbance required to cross a threshold to an alternative stable state. Reprinted from Laycock (1991) with permission of the Society for Range Management.

characteristics (Van de Koppel, Rietkerk & Weissing 1997; Archer, Boutton & Hibbard 2001).

Thresholds are primarily applied to woody plant invasion of grasslands and savannas (Archer 1994; Archer, Schimel & Holland 1995). Thresholds are most apparent in these cases because various growth forms track climatic change at different rates and, in the case of woody plants, the effects of previous events disappear less rapidly than in the case of herbaceous plants (Chesson & Case 1986). Once established, woody plants can modify the site to perpetuate woody plant dominance (Archer 1994; Archer, Schimel & Holland 1995)
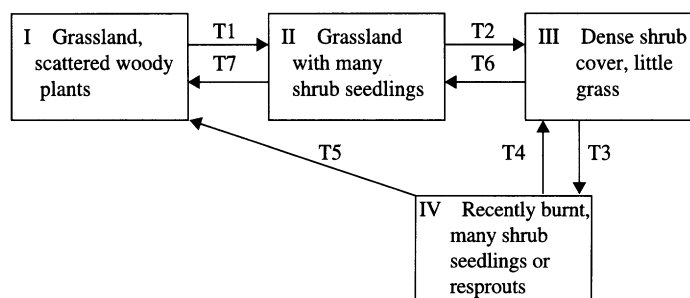
I Grassland, scattered woody plants —T1→ / ←T7— II Grassland with many shrub seedlings —T2→ / ←T6— III Dense shrub cover, little grass

T5 — T4 — T3

IV Recently burnt, many shrub seedlings or resprouts

Fig. 3. State-and-transition model depicting four stable vegetation states (numerals) and the potential transitions (T) between them. Reprinted from Westoby, Walker & Noy-Meir (1989) with permission of the Society for Range Management.

but this does not necessarily imply that ecosystem function has been impaired with respect to biodiversity, productivity, nutrient cycling and other important ecosystem attributes, as in the case of desertification (Archer, Boutton & Hibbard 2001; Norris et al. 2001). Surpassing a threshold from a grassland to woodland state defines the existence of a non-equilibrium system (i.e. multiple stable states) but it does not necessarily imply that the ecosystem has shifted from equilibrium to non-equilibrium dynamics, because the capacity for internal regulation may be as great or greater than in the previous state (Table 1). This illustrates that an array of thresholds exists that can variously affect ecosystem structure and function.

Although thresholds are currently distinguished on the basis of the reversibility of change between dominant growth forms (Friedel 1991; Laycock 1991), it may be more appropriate to interpret thresholds on the basis of modifications to the prevailing disturbance regimes (Holling 1973; Peterson, Allen & Holling 1998). In the case of grassland conversion to shrubland, what has often changed is the frequency and intensity of fire, e.g. fire threshold (Fuhlendorf, Smeins & Grant 1996; Fuhlendorf & Smeins 1997). Grazing is involved secondarily in determining the rate at which fire thresholds are surpassed via a reduction of fuel loads, reduced competitive suppression of woody seedlings and the modification of seed dispersal (Archer & Smeins 1991; Archer 1994). In cases where a fire threshold has been surpassed, the removal of grazing would not be expected to reverse the prior change in plant growth form without reinstatement of the fire regime (West & Yorks 2002). Threshold evaluation on the basis of disturbance regimes will more explicitly identify the driver of vegetation change and provide additional insight into the ecological processes establishing the occurrence of thresholds.

STATE-AND-TRANSITION MODEL

The state-and-transition model was presented as a qualitative model that possessed the capacity and flexibility to accommodate various types of knowledge and information associated with vegetation management on rangelands (Westoby, Walker & Noy-Meir 1989) (Fig. 1a–d). This model was especially designed for application in rangeland systems characterized by event-driven vegetation dynamics that were not effectively addressed by the range model. However, the state-and-transition model was not intended to provide a replacement for the range model in all rangeland ecosystems and it can accommodate both equilibrium and non-equilibrium vegetation dynamics (Westoby 1979/80; Westoby, Walker & Noy-Meir 1989).

State-and-transition models were intended to function on the basis of managerial, rather than ecological, criteria. The information required to develop these models includes knowledge of (i) potential alternative vegetation states on a site, (ii) potential transitions between states and (iii) opportunities to achieve favourable transitions between vegetation states and hazards to avoid unfavourable transitions (Fig. 3). Evaluation of vegetation dynamics within states, in addition to between states, and the application of the threshold concept to between-state transitions represent important developments since the model was initially introduced (Bestelmeyer et al. 2003; Stringham, Krueger & Shaver 2003).

The distinction between the range and the state-and-transition models directly reflects their origins in the equilibrium and non-equilibrium paradigms, respectively. The range model is largely a univariate approach that emphasizes grazing as the primary driver of vegetation dynamics. It is our assessment that the univariate nature of the range model does not imply that early rangeland ecologists perceived the disturbances of fire and climatic variability as being unimportant, but rather that they were not subject to managerial control (Sampson 1923). However, these disturbances may have been envisaged as acting along the same univariate dimension as grazing. The state-and-transition model accommodates additional complexity by utilizing a multivariate approach that explicitly incorporates multiple dimensions (e.g. fire and climatic variability), in addition to grazing, and relaxes the assumptions concerning system predictability, stability and the potential number of equilibrium states. Recognition that the state-and-transition model encompasses the range model may partially minimize the dichotomy that has developed between these two methodologies.
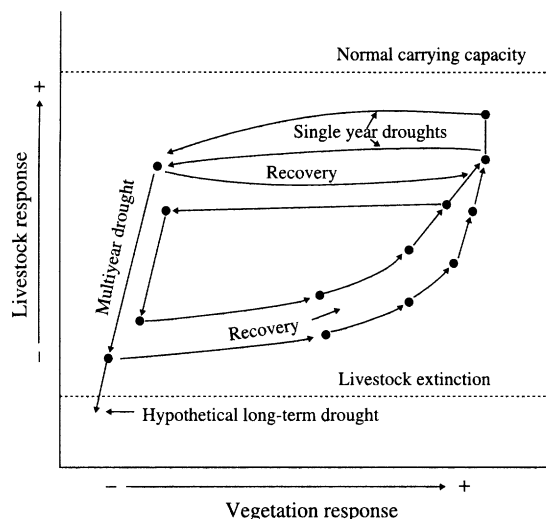
Fig. 4. Illustration of vegetation and livestock dynamics within persistent non-equilibrium systems. Multiyear drought occurring on approximately decadal time frames decouple plant–herbivore interactions by inducing animal mortality and providing vegetation with a recovery period. Reprinted from Ellis & Swift (1988) with permission of the Society for Range Management.

PERSISTENT NON-EQUILIBRIUM MODEL

This model assumes that arid systems (< 300 mm year) are so constrained by the amount and variability of precipitation that these events influence plant and animal dynamics to a greater extent than plant competition and plant–herbivore interactions. Large fluctuations in primary productivity associated with low and erratic precipitation regimes are hypothesized to prevent herbivore populations from effectively tracking forage availability and thereby minimize negative feedbacks between grazing intensity and vegetation dynamics (Ellis & Swift 1988). The occurrence of frequent multiyear droughts contributes to herbivore mortality and prevents herbivore numbers from attaining carrying capacity in these variable environments (Fig. 4). This rationale is used to support the hypothesis that free-roaming herbivores have a lesser impact on vegetation in non-equilibrium systems than they do in equilibrium systems. However, this model does not explicitly define a pattern of vegetation dynamics or the role of species composition on primary or secondary productivity.

An alternative interpretation is that the impact of grazing may be greater than in equilibrium systems because grazing intensity increases prior to herbivore mortality during periodic multiyear droughts. This effect may be magnified by the occurrence of high production zones within a landscape that can support high herbivore numbers and delay animal mortality during drought periods (Illius & O'Connor 1999, 2000). These authors concluded that free-roaming herbivores remain in equilibrium with key resource areas, even though they may not be in equilibrium with many other areas of the landscape. This implies that both equilibrium and non-equilibrium dynamics occur in plant–herbivore

interactions in rangelands characterized by low and highly variable precipitation regimes.

Paradigm evaluation

Why has it proven so difficult to evaluate the effectiveness of the equilibrium and non-equilibrium paradigms on rangeland vegetation dynamics? We contend that several interrelated issues have contributed to the complexity of the rangeland debate. First, the evidence or criteria necessary to distinguish between vegetation dynamics associated with the two paradigms has not been clearly defined (Walker & Wilson 2002). Consequently, the controversy has become confounded with the application of various measures of vegetation dynamics, spatial and temporal scales, and management systems. Secondly, the limited availability of long-term vegetation data has prevented rigorous evaluation of the theoretical interpretations associated with these two paradigms (Petraitis & Latham 1999; Brown et al. 2001a). Thirdly, the theoretical literature has established that scale is of paramount importance to the interpretation of equilibrium and non-equilibrium systems, but empirical tests of scale issues have been limited (Brown 1994; Fuhlendorf, Smeins & Grant 1996). The absence of clear criteria and the presence of several confounding variables have created the situation where 'one person's threshold is another's continuum' (Stafford Smith 1992).

APPROPRIATE EVIDENCE

The empirical evidence currently utilized to distinguish between equilibrium and non-equilibrium vegetation dynamics can be placed into three categories. First, species or functional group replacement through time following a reduction in grazing intensity or the exclusion of grazing, or through space in communities arrayed along a grazing intensity gradient established by distance from water (Fernandez-Gimenez & Allen-Diaz 1999; Ryerson & Parmenter 2001). Secondly, the strength of the correlation between various attributes of vegetation change with grazing intensity compared with interannual precipitation patterns through time (Fynn & O'Connor 2000; Fuhlendorf, Briske & Smeins 2001). Thirdly, the existence of event-driven vegetation dynamics, which often involves drought-induced plant mortality or episodic plant recruitment during favourable precipitation years (Friedel 1991; Walker 1993a; Watson, Westoby & Holm 1997a). All three categories of evidence assess the reversibility of vegetation dynamics, based on the relative strength of plant competition and plant–herbivore interactions compared with climatically induced vegetation change.

A critique of the current paradigms demonstrates that they are distinguished by varying degrees of ecosystem organization and regulation that uniquely affect ecosystem behaviour following disturbance. This raises two fundamental questions regarding the evidence

required to resolve the rangeland debate. Do species fluctuations establish the explanation for a community phenomenon or are they merely incidental to the explanation (Chesson & Case 1986)? Do vegetation dynamics constitute sufficient criteria to distinguish between equilibrium and non-equilibrium systems? A growing body of literature suggests that while species composition may vary substantially in response to disturbances, ecosystem variables, including species richness, productivity and energy use, may remain relatively constant (Chesson & Case 1986; Wardle *et al.* 1999; Brown *et al.* 2001b). It has even been hypothesized that species fluctuations may represent a compensatory mechanism that contributes to ecosystem stability (i.e. homeostasis) in numerous ecosystems (Morgan Ernest & Brown 2001). These interpretations suggest that exclusive emphasis on vegetation dynamics may be insufficient criteria to evaluate these two paradigms.

APPROPRIATE SCALES

Ecological patterns and processes are often scale dependent, indicating that as the spatial and temporal dimensions change, the pattern, rate and direction of change will also vary. All patterns and processes are best described at a single inherent scale, but no single scale exists that can collectively describe population, community and landscape patterns and processes (Wiens *et al.* 1986; Levin 1992). The theoretical interpretations of the equilibrium and non-equilibrium paradigms explicitly emphasize the importance of scale in their determination (O'Neill *et al.* 1986; Wiens 1989; Allen & Hoekstra 1992; Levin 1992; O'Neill 2001), but relatively few quantitative investigations have tested these predictions until recently (Wu & Loucks 1995; Fuhlendorf & Smeins 1996, 1999; Landsberg *et al.* 2002). For example, Ryerson & Parmenter (2001) have clearly demonstrated that the occurrence of species-specific and site-specific vegetation changes following the removal of herbivores was not accompanied by a change in total perennial basal cover at the landscape scale.

Spatial scale

Explicit consideration of spatial scale would eliminate much of the confusion associated with the rangeland debate. For example, the range model was developed explicitly to evaluate vegetation dynamics on specific sites that were defined on the basis of homogeneity of local topo-edaphic conditions and precipitation regimes (i.e. range sites; Dyksterhuis 1949). Application of the range model across various sites within landscapes confounds the critical issue of spatial scale because it assumes that successional rates and patterns will be similar on all sites (Fuhlendorf & Smeins 1998). Vegetation dynamics are currently expressed as a shifting mosaic of patches at various stages of succession that are responding to disturbance regimes, resource
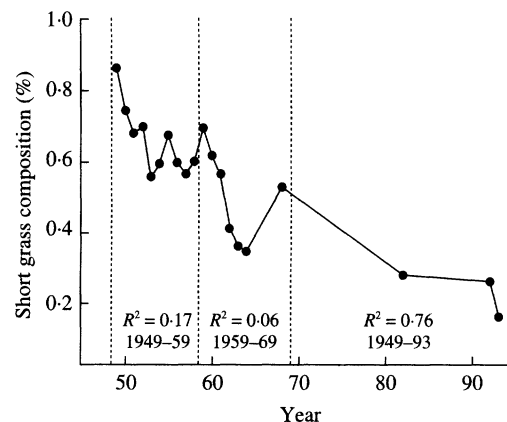

Fig. 5. Long-term response of a short-grass response group to the elimination of livestock grazing in a juniper–oak savanna near Sonora, Texas, USA. The entire record of vegetation change is characterized by long-term continuous and directional vegetation response to the elimination of grazing, but it contains intervals of rapid vegetation change and stable community composition.

heterogeneity and interspecific competitive interactions (White & Pickett 1985; Wu & Loucks 1995). The extensive use of individual sites as management units has probably contributed to the perception that non-equilibrium vegetation dynamics occur more frequently than if larger land areas had been evaluated (Ryerson & Parmenter 2001; Landsberg *et al.* 2002). Range sites continue to be used as the basic land unit for vegetation evaluation in many rangelands throughout the world (Bestelmeyer *et al.* 2003; Stringham, Krueger & Shaver 2003).

Temporal scale

The importance of the period of record of vegetation dynamics is illustrated by the response of herbaceous vegetation to livestock removal in the investigation of Fuhlendorf, Briske & Smeins (2001). Short grass composition decreased rapidly over the first several years following the elimination of grazing, but the drought of the 1950s halted this response and a relatively stable herbaceous composition resulted (Fig. 5). A resumption of normal precipitation in the 1960s was associated with a large and rapid decrease in short grass composition followed by a rapid increase in the last half of the decade. Interpretation of vegetation dynamics during these respective periods would suggest rapid directional change that was suspended during the 1950s drought; rapid non-directional change then occurred during the 1960s, followed by gradual, directional change during the next two decades. However, the vegetation trajectory encompassing all time periods differs from that associated with all but the last segment of the entire 44-year record. Vegetation dynamics were often characterized by intervals of static to very gradual change in vegetation composition and structure, indicating that even herbaceous vegetation dynamics occur on prolonged temporal scales in semi-arid
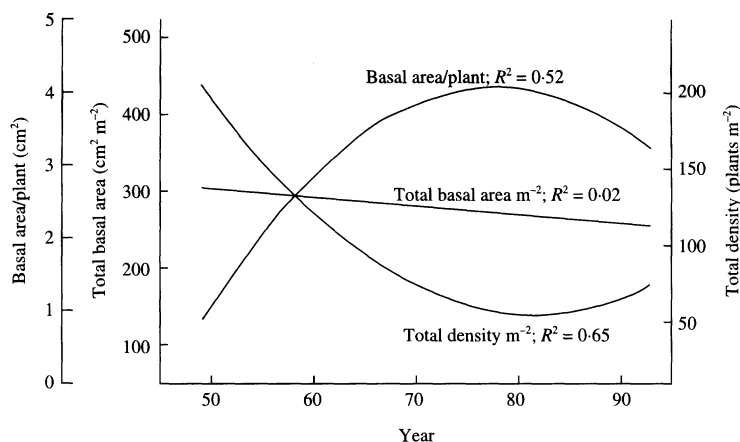
Fig. 6. Regression fitted responses of basal area per plant, total plant basal area, and total density of perennial grasses following removal of grazing in a juniper–oak savanna near Sonora, Texas, USA. Note that all three community attributes show distinct temporal responses to the elimination of livestock grazing. Reprinted from Fuhlendorf, Briske & Smeins (2001) with permission of Opulus Press.

rangelands (Wiegand & Milton 1996; Anderson & Inouye 2001; Ryerson & Parmenter 2001).

VEGETATION ATTRIBUTES

Unique responses among vegetation attributes to grazing and climate have most probably provided conflicting interpretations for these two ecological paradigms. In the record of vegetation change presented by Fuhlendorf, Briske & Smeins (2001), mid- and short-grass response group composition was affected primarily by the removal of grazing, total plant basal area was affected primarily by interannual precipitation, and grass density was significantly affected by both grazing removal and climate (Fig. 6). This demonstrates that total basal area is not an effective indicator of grazing intensity and suggests that extensive use of this community attribute may have contributed to the interpretation that vegetation dynamics are more responsive to climate than to grazing. On the other hand, response group composition and mean basal area per plant were much more responsive to grazing than to interannual precipitation over the long-term. This suggests that these structural attributes would provide effective indicators for monitoring vegetation dynamics in response to grazing. Recognition of distinct responses among various community attributes to grazing and climatic variability supports the conclusion of Fernandez-Gimenez & Allen-Diaz (1999) that the evaluation of a broader set of vegetation variables, including individual species' attributes or specific functional groups, may lead to the conclusion that vegetation dynamics are impacted by both grazing and climatic variability, rather than solely by climatic variability.

MANAGERIAL INVOLVEMENT

The interpretation of equilibrium and non-equilibrium vegetation dynamics may be strongly influenced by the degree of managerial involvement imposed within a system (Fuhlendorf, Briske & Smeins 2001). Free-roaming herbivores have the ability to access various plant communities within a landscape, including key resource areas, to optimize nutrient intake (Illius & O'Connor 1999, 2000). This is clearly not the case in most commercial ranching systems. However, commercial ranching systems impose various management options to minimize fluctuations in livestock numbers, in contrast to subsistence, nomadic livestock systems. This makes it difficult to compare vegetation dynamics directly in these two distinct management systems (Ellis & Swift 1988). Confined livestock grazing, supported by water development, veterinary care and supplemental feeding, will have a greater potential to impact vegetation dynamics adversely than pastoralist systems, where herbivore numbers are directly influenced by the prevailing environmental conditions. The continuous presence of livestock in managed systems reduces the opportunity for long-term vegetation recovery compared with less intensively managed systems (Fig. 4). However, current evidence indicates the occurrence of both equilibrium and non-equilibrium dynamics in pastoral (Illius & O'Connor 1999) and commercial systems (Fuhlendorf, Briske & Smeins 2001).

Mutual exclusivity between paradigms

The rangeland debate has largely contrasted the relative ecological and managerial merits of the range and state-and-transition models (Westoby, Walker & Noy-Meir 1989; Laycock 1991; Brown 1994). Given that these two models are conceptually related to the equilibrium and non-equilibrium paradigms, respectively, the debate has implicitly established a mutually exclusive relationship between the two current paradigms. We challenge this interpretation of mutual exclusivity, based on an evaluation of the available theoretical and empirical evidence.

Table 2. Vegetation, life form, location, duration of vegetation record (year), mean annual precipitation (PPT in mm), and citation for 11 investigations documenting the occurrence of both equilibrium and non-equilibrium vegetation dynamics. Equilibrial dynamics are based on significant changes in species composition following herbivore removal or the imposition of various grazing intensities unless otherwise indicated. Non-equilibrial dynamics are based on the absence of significant compositional change in response to herbivore removal or grazing intensity or a significant correlation with interannual precipitation. Life form: A = annual, H = herbaceous perennial, W = woody

Vegetation	Life form	Location	Years	PPT	Reference
Savanna	H	Texas, USA	44	600	Fuhlendorf, Briske & Smeins (2001)
Desert–woodland gradient	A, H, W	New Mexico, USA	20	255	Ryerson & Parmenter (2001)
Savanna	H	South Africa	10	570	Fynn & O'Connor (2000)
Steppe gradient*	A, H, W	Mongolia	2	95–230	Fernandez-Gimenez & Allen-Diaz (1999)
Acacia shrubland†	W	Western Australia	11	230	Watson, Westoby & Holm (1997b)
Grassland	A, H	Otago, New Zealand	6	340	Allen, Wilson & Mason (1995)
Karoo shrubland	A, H, W	South Africa	23	360	O'Connor & Roux (1995)
Desert shrub	H, W	New Mexico, USA	51	260	Gibbens *et al.* (1993)
Grassland	A, H, W	Montana, USA	25	340	Olson, White & Sindelar (1985)
Grassland‡	H	Serengeti, Africa	2	400–1000	McNaughton (1983)
Sagebrush steppe	A, H, W	Idaho, USA	45	220	Anderson & Inouye (2001)

*Based on compositional change to grazing intensity at three locations along a precipitation gradient.
†Based on the population dynamics of two evergreen shrubs.
‡Based on community ordination with grazing intensity and strength of competitive interactions.

THEORETICAL EVIDENCE

The majority of theoretical evidence suggests that equilibrium and non-equilibrium systems are not distinguished by unique processes or functions but rather by the evaluation of various temporal and spatial scales within ecosystems (Connell & Sousa 1983; O'Neill *et al.* 1986; Allen & Hoekstra 1992; Illius & O'Connor 1999). This interpretation is consistent with the conclusion that equilibrium may not represent a fundamental property of ecosystems but that it may emerge as a characteristic of increasing spatial scale (DeAngelis & Waterhouse 1987). The theoretical evidence clearly indicates that both equilibrium and non-equilibrium dynamics may operate in ecosystems, at various spatial and temporal scales, to influence vegetation dynamics. This interpretation re-emphasizes the validity of Wiens's (1984) initial assessment that ecosystems are distributed along a continuum of equilibrium to non-equilibrium behaviour (Table 1).

The hypothesis of dynamic equilibrium may have been the first ecological interpretation suggesting that community structure may be regulated by a combination of equilibrium and non-equilibrium dynamics (Huston 1979). This hypothesis indicates that communities primarily exist under non-equilibrium conditions, because competitive equilibrium, representing the process of species sorting on the basis of inherent competitive ability, is prevented by periodic disturbances that variously reduce population densities and the intensity of plant competition. However, stable species diversity and composition may still occur in the presence of non-equilibrium dynamics when competitive displacement among species is balanced by population reductions associated with disturbance. It is important to recognize that the dynamic equilib-

rium hypothesis suggests that communities may be structured by processes both internal (e.g. herbivory) and external (e.g. climatic variability) to the ecosystem and that the relative expression of equilibrium and non-equilibrium dynamics are assumed to vary with the time interval following successive disturbances. This hypothesis suggests that communities may be structured by a combination of both equilibrium and non-equilibrium dynamics and that the outcome of this interaction may contribute to a stable species composition.

EMPIRICAL EVIDENCE

Limited experimental evaluation of these two broad paradigms has undoubtedly contributed to both the intensity and longevity of the rangeland debate (Petraitis & Latham 1999; Brown *et al.* 2001b). However, an increasing amount of recent empirical evidence supports the theoretical interpretation that both equilibrium and non-equilibrium dynamics operate in rangeland systems at various spatial and temporal scales (Table 2). These records of vegetation change include both herbaceous and woody life forms in regions encompassing a broad range of annual precipitation, and several of them are based on vegetation records lasting 10 years or more that have recently been published (1995 onwards; Table 2). However, we do not intend to imply that vegetation dynamics always respond to the exclusion of grazing over comparable temporal scales, because this is clearly not the case (Milchunas *et al.* 1989; Laycock 1991; Yorks, West & Capels 1992).

A compilation of empirical data from numerous investigations of plant–herbivore interactions further demonstrates the involvement of both grazing and

climate on vegetation dynamics in grazed ecosystems. These data indicate that the effect of herbivores on plant biomass increases as precipitation decreases, but that the ability of herbivores to modify species composition increases with increasing precipitation (Chase *et al.* 2000). These data illustrate two important points that are relevant to the rangeland debate. First, herbivores affect vegetation over a broad range of primary productivity, even though the intensity of plant–herbivore interactions may vary. Secondly, herbivory may uniquely affect primary productivity and species composition at various locations along productivity gradients. The disproportionate effect of herbivory on productivity and composition probably results from an increasing expression of selective herbivory with increasing primary productivity. It can be concluded from these generalized patterns of plant–herbivore interactions that both herbivory and precipitation interact to structure plant communities (Chase *et al.* 2000). We argue that a similar conclusion can be drawn regarding the application of the equilibrium and non-equilibrium paradigms to vegetation dynamics on rangelands, based on the involvement of similar ecological processes.

RELATIVE EFFECTS OF EQUILIBRIUM AND NON-EQUILIBRIUM DYNAMICS

Assuming that both equilibrium and non-equilibrium dynamics operate in rangeland systems, the critical question becomes, 'what is their relative effect on vegetation dynamics?' The current empirical evidence does not provide a clear answer to this question, but we will draw a general inference from the vegetation record of Fuhlendorf, Briske & Smeins (2001). The reciprocal and directional response of the short- and mid-grass response groups to the imposition of three grazing regimes indicates that grazing intensity established the long-term direction of compositional and structural change (Fig. 7). However, a severe episodic drought substantially influenced the short-term rate and trajectory of vegetation change. The drought of the 1950s reduced plant density to similarly low values in all three grazing regimes, but plant density recovered following the drought and eventually became proportional with grazing intensity during the subsequent decade. The intermittent influence of precipitation variability on vegetation dynamics has previously been recognized by Wiegand & Milton (1996) and Walker, Langridge & McFarlane (1997). The less persistent response of community composition to precipitation variability than to grazing intensity is partially a function of the non-selective, intermittent effects of drought compared with the more chronic, selective influence of grazing on individual species or species groups (Illius & O'Connor 1999). These data collectively indicate that climate and grazing variously interact to influence rangeland vegetation, because intensive selective grazing often establishes the long-
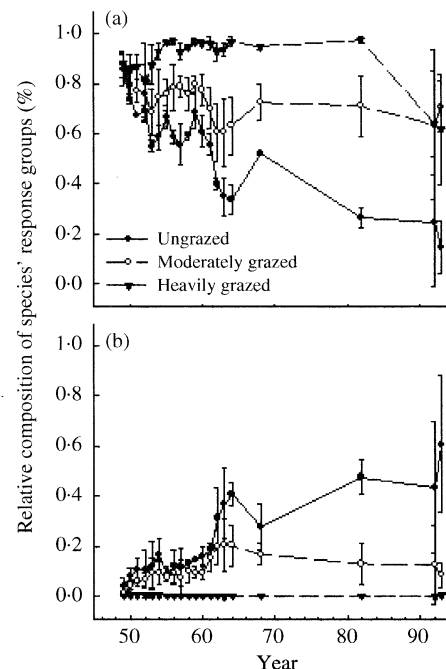
Fig. 7. Long-term response of (a) short-grass and (b) mid-grass response groups to three grazing intensities in a juniper–oak savanna near Sonora, Texas, USA. Data show a continuous and directional vegetation response to grazing intensity as indicated by the reciprocal response between short- and mid-grass response groups. However, the trajectory of this vegetation response is punctuated by episodic climatic events. Reprinted from Fuhlendorf, Briske & Smeins (2001) with permission of Opulus Press.

term trajectory of vegetation change, while episodic climatic events often exert short-term effects on this rate and trajectory (Fuhlendorf, Briske & Smeins 2001).

The combined effect of grazing and climatic variation on vegetation dynamics supports the inference that stochastic climatic variation does not maintain a system in a perpetual non-equilibrium state (Wiens 1984), but rather superimposes fluctuations on an otherwise directional response of community composition to grazing intensity. This interpretation supports the hypothesis of Illius & O'Connor (1999) that the occurrence of climatic variability does not justify the assumption that grazing intensity has a negligible impact on vegetation dynamics. However, in environments characterized by lower and more variable precipitation more time would be required to disentangle the effects of grazing and climate.

Synthesis and applications

A critique of the equilibrium and non-equilibrium paradigms indicates that neither paradigm alone is sufficiently comprehensive to interpret and evaluate vegetation dynamics effectively in all rangeland ecosystems (Mentis *et al.* 1989; Lockwood & Lockwood 1993; Wu & Loucks 1995; Stafford Smith 1996; Fernandez-Gimenez & Allen-Diaz 1999). Application of the equilibrium paradigm is restricted by assumptions

of high stability, continuous change and a single equilibrium point. However, these assumptions should not be taken to imply that this paradigm is invalid or inappropriate in all situations (Westoby 1979/80; O'Neill *et al.* 1986; Westoby, Walker & Noy-Meir 1989; Sutherland 1990; Pickett & Ostfeld 1995). This interpretation is substantiated by the occurrence of intense plant competition and plant–herbivore interactions in numerous ecosystems (O'Neill *et al.* 1986; Illius & O'Connor 1999; Walker & Wilson 2002) and this may explain why the range model is often viewed as an appropriate interpretation in more productive ecosystems (Díaz, Noy-Meir & Cabido 2001; Vesk & Westoby 2001; Stringham, Krueger & Shaver 2003).

At the other extreme, the non-equilibrium paradigm more effectively describes the occurrence of discontinuous, non-reversible vegetation dynamics that have been documented to occur in rangeland ecosystems (Westoby, Walker & Noy-Meir 1989; Walker 1993a). However, rigid adherence to the non-equilibrium paradigm will overemphasize event-driven vegetation dynamics and de-emphasize the importance of continuous and reversible change characteristic of numerous ecosystems, at various temporal and spatial scales (O'Neill *et al.* 1986; Watson, Westoby & Holm 1997a,b; Morgan Ernest & Brown 2001). Conclusive evidence does not exist to demonstrate that the non-equilibrium paradigm more effectively defines vegetation dynamics than the equilibrium paradigm in all rangeland ecosystems.

This interpretation supports a dualistic approach as the most appropriate course of action to evaluate vegetation dynamics effectively on rangelands (Chesson & Case 1986; Lockwood & Lockwood 1993; Wu & Loucks 1995; Illius & O'Connor 1999; Walker & Wilson 2002). The appropriate question appears to be, 'when do equilibrium and non-equilibrium dynamics apply?', rather than, 'do equilibrium or non-equilibrium dynamics apply?' We conclude that this debate would be best resolved and that rangeland ecology would be best served by the development of models that can accommodate both the equilibrium and non-equilibrium paradigms for the evaluation of vegetation dynamics in variable rangeland environments. State-and-transition models can support paradigm integration because they can accommodate both equilibrium and non-equilibrium vegetation dynamics (Stafford Smith 1996; Watson, Burnside & Holm 1996; Bestelmeyer *et al.* 2003).

However, considerable uncertainty exists regarding the current application and future development of state-and-transition models in rangeland ecology. Recent application of these models frequently invokes both a methodology and a theory founded on an extension of the non-equilibrium paradigm (Brown 1994; Allen-Diaz & Bartolome 1998). The tendency to link method with theory may have developed in response to (i) the linkage that existed between the range model and successional theory (Joyce 1993), and (ii) the premise that the art of rangeland management should be supported with the science of rangeland ecology (Provenza 1991). It is difficult to envisage how rangeland ecology and management can develop in parallel if state-and-transition models are not at least implicitly linked with ecological theory (Bestelmeyer *et al.* 2003). A linkage between model and theory will require greater quantification of both states and transitions and more explicit definition of spatial and temporal scale (Wu & Loucks 1995).

An important aspect of the rangeland controversy is the ability of these two paradigms to support vegetation management effectively. The adverse consequences associated with the application of the equilibrium paradigm to various rangeland ecosystems has been widely referenced (Ellis & Swift 1988; Mentis *et al.* 1989; Walker 1993a). However, exclusive application of the non-equilibrium paradigm may also compromise effective vegetation management in various rangeland ecosystems by overemphasizing event-driven vegetation dynamics and discounting the occurrence of continuous vegetation dynamics that occur between episodic events (Watson, Burnside & Holm 1996; Fernandez-Gimenez & Allen-Diaz 1999). In this context, Watson, Burnside & Holm (1996) make an important distinction between the occurrence of episodic events and the long-term consequences of those events that may be partially characterized by continuous vegetation dynamics. For example, even woody plant invasion of grasslands and savannas is often characterized by a period of continuous vegetation change (Archer 1994; Watson, Westoby & Holm 1997a).

Watson, Burnside & Holm (1996) have developed an insightful assessment of the managerial significance of equilibrium and non-equilibrium vegetation dynamics. These authors emphasize the importance of equilibrium dynamics to effective vegetation management prior to crossing a threshold between stable plant communities, in addition to non-equilibrium dynamics that emphasize thresholds separating multiple stable communities. They contend that effective vegetation management enables managers to 'condition the resource' to take maximum advantage of the occurrence of favourable events and potentially to increase their frequency by lowering the response threshold of systems to these events (Watson, Burnside & Holm 1996). Similarly, effective management may minimize the negative consequences of unfavourable events by increasing the response thresholds of systems to them.

Exclusive emphasis on event-driven dynamics may shift the responsibility for vegetation management from rangeland managers to the vagaries of nature and imply that management is of little consequence (Watson, Burnside & Holm 1996). The perception that vegetation dynamics are 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 (Stafford Smith 1996; Watson, Burnside & Holm 1996). The clear implication is that both event-driven and continuous vegetation dynamics

must be incorporated into vegetation management on rangelands.

This critique supports the conclusion that a paradigm shift (*sensu* Kuhn 1996) has not taken place in rangeland ecology. If a paradigm shift had occurred, it would imply that the rangeland profession had unconditionally accepted the non-equilibrium paradigm as a more effective interpretation of vegetation dynamics in all rangeland ecosystems. Alternatively, the debate has forced a more comprehensive interpretation of vegetation dynamics along the entirety of the equilibrium-non-equilibrium continuum (Pickett & Ostfeld 1995; Fiedler, White & Leidy 1997). We contend that rangeland ecology would not benefit from the replacement of the equilibrium by the non-equilibrium paradigm, because it would only shift our perception of vegetation dynamics from one end of this continuum to the other.

The rangeland debate appears to more clearly fit the interpretation of an ecological dialectic, where a profession assigns importance to various processes or components in nature rather than embracing its internal contradictions (Naeem 2002). This phenomenon produces cycles of thesis (e.g. equilibrium) and antithesis (e.g. non-equilibrium) that frequently culminate in a synthesis of the opposing views. Rangeland ecology may have experienced such a dialectic debate (e.g. analysis, criticism, synthesis). This interpretation is supported by the notion that paradigm shifts are unlikely to occur in a multiple causation discipline like ecology (Paine 2002).

Acknowledgements

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