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Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia

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Summary

1. Few studies have tested the applicability of current non-equilibrium models of rangeland vegetation dynamics to a particular ecosystem, or across a range of systems that might be expected to respond differently to grazing. This study assessed the extent to which the non-equilibrium persistent (NEP) model of rangeland vegetation dynamics applies to three distinct Mongolian rangeland ecosystems, the desert-steppe, steppe and mountain-steppe.

2. Standing biomass, vegetation cover and composition, and species richness and diversity were examined along grazing pressure gradients in ecological zones of differing productivity and interannual variability in precipitation.

3. In the desert-steppe, biomass, functional group cover, richness and diversity did not vary along grazing pressure gradients, but all vegetation variables except the cover of weedy annuals and unpalatable forbs varied significantly between years. Vegetation dynamics in this zone largely conformed to the NEP model of rangeland dynamics.

4. In the mountain-steppe, grass and total biomass, total vegetative cover, the cover of grasses, weedy annuals and unpalatable forbs, and richness and diversity varied along grazing pressure gradients. With increasing grazing pressure, grasses decreased and forbs and weedy annuals increased, as the conventional range condition (RC) model predicts. Interannual variation in precipitation influenced total vegetative cover, species and functional group cover, and richness and diversity.

5. In the steppe, forb biomass, grass, forb, unpalatable forb and weedy annual cover, and diversity varied along grazing pressure gradients. Grass biomass and total vegetative cover responded interactively to rainfall and grazing. Forb biomass, grass, forb and weedy annual cover and richness varied between years. Grasses decreased and forbs and weedy annuals increased with increasing grazing pressure, conforming to the RC model.

6. Ecosystem response to rainfall and grazing is complex, and interpretation of the response depends on the specific variables examined. The recent paradigm shift in rangeland science from the RC model to non-equilibrium models has been embraced with such enthusiasm by some that the concept of non-equilibrium rangelands may be as much in danger of being misapplied as equilibrium-based models have been.

Key-words: grazing gradients, range condition, species diversity.

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Introduction

Two equilibrium-based ecological models have dominated conventional range science and management: the Clementsian successional model of vegetation change (Clements 1936; Ellison 1960) and the classical model of plant–herbivore population dynamics (Caughley 1979). Both models posit tightly coupled relationships between the abundance of herbivores and the productivity and species composition of plants. This presumed relationship between grazing intensity and vegetation formed the basis of the range condition (RC) model of vegetation dynamics (Dyksterhuis 1949). The RC model predicts that as herbivore numbers increase, plant biomass and cover decline and species composition shifts from dominance by perennial grasses and forbs ('climax' species) towards dominance by unpalatable forbs and weedy annuals. When grazing is decreased or removed, biomass and cover are predicted to increase and species composition shifts back towards late-successional stages. Although the RC model does not specifically address species richness and diversity, others have hypothesized that diversity and richness should peak at intermediate grazing intensities and decline with heavy grazing (Harper 1969; Coppock *et al.* 1983; Milchunas, Sala & Lauenroth 1988).

Clementsian succession and its application through the RC model to range management have been widely criticized (Gleason 1926; Connell & Slayter 1977; Smith 1988; Westoby, Walker & Noy Meir 1989; Friedel 1991). Equilibrium-based theoretical models and the resource management measures based on them have failed to predict successfully the behaviour of complex natural systems (Holling 1973; May 1977; Connell & Sousa 1983). Alternative models for addressing rangeland dynamics, such as the state and transition (Westoby, Walker & Noy Meir 1989; Huntsinger & Bartolome 1992; Allen-Diaz & Bartolome 1998), threshold (Friedel 1991; Laycock 1991) and catastrophe (Lockwood & Lockwood 1993) models, have been proposed. These closely related models focus on describing quasi-stable vegetation states, predicting the circumstances that trigger transitions to specific different states, and modelling these changes. They emphasize the non-linearity of vegetation responses to grazing and other environmental perturbations. Another model is the non-equilibrium persistent (NEP) model of rangeland dynamics (Ellis & Swift 1988; Behnke & Scoones 1993), which focuses on effects of abiotic factors on plant community and herbivore population dynamics.

The NEP model of rangeland dynamics draws on the ecological literature on non-equilibrium dynamics (especially Wiens 1984) and on Ellis and Swift's observations during a decade of fieldwork in Africa. Ellis & Swift (1988) proposed that many rangeland ecosystems are dominated by density-independent and abiotic factors, rather than density-dependent and biological interactions. Despite high variability in interannual and interseasonal productivity, and fluctuating livestock populations, these ecosystems and the pastoralists they support persist. Proponents of the NEP model (Ellis & Swift 1988; Behnke & Scoones 1993) suggest that equilibrium models, such as the RC model, work in systems where conditions for plant growth are relatively constant from one year to another, allowing herbivore populations to increase until they are stabilized by density-dependent limitations. Most rangelands, however, exhibit dramatic fluctuations in rainfall and plant productivity, as well as frequent perturbations such as extended droughts or severe winter storms. Ellis & Swift (1988) posit that 'under these conditions' changes in forage quantity are too rapid and great in magnitude to be closely tracked by animal populations. Thus plant biomass, cover and species composition are driven primarily by climatic factors, and herbivory plays a relatively small role in determining the productivity and composition of vegetation.

Following Wiens (1984) and DeAngelis & Waterhouse (1987), Ellis & Swift (1988) suggest that in non-equilibrium rangeland ecosystems: (i) plant–herbivore interactions are loosely coupled; (ii) herbivore populations are controlled by density-independent factors; (ii) carrying capacity is too dynamic for close animal population tracking; (iv) plant biomass is abiotically controlled; and (v) competition among plant species is not an important force in structuring communities. In contrast, equilibrium rangeland ecosystems are characterized by (i) tightly coupled plant–herbivore interactions; (ii) density-dependent controls on herbivore populations; (iii) animal populations that fluctuate in response to changing carrying capacity; (iv) herbivore-controlled plant biomass; and (v) competition as an important structuring force in plant communities.

Ellis (1995) attempts to sharpen predictions about where non-equilibrium dynamics are likely to occur, based on coefficients of variation in annual precipitation, mean annual precipitation, and the presence or absence of El Niño-Southern Oscillation effects (which increase variability even at fairly high mean annual rainfall levels). Ellis & Chuluun (1993) and Ellis (1995) suggest that in Mongolia non-equilibrium dynamics are likely to occur where the coefficient of variation of annual precipitation is greater than 33% and mean annual precipitation is less than 250 mm. Existing studies testing the predictions of the NEP model have focused on livestock populations and were mainly conducted in Africa (Behnke & Scoones 1993; Coppock 1993; Scoones 1993; Cincotta, Yangqing & Xingmin 1992 is an exception). The evidence presented in those studies was marshalled in a post-hoc manner, rather than gathered with the intent to test a specific ecological hypothesis.

This study was conducted specifically to test the applicability of the NEP model of rangeland dynamics to three ecosystems that the model predicts should respond differently to livestock grazing: the desert-steppe, steppe and mountain-steppe ecological zones of Mongolia. We expected that the desert-steppe and steppe zones would fit the NEP model predictions, while the mountain-steppe would display equilibrium dynamics following the traditional RC model. Our expectations were initially based on Ellis's (1995) prediction of mean annual precipitation and interannual variability in precipitation in each system. Following the NEP model, we hypothesized that plant biomass, vegetation cover and composition, and species richness and diversity should not vary along a grazing pressure gradient in the desert-steppe and steppe zones of Mongolia. Conversely, these variables should vary along a grazing pressure gradient in the mountain-steppe zone, with greater grazing pressure resulting in decreased biomass and cover, and shifts in species composition consistent with the RC model. We expected species richness and diversity to increase with moderate grazing pressure.

MONGOLIAN PASTORAL ECOSYSTEMS

Approximately 75% of Mongolia's 1·56 million square kilometres is grassland and shrubland grazed by some 30 million head of domestic livestock (cattle, camels, horses, sheep and goats) in addition to wild herbivores (including large grazers and small mammals). Close to 20% of the country's human population are pastoralists and half the population depends directly or indirectly on the pastoral economy for its livelihood (Mongolian Business Development Agency (MBDA) & European Union Tacis Program 1996). Mongolia's pastoralists pursue a semi-nomadic lifestyle, moving their households and livestock an average of four times yearly among seasonal pastures selected to meet the nutritional and physiological demands of their herds, conserve pasture resources, and avoid herd and pasture devastation from frequent droughts and winter storms. Due to the very recent accessibility of Mongolia to Western scientists (since 1991) and the logistical challenges of conducting fieldwork there, relatively little is known about the vegetation and ecological conditions and dynamics of the Mongolian steppe. Current and high quality ecological data are particularly important in light of proposed changes to existing rangeland tenure, including formal pasture leasing and monitoring.

Mongolia's vegetation has been described in general (Kalinina 1974; Yunatov 1977; Ulziikhutag 1989; Lavrenko & Karamysheva 1993). Some plant communities have been classified (Pacyna 1986; Hilbig 1995; Wallis de Vries, Manibazar & Dugerlham 1996) and the seasonal production dynamics of several communities have been studied (Breymeyer & Klimek 1983; Tsogoo 1990; Lavrenko & Karamysheva 1993). However, few experimental or observational studies have been conducted to determine the effects of grazing (or release from grazing) on vegetation productivity or species composition. The available studies in the mountain-steppe (Chogni 1989; Tsogoo 1990; Lhagvajav 1992; Tserendash & Erdenebaatar 1993) and Inner Mongolian steppe (Yong-hong 1989; Poissonet & Bo 1990; Zouzhong & Xiangming 1993; Wei & Skarpe 1995) demonstrate that the productivity of these two Mongolian ecosystems is strongly influenced by abiotic factors, particularly the timing and amount of rainfall. The results of grazing exclusion experiments in both the mountain-steppe and steppe indicate that some of these communities respond to grazing removal as the RC model predicts, suggesting that these systems are characterized by equilibrium dynamics (Tserendash & Erdenebaatar 1993). No studies were found on vegetation change in the Mongolian desert-steppe, nor were any studies located that explicitly examined interactions between rainfall variability and grazing in Mongolia.

Methods

STUDY AREAS

Using 25–40 years of weather data from established government weather stations, we selected three study areas, one each in the desert-steppe, steppe and mountain-steppe ecological zones, to cover a precipitation gradient that would include a continuum of ecosystems from non-equilibrium to equilibrium, according to Ellis's (1995) predictions about the mean annual precipitation ($<$ 250 mm) and precipitation CV ($>$ 33%) of non-equilibrium ecosystems in Mongolia. Plots were located in two districts of Bayankhongor Aimag (province), Mongolia (an area bounded by 45°15′ N and 46°30′ N latitude and 100°E and 100°40′ E longitude) (Fig. 1). All three ecological zones are dominated by perennial grasses (see Table 1 for a summary of site characteristics). The three study areas have been grazed by domestic livestock under a nomadic or semi-nomadic pattern of land use for at least 500 years, possibly for several millennia. Although grazing practices vary somewhat depending on local geography, the basic pattern of seasonal use is similar in all three zones, with summers spent in the vicinity of natural water sources and wells, and winters, when herds can usually rely on snow fall for water, spent in sheltered, often mountainous, terrain, sometimes distant from water. Mongolia's climate is continental, with cold dry winters and warm wet summers. Mean annual temperatures and precipitations are −1·7 °C and 230 mm in the mountain-steppe, 1·6 °C and 200 mm in the steppe and 4·8 °C and 95 mm in the desert-steppe. Coefficients of variation for precipitation range from 28% in the mountain-steppe to 47–50% in the desert-steppe. Precipitation is unimodally distributed, with peak rainfall occurring in July. In the first year of the study, 1994, all sites received above average precipitation. In the second year, spring and summer precipitation was below

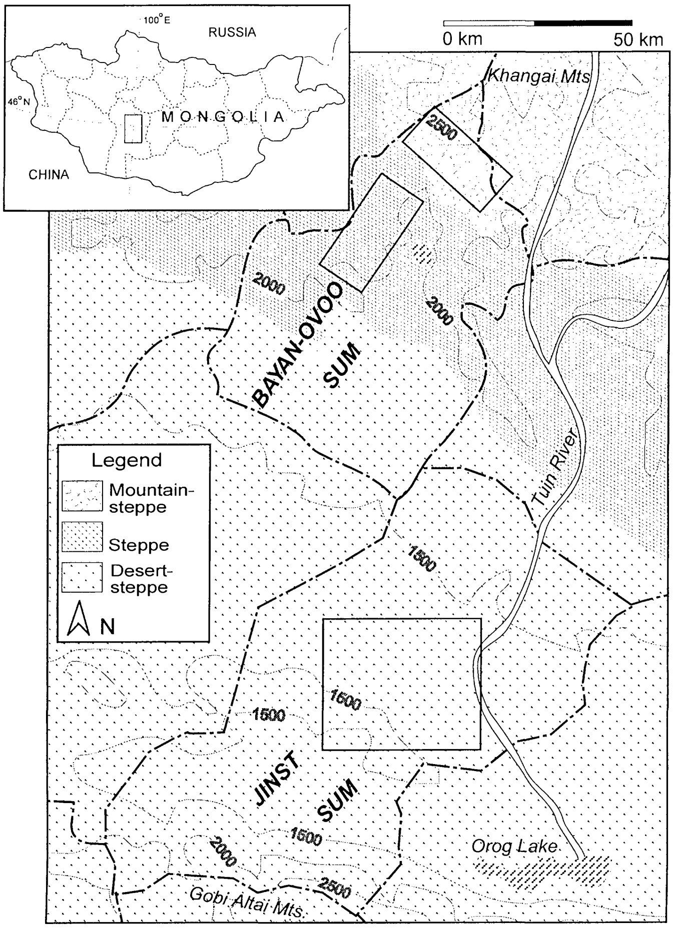

Fig. 1. Map of the study location. Rectangles indicate study areas for each of the three ecological zones.

average (Table 2). (Most available studies from the Inner Mongolian steppe report that spring or early summer precipitation is a more important determinant of peak biomass than total annual precipitation; Dexin 1990; Shu 1990; Zhongling & Zhonhou 1990). This interannual variability during the course of the study allowed a comparison of annual precipitation and grazing effects on vegetation. Livestock density in the desert-steppe site was 3·2 ha sheep forage unit^{-1}. The livestock density over all of Bayan-Ovoo Sum (steppe and mountain-steppe together) was 2·8 ha sheep forage unit^{-1}. (The equivalencies for Mongolian sheep forage units are: sheep = 1·0, camel = 5·0, horse = 7·0 cattle = 6·0, goat = 0·9.)

SAMPLING METHODS

We used grazing gradients from water sources to areas distant from water to examine the effects of livestock grazing pressure on vegetation. Livestock density and grazing pressure are usually highest close to water and decrease with distance away from water (Valentine 1945). Many ecological studies have sampled vegetation and soils along gradients from water sources to determine the effects of grazing pressure on rangeland structure and function (Andrew & Lange 1986a; Tolsma, Ernst & Verwey 1987; McClaran & Anable 1992).

Within each of the three ecological zones, all functioning wells and water sources were mapped on a 1 : 100 000 topographic map. The area surrounding each water source was stratified into three concentric categories: $<$ 500 m from water, 500–2000 m from water and $>$ 2000 m from water. An equal number of replicate plots was selected randomly in each distance-from-water category in each zone. In the steppe and mountain-steppe 15 plots were sampled: five replicates in each of the three distance-from-water categories. In the desert-steppe zone, 27 plots were sampled, nine in each distance-from-water category. A larger number of replicate plots was sampled in the desert-steppe to increase the power of statistical analyses because of the expected variability of the arid zone. Permanent plots with a 200-m radius were established from a fixed centre point in each plot (recorded by global

Table 1. Site characteristics of the desert-steppe, steppe and mountain-steppe ecological zones in Jinst and Bayan-Ovoo Sums, Bayankhongor Aimag

	Desert-steppe	Steppe	Mountain-steppe
Mean annual precipitation (min–max)*	95 mm (39–143)	200 mm (110–340)	230 mm (144–450)
Coefficient of variation†	47–50%	30%	28%
Mean January temperature	−18 °C	−18 °C	−25 °C
Mean July temperature	21 °C	16 °C	13 °C
Elevation	1380 m	2000 m	2200–2800 m
Soils‡	Desert grey	Chestnut	Chestnut and dark chestnut
Dominant plant species§	grasses: *Stipa gobica*, *S. glareosa*	grasses: *Stipa krylovii*, *Cleistogenes squarrosa*, *Agropyron cristatum*	grasses: *Festuca lenensis*, *Koelaria macrantha*, *Poa attenuata*
	forbs: *Artemisia xerophytica*, *Allium polyrrhizum*, *A. mongolicum*	forbs: *Cymbaria dahurica*, *Thermopsis dahurica*, *Oxytropis* spp.	forbs: *Artemisia frigida*, *Leontopodium leontopodoides*, *Oxytropis* spp.
	shrubs: *Caragana* spp., *Artemisia* spp.	shrubs: *Caragana* spp.	
Typical dry yield of pastures¶	50–250 kg ha^{-1}	300–400 kg ha^{-1}	500–800 kg ha^{-1}

*Source for climate data: Hydrometeorological Institute, Ministry of Nature and Environment.
†Coefficient of variation for the desert-steppe based on data from Saikhan-Ovoo and Gurvansaikhan Sums in Dundgov Aimag, at the same latitude and of similar elevation and vegetation type as Jinst Sum. Substitution of these data for the calculation of the CV was made due to missing rainfall data for a number of months in the Jinst data set.
‡Source: Sodnom & Yanshin (1990).
§ Source: Fernandez-Gimenez (1997).
¶ Source: Purev (1990).

positioning system, GPS). Within-plot samples were taken along five 50-m transects located at 0, 50, 100, 150 and 200 m from the plot centre. Sampling was conducted from 18 July to 19 August 1994 and from 16 July to 6 August 1995, beginning in the desert-steppe and ending in the mountain-steppe.

Biomass

Standing biomass, including both green and brown material, was clipped at 1·0 cm height in four systematically located circular 0·125-m^2 quadrats along each transect, for a total of 20 clipped samples per plot, then oven-dried for 48 h at 60 °C in the laboratory. Samples were separated into 'graminoid' and 'forb' fractions and weighed separately. Woody parts of subshrubs were included in the forb fraction. The biomass of large woody plants was not measured.

Species and functional group cover

We used the line-point method to estimate the foliar cover of species (Goodall 1952; Fisser & Van Dyne 1966; Mueller-Dombois & Ellenberg 1974; Mitchell, Brady & Bonham 1994). Points were located every half metre along each transect and the first surface intercepted by the point was recorded (plant species, litter, bare ground, rock) for a total of 500 points per plot. Where both shrub and understorey layers

Table 2. Mean spring precipitation (mm) compared with spring precipitation in 1994 and 1995. Means are based on 30 years of data from Jinst Sum (desert-steppe), 32 years from Bayankhongor Aimag Center (steppe), and 38 years in Galuut Sum (mountain-steppe)

Weather station	Mean April–May precipitation	1994 April–May precipitation	1995 April–May precipitation
Jinst Sum (desert-steppe)	8·8	11·5	0·1
Bayankhongor Aimag Center (steppe)	21·8	38·5	2·8
Galuut Sum (mountain-steppe)	20·8	35·2	2·4

of vegetation were present, both layers were recorded. Nomenclature follows Grubov (1982). Species were classified into functional groups based on key attributes including life history (perennial or annual/biennial/ephemeral); growth form (graminoid, forb, shrub); palatability; and whether or not the plant was a known 'weed', ruderal or disturbance indicator.

DATA ANALYSIS

All dependent variables were assessed for normality of distribution and heterogeneity of variances. Log, $\log(y + 1)$ or square-root transformations were performed where needed. Species with extremely skewed distributions or very small cover values were combined into taxonomic groups and analysed together (e.g. *Carex* spp., *Allium* spp.). The two most common grasses in the desert-steppe zone, *Stipa gobica* and *S. glareosa*, were also combined because they were difficult to distinguish after seed set, when sampling took place. Richness (R) was calculated as the sum of all taxa occurring on transects on a given plot. The Shannon–Wiener diversity index was used as the measure of diversity ($H' = -\Sigma p_i \ln p_i$; where p_i = the proportion of cover of the ith species) (Magurran 1988).

Repeated measures ANOVA (SYSTAT Inc. 1992) was used to compare the effects of distance from water (our proxy for grazing pressure) and year (our proxy for annual precipitation) on standing biomass, total vegetative cover, individual species cover, plant functional group cover, and richness and diversity within each ecological zone. Both year and distance from water were considered fixed effects for ANOVA. Statistical tests were considered significant at $P < 0{\cdot}05$.

Results

BIOMASS AND TOTAL VEGETATIVE COVER

In the desert-steppe, total and grass biomass and total vegetative cover were significantly greater in 1994 than in 1995 (Tables 3 and 4 and Fig. 2). Total cover increased significantly with distance from water, but not grass, forb or total biomass (Table 4). In 1994, forb biomass in the > 2000 m-from-water category increased, while in 1995 it remained low, resulting in a significant water × year interaction effect.

In the steppe, total biomass and total vegetative cover were significantly greater in 1994 than in 1995 (Tables 3 and 4 and Fig. 2). Grass biomass and total vegetative cover in the steppe zone increased significantly with distance from water, while forb biomass significantly decreased with distance from water. The increase in grass biomass in the > 2000 m-from-water category was greater in 1994 than in 1995, resulting in a significant water × year interaction effect. Also, due to much greater cover values in the < 500-m category in 1994 than in 1995, there was a significant water × year interaction effect on cover in the steppe.

In the mountain-steppe zone, only total vegetative cover was significantly greater in 1994 than 1995 (Table 3). Total and grass biomass and total vegetative cover increased significantly with distance from water in both years. (Forb biomass did not vary with distance from water.) However, there were significant water × year interaction effects on total and grass biomass.

SPECIES COVER

In the desert-steppe zone, 24 species had sufficient cover to meet statistical assumptions when cover values were ($\log(y + 1)$) transformed (Table 4). Of these, two species had significantly higher cover with increasing distance from water, *Artemisia schisinskii* (a palatable shrub) and *Asparagus gobica* (a marginally palatable forb). No other species differed in cover with distance from water in the desert-steppe. Eight of the 24 species had significantly greater cover in 1994 than 1995 (*Allium mongolica*, *A. polyrrhizum*, *Anabasis brevifolia*, *Artemisia xerophytica*, *Iris bungei*, *Oxytropis aciphylla*, *Scorzonera pseudodivaricata* and *Stipa gobica*/*glareosa*). Only one of these taxa, *Scorzonera pseudodivaricata*, is short-lived; three are subshrubs (*Anabasis brevifolia*, *Oxytropis aciphylla* and *Artemisia xerophytica*); three are perennial bulbs (*Allium mongolica*, *A. polyrrhizum* and *Iris bungei*); and one is a perennial bunch grass (*Stipa gobica*/*glareosa*).

In the steppe zone, four of the 28 taxa analysed differed significantly in cover with distance from water. *Artemisia glauca* (an unpalatable perennial forb and disturbance-indicator), *Stipa krylovii* (a perennial bunchgrass) and *Thermopsis dahurica* (a palatable perennial forb) increased in cover with increasing distance from water (Table 4). *Lepidium densiflorum* (an unpalatable annual weed) decreased with distance from water. Fourteen of the 28 steppe zone taxa had significantly greater cover in 1994 than in 1995 (*Allium* spp., *Carex* spp., *Leguminosae*, *Agropyron cristatum*, *Artemisia adamsii*, *A. glauca*, *Carex duriuscula*, *Caragana pygmea*, *Dontostemon integrifolius*, *Lepidium densiflorum*, *Ptilotrichum canescens*, *Scorzonera divaricata*, *Stipa krylovii* and *Thymus gobicus*). Four of these taxa are annual or biennial forbs, three are perennial grasses or sedges, two are subshrubs, and four are perennial forbs.

In the mountain-steppe zone, 13 of 33 taxa analysed differed significantly in cover with distance from water (Table 4). Lichens, *Amblynotus rupestris* (perennial forb), *Ephedra monosperma* (perennial forb), *Festuca lenensis*, *Koelaria macrantha*, *Stipa*

Table 3. Results from repeated-measures analysis of variance of the effects of distance from water and year on biomass total vegetation cover and species richness and diversity

		Desert-steppe		Steppe		Mountain-steppe	
Variable	Source	d.f.	*F*	d.f.	*F*	d.f.	*F*
Grass biomass	water	2	2·54	2	4·24*	2	7·39**
	year	1	41·31***	1	14·22**	1	0·13
	water × year	2	0·81	2	11·54**	2	5·59*
	between error†	23		12		12	
	within error	23		12		12	
Forb biomass	water	2	0·12	2	5·48*	2	0·52
	year	1	44·07***	1	4·37	1	0·97
	water × year	2	3·33*	2	2·59	2	3·67
	between error	23		12		12	
	within error	23		12		12	
Total biomass	water	2	2·05	2	2·84	2	8·41**
	year	1	66·86***	1	12·20**	1	0·09
	water × year	2	1·07	2	1·50	2	6·95*
	between error	23		12		12	
	within error	23		12		12	
Total vegetative cover	water	2	5·20**	2	10·73**	2	7·15**
	year	1	35·46***	1	90·08***	1	4·95*
	water × year	2	0·54	2	12·34**	2	1·44
	between error	24		12		12	
	within error	24		12		12	
Diversity	water	2	0·86	2	5·86*	2	6·25*
	year	1	23·45***	1	3·18	1	9·85**
	water × year	2	0·30	2	0·80	2	1·89
	between error	24		12		12	
	within error	24		12		12	
Richness	water	2	0·14	2	2·52	2	6·48*
	year	1	23·35***	1	18·65**	1	3·40*
	water × year	2	0·30	2	0·19	2	3·65
	between error	24		12		12	
	within error	24		12		12	
Species cover	water		2 of 24 taxa	4 of 28 taxa		13 of 33 taxa	
	year		8 of 24 taxa	14 of 28 taxa		11 of 33 taxa	
	water × year						

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Between error is the between plot error in repeated-measures ANOVA. Within error is the within plot error in repeated-measures ANOVA.

krylovii (perennial grasses) and *Thermopsis dahurica* (perennial forb) increased in cover with increasing distance from water. Mosses, *Carex* spp., *Potentilla* spp., *Artemisia adamsii* (a weedy annual), *Carex duriuscula* (a grazing-tolerant sedge) and *Potentilla strigosa* (perennial forb) had greatest cover close to water. Eight of the 33 mountain-steppe taxa had significantly greater cover in 1994 than in 1995 (lichens, *Carex* spp., *Arenaria capillaris*, *Artemisia frigida*, *Aster alpinus*, *Potentilla strigosa* (all four perennial forbs), *Carex duriuscula and Festuca lenensis*). Three taxa in the mountain-steppe zone had significantly greater cover in 1995 than in 1994 (mosses, *Agropyron cristatum* and *Poa attenuata*).

FUNCTIONAL GROUP COVER

In the desert-steppe zone, none of the functional groups varied in cover with distance from water. Grasses, forbs, palatable annuals, palatable perennials and subshrubs had significantly higher cover values in 1994 than in 1995 (Table 5 and Fig. 3).

In the steppe zone, grass cover increased significantly with distance from water. Forbs, unpalatable forbs and weedy annuals decreased in cover significantly with increasing distance from water. All functional groups except palatable perennials had significantly higher cover values in 1994 than 1995 in the steppe zone. Palatable perennials did not vary significantly in cover between years.

In the mountain-steppe zone, grasses increased in cover significantly with increasing distance from water. Unpalatable forbs and weedy annuals had significantly greater cover values close to water. Forbs, palatable perennials and weedy annuals had significantly greater cover in 1994 than 1995. Grass, palatable annual and unpalatable forb cover did not vary significantly between years.

Table 4. Summary of the effects of water (grazing) and year (precipitation) on vegetation variables. ↑ indicates that the variable increases with increasing distance from water. ↓ indicates that variable decreases with increasing distance from water

	Desert-steppe			Steppe			Mountain-steppe		
	Water	Year	Interaction	Water	Year	Interaction	Water	Year	Interaction
Biomass									
Grass	NS	94 > 95		↑	94 > 95	Yes	↑	NS	Yes
Forb	NS	94 > 95	Yes	↓	NS		NS	NS	
Total	NS	94 > 95		NS	94 > 95		↑	NS	Yes
Total vegetative cover	↑	94 > 95		↑	94 > 95	Yes	↑	94 > 95	
Functional group cover									
Grasses	NS	94 > 95		↑	94 > 95		↑	NS	
Forbs	NS	94 > 95		↓	94 > 95		NS	94 > 95	
Weedy annuals	NS	NS		↓	94 > 95		↓	94 > 95	
Species cover	2 ↑	8 > in 94		3 ↑	14 > in 94		7 ↑	8 > in 94	
	0 ↓	than 95		1 ↓	than 95		6 ↓	3 > in 95	
Richness	NS	94 > 95		NS	94 > 95		↓	95 > 94	
Diversity	NS	94 > 95		↑	NS		↓	95 > 94	

SPECIES RICHNESS AND DIVERSITY

The patterns of species diversity and richness along distance-from-water gradients differed substantially among the three ecological zones (Fig. 4). In the desert-steppe zone, both richness and diversity were significantly lower in 1995 than in 1994, but did not vary with distance from water. In the steppe zone, diversity increased significantly with increasing distance from water. Richness was significantly lower

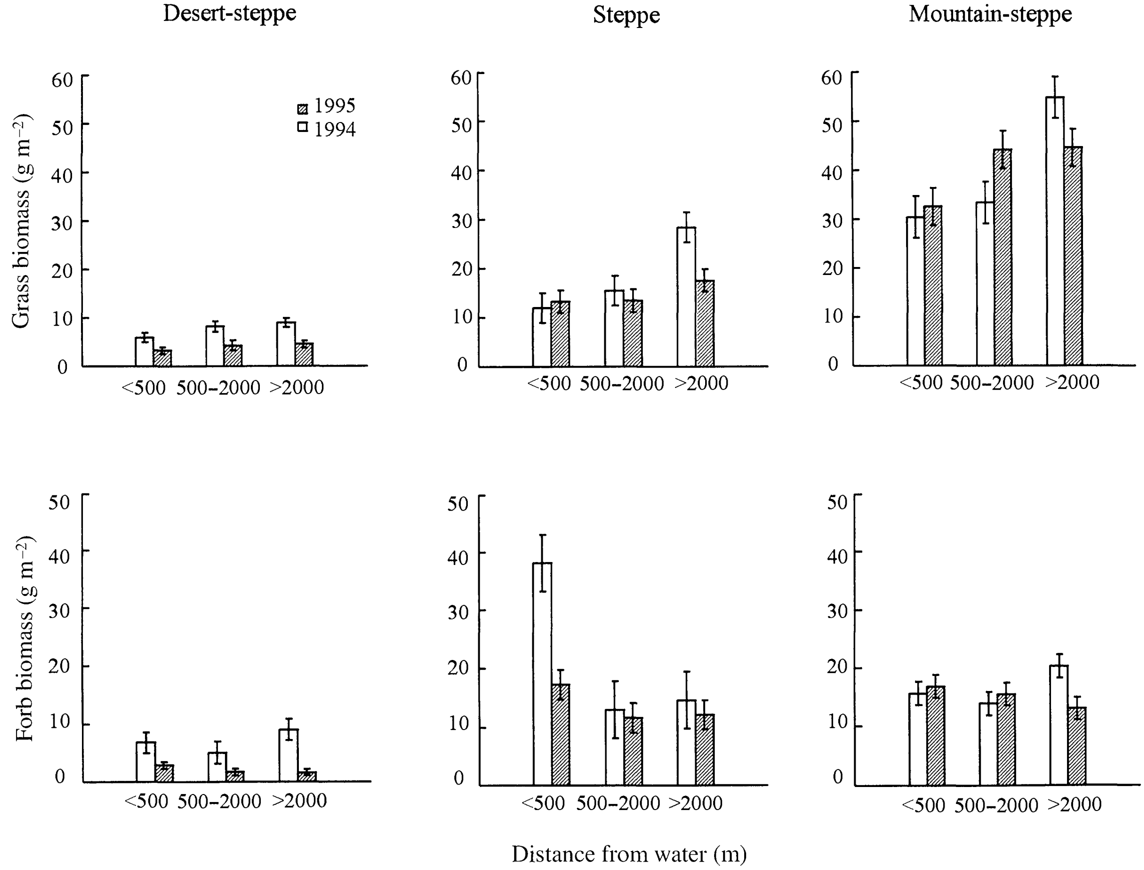

Fig. 2. Changes in grass and forb biomass (g m^{-2}) with distance from water (our proxy for grazing pressure) in wet (1994) and dry (1995) years in the desert-steppe, steppe and mountain-steppe ecological zones. Each bar represents the mean ± 1 SE of five (steppe and mountain-steppe) or nine (desert-steppe) plots.

Table 5. Results from repeated-measures analysis of variance of the effects of distance from water and year on functional group cover

		Desert-steppe		Steppe		Mountain-steppe	
Variable	Source	d.f.	*F*	d.f.	*F*	d.f.	*F*
Grass cover	water	2	1·13	2	46·45***	2	5·72*
	year	1	57·65***	1	8·28*	1	2·90
	water × year	2	3·24	2	2·15	2	0·19
	between error†	24		12		12	
	within error	24		12		12	
Forb cover	water	2	0·43	2	20·32***	2	1·07
	year	1	47·24***	1	19·79***	1	9·06**
	water × year	2	0·60	2	0·15	2	3·05
	between error	24		12		12	
	within error	24		12		12	
Weedy annual cover	water	2	0·71	2	12·31***	2	4·60*
	year	1	1·81	1	10·89**	1	4·59*
	water × year	2	0·91	2	2·89	2	0·10
	between error	24		12		12	
	within error	24		12		12	
Palatable annual cover	water	2	0·61	2	3·69	2	1·46
	year	1	8·64**	1	15·11**	1	0·52
	water × year	2	0·47	2	0·55	2	2·29
	between error	24		12		12	
	within error	24		12		12	
Palatable perennial cover	water	2	0·23	2	0·24	2	0·07
	year	1	39·08***	1	2·71	1	17·81***
	water × year	2	0·15	2	0·65	2	2·02
	between error	24		12		12	
	within error	24		12		12	
Unpalatable forb cover	water	2	0·12	2	8·75**	2	5·53**
	year	1	1·99	1	13·86**	1	0·20
	water × year	2	0·42	2	3·01	2	0·44
	between error	24		12		12	
	within error	24		12		12	
Subshrub cover	water	2	0·32				
	year	1	25·89***				
	water × year	2	0·71				
	between error	24					
	within error	24					

*$P \le 0·05$, **$P \le 0·01$, ***$P \le 0·001$.

† Between error is the between plot error in repeated-measures ANOVA. Within error is the within plot error in repeated-measures ANOVA.

in 1995 than in 1994. In the mountain-steppe zone, diversity and richness were significantly greater in the plots closest to water and declined with increasing distance from water. This pattern was the opposite of that observed in the steppe zone. Diversity and richness were significantly greater in 1995 than in 1994 in the mountain-steppe.

Discussion

The NEP model predicts that in arid and highly variable ecosystems abiotic factors such as precipitation have a greater influence on vegetation biomass and species composition than grazing. The model also predicts that in moist and constant environments, grazing plays a greater role in regulating vegetation productivity and composition. Thus we hypothesized that vegetation variables in the desert-steppe and steppe would not vary along a grazing pressure gradient (distance from water) but would be abiotically controlled. Conversely, we hypothesized that vegetation biomass and cover in the mountain-steppe would vary along a grazing pressure gradient.

The classic RC model (Dyksterhuis 1949) predicts that increasing livestock grazing leads to decreases in perennial grasses and increases in weedy annuals. We expected that in the mountain-steppe zone, species cover and composition changes with grazing would be in line with the predictions of the RC model, while in the steppe and desert-steppe they would not.

The picture of ecosystem response that emerges from our results is much more complicated than

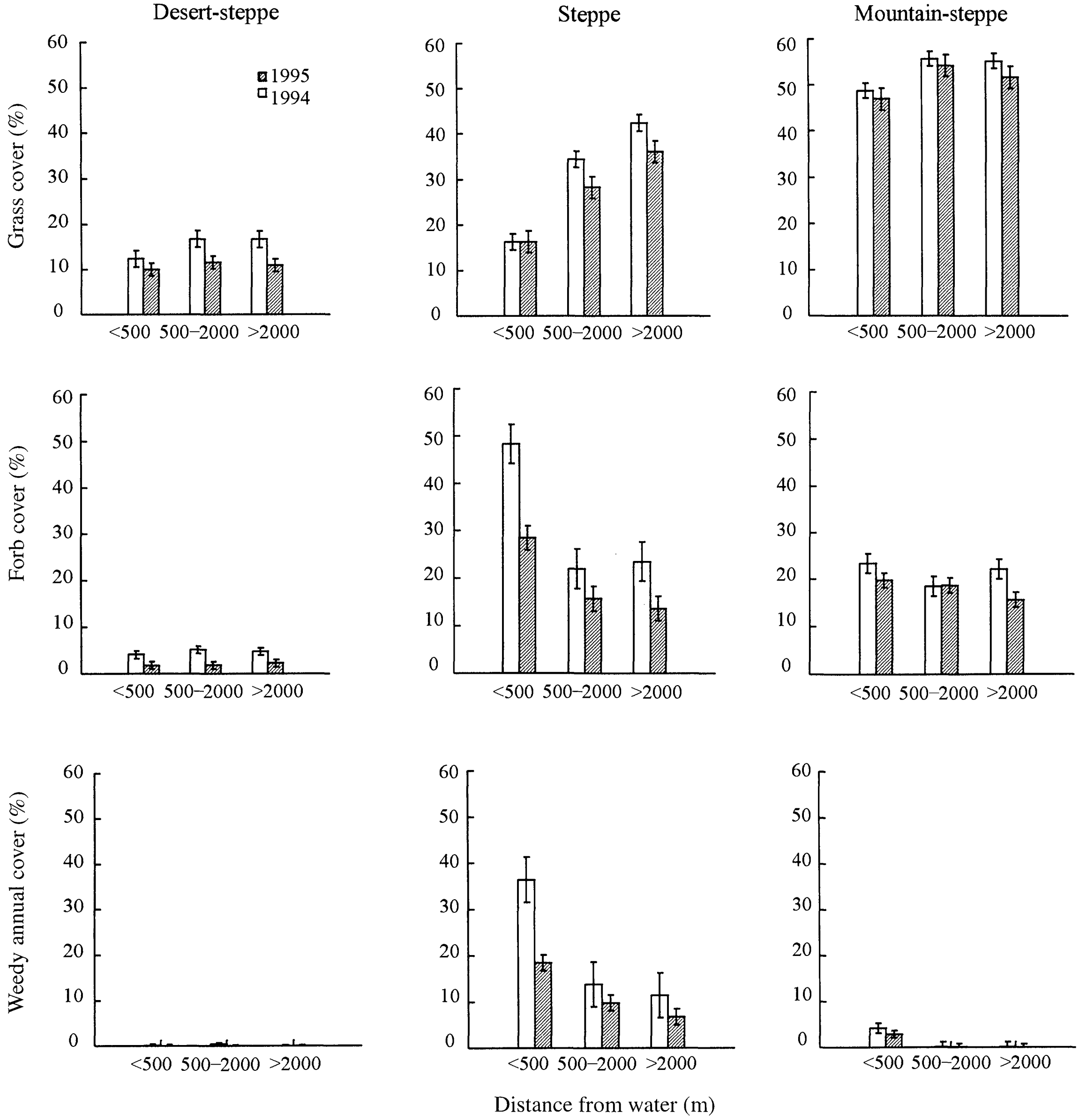

Fig. 3. Changes in functional group (grass, forb and weedy annual) cover with distance from water (our proxy for grazing pressure) in wet (1994) and dry (1995) years in the desert-steppe, steppe and mountain-steppe ecological zones. Each bar represents the mean ± 1 SE of five (steppe and mountain-steppe) or nine (desert-steppe) plots.

either model suggests. Evaluation of all the variables collected in the desert-steppe suggests that, as we hypothesized, this system largely conforms with the predictions of the NEP model. In this arid and variable system, biomass, functional group cover, richness and diversity showed no distance-from-water effects, indicating that grazing apparently has little influence on these variables in the desert-steppe. As the NEP model predicts, all vegetation variables in the desert-steppe varied significantly between years, except for the cover of weedy annuals and unpalatable forbs, suggesting that interannual variation in precipitation is an important determinant of vegetation biomass and species composition in the desert-steppe zone. However, total vegetative cover and cover of two individual species did vary with distance from water.

In the wetter, less climatically variable mountain-steppe zone, grass and total biomass, total vegetative cover, the cover of grasses, weedy annuals, unpalatable forbs, and richness and diversity all varied with distance from water, as the RC model predicts. However, the interpretation of changes in grass and total biomass was confounded by a significant interaction between grazing and year. Total vegetative cover, the cover of forbs, weedy annuals

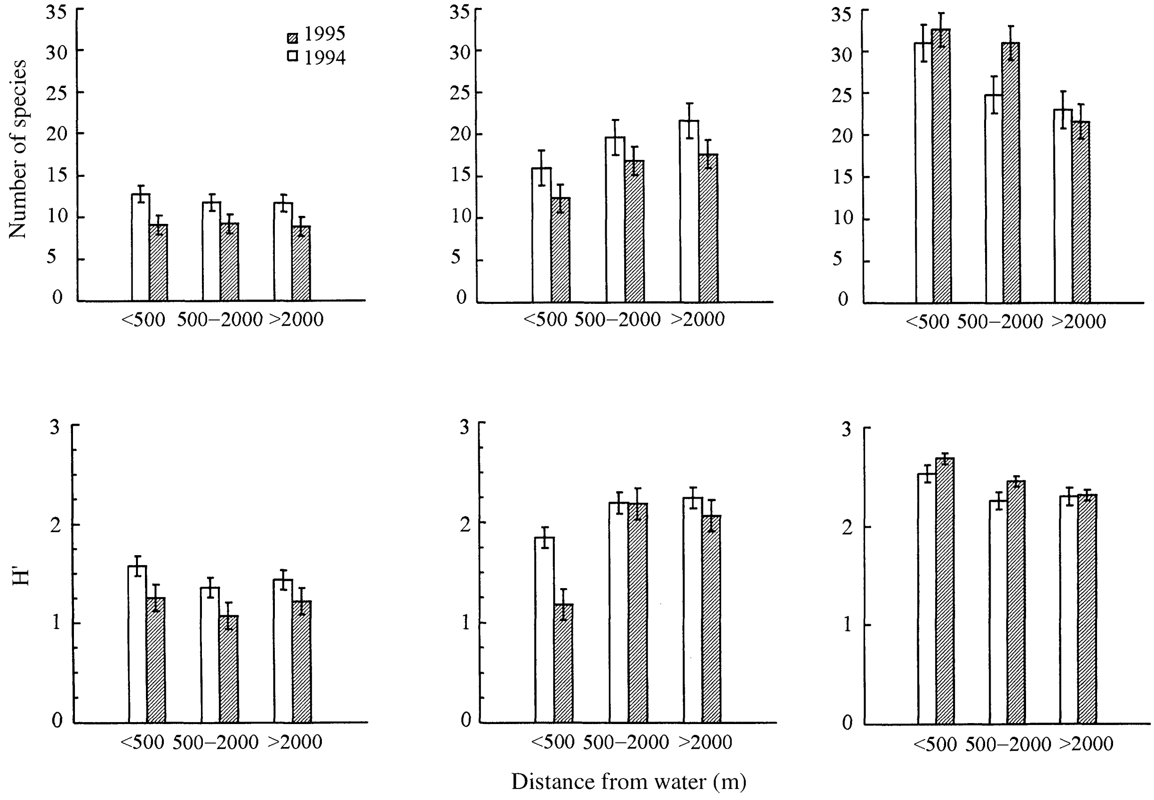

Fig. 4. Changes in richness and diversity (H′) with distance from water (our proxy for grazing pressure) in wet (1994) and dry (1995) years in the desert-steppe, steppe and mountain-steppe ecological zones. Each bar represents the mean ± 1 SE of five (steppe and mountain-steppe) or nine (desert-steppe) plots.

and palatable perennials, the cover of 11 individual species, richness and diversity also varied with year, a response that is not directly addressed in the RC model. Overall, with increasing grazing pressure, grasses decrease and forbs and weedy annuals increase. It appears that while grazing plays a more important role in determining biomass, cover and vegetation composition in the mountain-steppe than in the desert-steppe, interannual variation in precipitation is still an important determinant of total vegetative cover, species and functional group cover, and richness and diversity, in this zone. These results support the findings of the few studies available from the mountain-steppe zone (Tsogoo 1990; Tserendash & Erdenebaatar 1993) which also report interannual changes in biomass and species composition related to variation in precipitation.

Our results from the steppe zone were also mixed. Grass biomass and total vegetative cover responded interactively to rainfall and grazing. The interaction effect on total cover was due to the extremely dense cover of weedy annuals in the highly disturbed plots close to water during the high rainfall year. Cover in these plots diminished sharply in the dry year. Four functional groups (grasses, forbs, unpalatable forbs and weedy annuals) varied significantly with distance from water, and cover in all functional groups except palatable perennials varied between years. Here again, as in the mountain-steppe, the pattern of vegetation change fits the classic RC model, with decreasing grass cover and increasing forb and annual weed cover as grazing pressure increases. In this system, it seems that both grazing and variation in precipitation play important roles in determining vegetation biomass and composition.

In all three ecological zones, interannual variation in precipitation would probably affect the annual component of the flora, with a wet year resulting in greater biomass, greater total vegetative cover and potentially greater diversity than a dry year (Heady *et al.* 1992; O'Connor & Roux 1995). Annuals comprise only a small fraction of the total vegetative cover in the desert-steppe and mountain-steppe (5% or less of relative cover in both cases), while they are much more prevalent in the steppe zone (22–34% of relative cover).

Others have found that the cover of perennial grasses in some systems exhibits a 1-year lag in response to decreased rainfall (Allen-Diaz & Jackson 2000). A lag effect might explain the lack of variation between years in grass cover in the mountain-steppe. However, individual perennial grass and forb species had greater cover in 1994 than 1995 in all three ecological zones. Total vegetative cover was greater in the wet year than the dry year in all three zones, suggesting that, overall, vegetation cover in all three zones is sensitive to interannual changes in rainfall, and responds without a lag time. We acknowledge that the short duration of this study is potentially a significant limitation. A longer time series of data is needed to more definitively determine the factors, biotic and abiotic, driving vegetation productivity and composition in each zone over the long-term. It is also important to note that this study, like the research in Kenya that inspired the NEP model, took place in a highly seasonal system, while other non-equilibrium models, such as the state and transition and threshold models, were developed in aseasonal systems. The applicability of the NEP model needs further testing in systems characterized by non-seasonal, episodic productivity.

In addition to our hypotheses based on NEP and RC model predictions, we also expected that species richness and diversity would peak at moderate levels of grazing, as predicted by the intermediate disturbance hypothesis (Harper 1969; Connell 1978; Coppock *et al.* 1983; Milchunas, Sala & Lauenroth 1988). The predicted pattern did not occur in any of the three ecological zones. In the desert-steppe there were no differences in richness or diversity with increasing grazing pressure. In the mountain-steppe, richness and diversity increased significantly with increasing grazing pressure, peaking in the most heavily grazed plots. In the steppe, the reverse pattern was detected, with maximum diversity and richness found in the least-grazed plots. Although the mechanisms driving shifts in diversity with changing grazing pressure and precipitation are not clear, the fact that diversity and richness do not vary with grazing pressure in the desert-steppe lends support to the hypothesis that in this arid and variable ecosystem, grazing has little effect on vegetation composition.

Conclusions and management implications

Several lessons emerge from our attempt to test the NEP model of rangeland vegetation dynamics in the field. First, given the predictions of the model, it was difficult to devise simple, mutually exclusive, alternative hypotheses that would clearly support or refute the model. Rather, in all three zones, some of our expected outcomes were affirmed and some were not, preventing clear acceptance or rejection of the NEP model for any zone. We relied on the preponderance of the evidence to conclude that the desert-steppe zone exhibits many characteristics of a non-equilibrium rangeland, as the NEP model predicts, and few equilibrium system traits. The steppe and mountain-steppe both possess at least some important features of equilibrium rangelands, notably the response to grazing of functional group and individual species cover, as the traditional RC model predicts. Our interpretation is not clear-cut, however, because the steppe and mountain-steppe are also strongly influenced by interannual variation, a characteristic of non-equilibrium rangelands according to the NEP model.

This brings us to the second lesson: the specific vegetation variables investigators choose to sample influence whether the model in question is supported or refuted. This is not a new lesson for ecologists, but seems to be one we must remind ourselves of often. For example, if we had focused only on total biomass and species cover we would have concluded that both the steppe and desert-steppe were non-equilibrium systems. If we had focused only on total vegetative cover and species cover, we might have concluded that all three ecological zones respond as predicted by the RC model. By partitioning biomass into grass and forb fractions, and looking at functional group cover as well as the cover of individual taxa, we discovered the complexity of ecosystem responses. Examining a wide range of vegetation variables led to a more complex interpretation of our results, suggesting that systems such as the mountain-steppe and steppe possess both equilibrium and non-equilibrium characteristics according to the NEP and RC models.

The work of Ellis & Swift (1988) and non-equilibrium theorists such as Wiens (1984) supports the view that a continuum of systems exists rather than a stark dichotomy between equilibrium and non-equilibrium rangelands. Nevertheless, 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 classic RC model as the basis for range management (Scoones 1995). This ‘paradigm shift’ in range science has been embraced with such enthusiasm by some that the concept of non-equilibrium rangelands may be as much in danger of being misapplied as equilibrium-based models have been. At the extreme are those who rely on the notion of non-equilibrium rangelands to argue that stocking rates are completely irrelevant to management in systems with extreme interannual variability.

The question remains, however, what are the management implications of determining whether a particular rangeland ecosystem is ‘equilibrium’, ‘non-equilibrium’ or at some intermediate point on the equilibrium–non-equilibrium continuum? Our data may help to locate the systems we studied along this continuum, but in terms of management the data are more useful than the classification of the system as equilibrium or non-equilibrium. We find ourselves (somewhat regretfully) back to the principle that what is most important to managers is historic, site-specific information including data on initial conditions and the response of a given system to climatic perturbations, grazing intensification and the removal of grazing. Sampling a wide variety of vegetation variables, at least initially, also helps to identify potentially useful indicators of range condition in a given system, or across systems.

In our study, total vegetative cover offered the most consistent response to grazing across ecosystems and years, with the single exception (1994 in the steppe) readily explainable. However, because total cover is sensitive to both grazing and yearly changes in precipitation, it is really only useful to management in the context of a long-term data set with corresponding rainfall data. We note that local nomadic herders in Mongolia, who can identify a large number of individual forage species and know their various nutritional values, rely primarily on total vegetative cover and its converse, the proportion of bare ground, in their assessment of pasture conditions (Fernandez-Gimenez 1997).

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