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Global assessment of the non-equilibrium concept in rangelands

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Abstract. The non-equilibrium concept of rangeland dynamics predicts that the potential for grazing-induced degradation is low in rangelands with relatively variable precipitation. To date, evidence in support of the non-equilibrium concept has been inconsistent. Using a standardized protocol, including a newly developed global map of rainfall variability, we reviewed the incidence of degradation in relation to rainfall variability across 58 published studies. We distinguished between (1) zonal degradation (i.e., degradation independent of water and key resources), (2) degradation in the presence of key resources, and (3) degradation in the presence of water. For studies not affected by proximity to permanent water or key resources, we found strong support for the non-equilibrium concept for rangelands. Zonal degradation was absent at CV (coefficient of variation) values above 33%, which has been proposed as a critical threshold. Grazing degradation was almost entirely restricted to areas with relatively stable annual precipitation as expressed by a low CV, or to rangelands with key resources or water points nearby. To better understand rangeland dynamics, we recommend that future studies use globally comparable measures of degradation and rainfall variability. Our work underlines that rangelands with relatively stable rainfall patterns, and those with access to water or key resources, are potentially vulnerable to degradation. Grazing management in such areas should incorporate strategic rest periods. Such rest periods effectively mimic natural fluctuations in herbivore populations, which are a defining characteristic of non-degraded rangelands occurring under highly variable precipitation regimes.

Key words: *climatic variability; degradation; drylands; grazing; rainfall; rangeland management.*

INTRODUCTION

Rangelands composed of large areas of natural or semi-natural vegetation occupy approximately two-thirds of Earth's land (White et al. 2000), and support large populations of both wild and domesticated herbivores (Olff et al. 2002). Many rangelands have a high economical value (Costanza et al. 1997), while also securing the livelihoods of at least one-third of the human population (Reynolds et al. 2007). Rangelands are dynamic ecosystems, with biomass, productivity, and herbivore numbers fluctuating through time (Illius and O'Connor 2000, Gillson and Hoffman 2007). These fluctuations can lead to various forms of degradation (Illius and O'Connor 1999, Dregne 2002), affecting soil (Illius and O'Connor 1999), vegetation (Miehe et al. 2010), wild fauna (Olff et al. 2002), domesticated livestock, and subsequently, human livelihoods (Walker and Janssen 2002).

Traditionally, rangeland dynamics had been conceptualized primarily from a biotic perspective, considering herbivore pressure to be the major driver of ecosystem dynamics (Briske et al. 2003, Vetter 2005). An alternative to this traditional view is the non-equilibrium concept, which was first proposed in the 1980s (Ellis and Swift 1988). The non-equilibrium concept of rangelands emphasizes the importance of abiotic variables (Illius and O'Connor 1999). Specifically, rainfall variability is considered a critical driver of rangeland dynamics, with a coefficient of variation (CV) of 33% being suggested as a threshold above which non-equilibrium conditions become relevant (Ellis and Swift 1988). Where rainfall variability is higher, the potential for degradation is considered to be relatively low because herbivore populations collapse in periods of drought, enabling vegetation to recover. By contrast, where rainfall variability is less pronounced, herbivore pressure may remain high even in drought periods, with ongoing grazing and browsing on the available plant biomass increasing the potential for degradation (Gillson and Hoffman 2007).

Despite its intuitive appeal, empirical studies testing the non-equilibrium concept have produced inconsistent results. Some studies have described grazing-induced degradation despite high rainfall variability, whereas others have found no evidence for degradation despite

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an apparently relatively stable climate (Vetter 2005). In this paper, we test whether existing inconsistencies can be explained by three variables: (1) rainfall variability, as estimated by global mapping; (2) the presence of key resources, such as readily available additional forage; and (3) the availability of water sources, which concentrate herbivores in spatially restricted spots. The importance of key resources and water sources has been discussed by many authors (e.g., Illius and O'Connor 1999, Vetter 2005), and there is little doubt that availability of such resources fundamentally changes rangeland dynamics at times of drought. However, a systematic assessment across a wide range of studies of grazing effects related to key resources and water availability is lacking to date. Perhaps more importantly, the extent of rainfall variability is (by definition) an important part of the non-equilibrium concept, but to date, no systematic global data-driven assessment exists of the effects of rainfall variability on rangeland dynamics. The lack of comparable criteria to assess rainfall variability could be one of the main reasons why support for the non-equilibrium concept has been inconsistent (Vetter 2005).

Our paper provides the first systematic global assessment of one of the key predictions of the non-equilibrium concept for rangeland dynamics. Using explicit criteria for degradation and a globally consistent method to quantify rainfall variability, we tested whether the incidence of rangeland degradation in published case studies is significantly related to (1) rainfall sums and rainfall variability (especially above and below the potential threshold of a CV of 33%); (2) the presence of key resources; and (3) the presence of water sources.

METHODS

Database of case studies

We created a database of case studies that had investigated the incidence of ecological degradation in rangelands. To select case studies, we searched the ISI Web of Science, using the following keywords: "non-equilibrium theory," or "non-equilibrium," or "disequilibrium" and "arid," or "rangelands," or "degradation." Non-equilibrium and disequilibrium were treated as synonymous because of ongoing debate about which is the more appropriate term (Illius and O'Connor 2000, Gillson and Hoffman 2007). After obtaining an initial list of potential case studies, we manually excluded those that were not specific case studies of rangeland dynamics in relation to ecological degradation (for example because they dealt with ecosystem dynamics more broadly, focused on community ecology, or focused on disciplines other than ecology). We manually added additional suitable case studies not included in the original database but contained in the reference lists of the reviewed publications. In all cases, obviously redundant studies (e.g., from two directly adjacent study areas) were not included (Appendix A).

For each case study, we recorded the coefficient of variation of the mean annual precipitation of the study area as stated by the authors; whether the authors had used any measures of the variability of precipitation; and whether grazing-induced degradation was observed. We are acutely aware that the term "degradation" is emotionally charged and can be highly subjective. Definitions vary among authors, and can range from loss in species diversity (West 1993) to the reduction of productivity (Wessels et al. 2007) or irreversible changes in soils (Illius and O'Connor 1999). We also cannot rule out a certain level of "observer bias," that is, given the subjective nature of degradation, some authors may be more likely to find evidence of degradation than others. To encompass a wide range of perspectives, we used a broad definition of degradation. Grazing-induced degradation was considered to be present if one or more of the following indicators were considered by the authors of the case study to be in a permanently or irreversibly degraded state: biodiversity, species composition, life form composition, biomass, aboveground net primary productivity, or soil properties. We believe that adopting this definition of degradation results in a conservative analysis with respect to the question whether degradation can occur under dry and highly variable rainfalls.

In cases where degradation was observed, we differentiated between three types of degradation: (1) zonal degradation occurred in rangelands where vegetation condition and thus forage availability largely reflected the regional macroclimate, with negligible influences of additional water sources, riparian ecosystems, or key resources; (2) degradation related to easily accessible key resources occurred in the presence of resources that ensure relatively high and stable availability of forage (e.g., salt meadows, mountain sites, or sites where supplementary forage is provided [Illius and O'Connor 1999]); and (3) degradation related to water sources, such as "sacrifice zones" around stock watering points, where damage is largely related to trampling and loss of vegetation and soil. Sacrifice zones typically refer to the immediate vicinity (~100 m) around water sources (Leggett et al. 2003).

Finally, we geo-referenced and mapped each case study. Studies covering extensive regions were digitized as polygons. Some studies sampled extensive spatial gradients (e.g., transects spanning dozens of kilometers with occasional survey sites along a pronounced climatic gradient (e.g., Fernandez-Gimenez and Allen-Diaz 1999). For such cases, individual points were sufficiently far apart to be considered ecologically independent judged by the spatial resolution of GIS layers being used. Hence, they were geo-referenced as multiple points.

Rainfall variability mapping

We produced a map of global rainfall variability. To do this, we used precipitation data from 18 669 climatic stations from the Global Historical Climate Network Dataset (GHCN) version 2, which has undergone

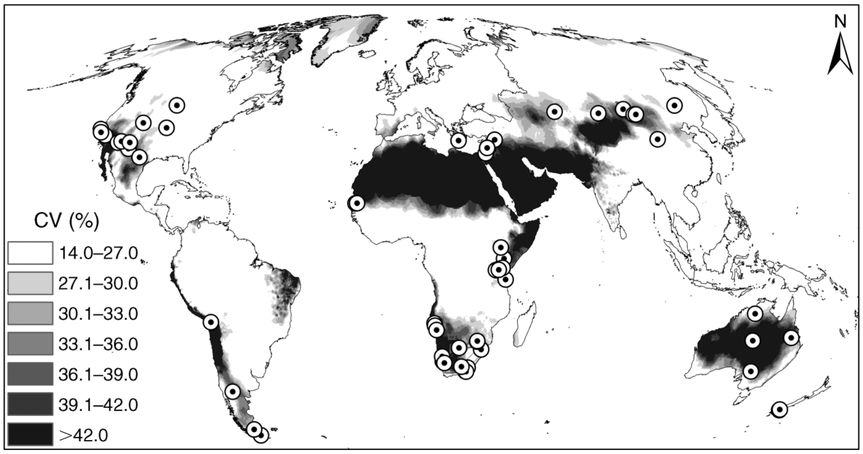

FIG. 1. Global map of the (interpolated) coefficient of variation (CV; %) of interannual precipitation. Dots indicate the locations of the case studies analyzed (see the Supplement for a high-resolution version of the climate layer alone). For a map showing only the difference between areas where zonal degradation may occur (CV < 33%), and areas where the likelihood of zonal degradation threat is low (CV > 33%), refer to Appendix C.

explicit quality control (data set *available online*).[7] For each station with more than 10 years of rainfall data, we calculated the coefficient of variation (CV) of rainfall, based on annual totals of precipitation. We refrained from restricting our analysis to stations with a longer (e.g., >25 years) observation period, since this would have substantially reduced data density. The CV is defined as the ratio of the standard deviation to the mean, divided by 100. We spatially interpolated the CV values by applying a standard kriging algorithm across the globe. We used a search radius setting of 10 points and a maximum search radius setting of 2000 km, regardless of rainfall regime. Mean precipitation rates were derived from Hijmans et al. (2005). Our method resulted in a continuous, global surface of rainfall variability, enabling us to estimate rainfall variability at virtually any point on the terrestrial part of the globe.

Data analysis

We used analysis of variance to test whether rainfall variability systematically differed between case studies experiencing one of three kinds of degradation (zonal, key resources, water sources) or no degradation. We also assessed the correlation between the CV of rainfall stated by the authors of individual case studies with our interpolated worldwide data set of the CV of rainfall. All statistical analyses were performed within the R environment (R Development Core Team 2009); kriging and mapping were conducted in Arc Map 8.2 (ESRI, Redlands, California, USA).

Results

We identified 58 case studies that explicitly examined the incidence of grazing-induced degradation in relation to rangeland dynamics (Fig. 1), of which 21 were carried out in Africa. Few studies ($n = 17$ studies) reported the CV of local rainfall (Fig. 2). For those that did, the CV of local rainfall given by the authors strongly correlated with our CV estimates ($P = 0.002$, correlation coefficient $= 0.61$). However, relative to the proposed critical threshold of rainfall variability of 33%, two studies were below this threshold according to the authors, but

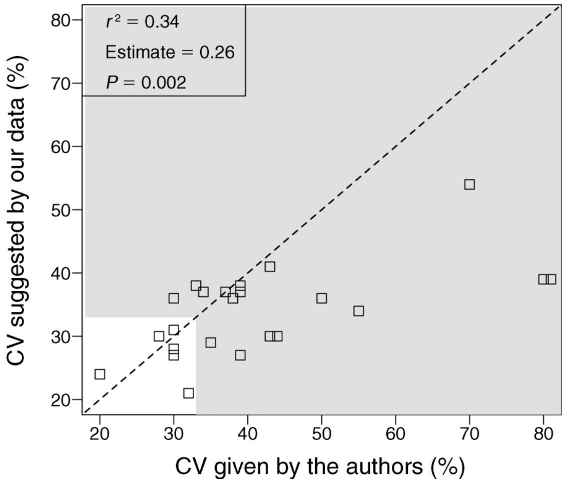

FIG. 2. Coefficients of variation (CV) of annual precipitation as reported in the analyzed studies, plotted against the CV values, based on our extrapolated layer ($n = 17$). Note that more than 17 points are shown, because for studies located along a large gradient we included both the minimum and maximum values of the CV. The light gray area demarcates sites above the proposed threshold of a CV of 33%, according to both reported and extrapolated data. The dotted line indicates whether extrapolated CV values were higher or lower than that suggested by the authors. Values in the upper left box summarize the results of a regression analysis of all plotted values.

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[7] http://www.ncdc.noaa.gov/pub/data/ghcn/v2

TABLE 1. Frequency of use of different rangeland health indicators, classified by whether or not degradation was observed in the 58 analyzed studies.

		Degradation observed?			
			Yes		
Rangeland health indicator	*n*	No	Key	Water	Zonal
Degradation class	58	9	7	8	34
Biodiversity	27	4	4	2	17
Species composition	34	5	3	4	23
Life form spectra	34	5	2	4	23
Plant height	10	0	2	0	8
Plant cover	48	8	6	8	26
Biomass	20	3	3	2	12
ANPP†	8	0	1	0	7
Soil	16	1	3	3	9

Notes: The column *n* indicates the number of studies in the respective class. Classes are no, no degradation observed; key, key resources present; water, around water sources; and zonal, zonal degradation occurs uncoupled from the availability of water or key resources.

† Aboveground net primary production.

were above the threshold according to our interpolations; and four studies were above the threshold according to the authors but below the threshold according to our spatially continuous surface.

Almost all papers employed multiple indicators of rangeland degradation, including vegetation cover, species composition, and composition of life forms (Table 1). Degradation was reported at 41 of 58 sites (84%).

Mean annual total precipitation differed significantly between classes of different types of degradation (ANOVA, $P = 0.002$). Degradation around water bodies and key resources occurred in areas with low annual rainfall, which was not significantly different from areas with no degradation. However, zonal degradation occurred in locations with significantly higher total annual precipitation (Fig. 3a).

The CV of rainfall also differed significantly between areas experiencing different types of degradation ($P < 0.001$). Notably, zonal degradation (i.e., degradation uncoupled from water or key resources) occurred almost exclusively in locations with a CV of rainfall of $\leq$33%. In areas with a higher coefficient of variation, degradation occurred only in the presence of key resources or at water-related piospheres. All studies without degradation occurred in locations where the CV of rainfall was >33% (Fig. 3b).

DISCUSSION

The non-equilibrium concept suggests that rangeland degradation is unlikely to occur where rainfall variability is high, because herbivore pressure during droughts is low relative to the available biomass (Illius and O'Connor 1999). A threshold value of the coefficient of variation of rainfall of 33% was suggested by the original proponents of the concept (Ellis and Swift 1988). The non-equilibrium concept states that below this value, degradation can occur if animal numbers are high enough. Here, we used a globally consistent rainfall database and consistently defined indicators of degradation to test the global applicability of the non-equilibrium concept. Our findings strongly support one of the key predictions of the concept. Zonal degradation (i.e., degradation despite no access to water or key resources) was entirely confined to areas where the CV of rainfall variability was below 33% (Fig. 3b).

Our analysis suggests that much of the debate about the applicability of the non-equilibrium concept (Briske et al. 2003, Vetter 2005) results from a lack of clarity

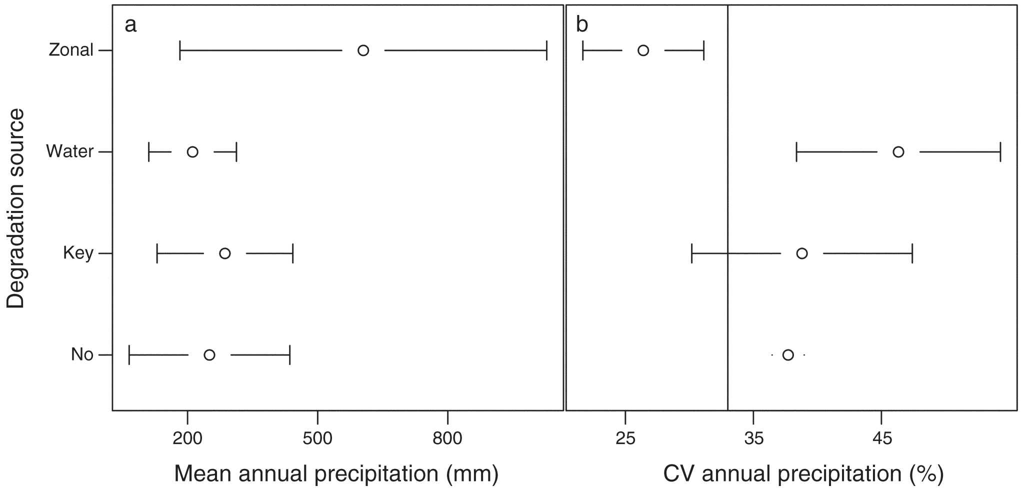

FIG. 3. Means (+SD) of (a) annual precipitation and (b) the coefficient of variation (CV) in precipitation for rangeland case studies reporting no degradation or degradation related to key resources, water sources, and zonal vegetation (see *Methods: Database of case studies* for definitions). For results of the Tukey post hoc test, which evaluates differences between the groups, see Appendix B.

about the conditions in which the concept can be expected to hold, and a lack of clarity about how to measure relevant quantitative data. Specifically, we believe there are four areas of concern where additional clarity would be beneficial.

First, the difference between mean annual rainfall and rainfall variability (Boone and Wang 2007) is sometimes confused. While the two variables are correlated, and yield broadly similar patterns regarding rangeland degradation (Fig. 3), the pattern is much clearer with rainfall variability. Notably, in its original form, the non-equilibrium concept postulated a link between rangeland degradation and rainfall variability, rather than mean annual rainfall. Retaining this original definition (Ellis and Swift 1988) evidently is important, because variability rather than aridity appears to be the primary driver of equilibrium (or non-equilibrium) conditions.

Second, consistent criteria are required to measure both sets of variables describing non-equilibrium dynamics, namely rainfall variability (on a globally comparable scale) and degradation. Reported violations of the non-equilibrium concept in the past could partly result from some authors of case studies assuming incorrect CV values for their study sites. In an attempt to provide consistent quantitative criteria of rainfall variability, we produced a global map of rainfall variability, and this is a likely reason why the patterns we found are very clear (Fig. 3b). Although spatial interpolation (by definition) cannot be entirely accurate at all locations, the difference between values reported by our GIS-layer compared to values given by the authors (Fig. 2) most frequently could be attributed to shorter measurement periods used in the case studies (e.g., three years), or large distances between case study areas and climate stations. Large distances to the nearest climate station result from the density of weather stations being low, which is often the case in drylands. In such cases, our interpolation approach based on several neighboring stations likely produces more accurate local estimates of rainfall variability than estimates from a single, relatively distant weather station. Finally, the CV of rainfall is not reported in many case studies, yet effects reported by some authors indicate they believe local rainfall variability to be very high when it may in fact be less high. We also attempted to use transparent criteria for what constitutes degradation. This is much more difficult because not all indicators of degradation are equally reliable, and degradation is a highly subjective concept. For future studies, we suggest that the most reliable indicator of degradation is soil condition: degraded soils cannot recover rapidly and thus are a highly reliable measure of degradation (Illius and O'Connor 1999). Soil restoration requires tremendous efforts as shown by examples from China, where soil degradation was eventually partly reversed due to immense restoration efforts (Zhang et al. 2005). By contrast, vegetation-related indicators and particularly plant biomass are less reliable, because under the right circumstances, they can recover relatively quickly.

The effect of grazing on biodiversity may differ widely, ranging from positive (Noy-Meir 1995) or unimodal responses (Milchunas et al. 2008) to negative effects (West 1993, Zhang et al. 2005). Effects of grazing are often positive where the rangeland vegetation has co-evolved with grazing and is adapted to it (Milchunas and Lauenroth 1993). Local adaptations or changes in plant community composition may prevent degradation; even when macroclimatic conditions are relatively stable (Mwalyosi 1992, Oliva et al. 1998, Hostert et al. 2003, Geerken and Ilaiwi 2004). Regardless of the indicator used, a transparent definition of degradation is vital to conduct a meaningful assessment of the non-equilibrium concept. Despite lasting changes of soil conditions being the most definite indicator of degradation, yet other indicators such as plant diversity and cover likewise confirmed the overall non-equilibrium concept.

Third, the availability of key resources and water sources fundamentally changes rangeland dynamics (Illius and O'Connor 1999). Degradation is common in the presence of key resources and water sources, which are considered a precondition for grazing under semi-arid or arid condition (Fensham et al. 1999, Bestelmeyer et al. 2006). A typical example of a stable key resource is the forage available in wet meadows located within rangelands (Buttolph and Coppock 2004); in addition, local degradation typically occurs around water sources (Hanan et al. 1991), settlements (Sullivan 1999), nomad tents (Evans and Geerken 2004), and stock posts (Zhao et al. 2007). Although the presence of key resources or water sources may lead to degradation, this does not necessarily imply that the non-equilibrium concept per se is incorrect.

Fourth, there are numerous additional variables that may influence the applicability of rangeland dynamics. Such variables include alterations to fire frequency (Thompson Hobbs et al. 1991, Fuhlendorf and Smeins 1997, Harrison et al. 2003), invasive plants (Huebner and Vankat 2003), or herbivores regimes (Tadey and Farji-Brener 2007), and the presence of snow (Begzsuren et al. 2004) or frost (Buttolph and Coppock 2004). These variables should not be considered part of the traditional non-equilibrium concept, and therefore their effects need to be studied on a case-by-case basis.

Management implications

The non-equilibrium concept has clear implications for sustainable rangeland management. Our work underlines that rangelands with relatively stable rainfall patterns, and those with access to water or key resources, are potentially vulnerable to degradation. Especially in settings with highly variable rainfall, stabilizing the number of grazing animals through access to water sources, key resources, or artificial fodder supplementation can have a potentially severe impact on rangeland condition (Illius and O'Connor 2000). Grazing management in such areas should incorporate strategic rest periods to enable sustainable long-term use (Müller et al. 2011). Such rest periods effectively mimic natural fluctuations in herbivore populations, which are an important characteristic of undegraded rangelands. In turn, rangelands under highly variable rainfall regimes are unlikely to suffer from degradation unless key resources or water points play an important role.

Our analysis clearly supported the primary focus of the non-equilibrium concept for rangelands on climatic variability, rather than aridity per se. We believe that our map of the CV provides a realistic global overview of rainfall variability. This can be translated into a map of locations not vulnerable and those potentially vulnerable to degradation (Fig. 1; Supplement). Our approach is based on a single, globally consistent method, and provides an easy means to check rainfall variability at any given location or compare different locations. On this basis, we hope our map will be a useful resource for both ecologists and land managers that may quickly check whether grazing degradation should be a main concern under their given climatic situation.

Conclusion

We found strong support for the non-equilibrium concept in rangelands, with zonal degradation (i.e., uncoupled from the presence of water or key resources) occurring almost exclusively in areas with a CV of rainfall of less than 33%. Consistent and transparent criteria to define both rainfall variability and degradation will be critically important in future research. Similarly, future research should carefully consider a priori whether the non-equilibrium concept reasonably can be expected to hold. For example, supplementation feeding of animals may be beyond the domain of the concept. From a management perspective, our work underlines that rangelands with relatively stable rainfall patterns, and those with access to water or key resources, are potentially vulnerable to degradation. Appropriately timed rest periods are important in such situations to avoid degradation.

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SUPPLEMENTAL MATERIAL

Appendix A

Literature covered by this review (*Ecological Archives* A022-025-A1).

Appendix B

Tukey post hoc test of the different categories from Fig. 3, tested against each other (*Ecological Archives* A022-025-A2).

Appendix C

Global annual mean precipitation map (based on Hijmans et al. 2005, in mm) combined with our product indicating areas with a precipitation CV $< 33\%$ (*Ecological Archives* A022-025-A3).

Supplement

High-resolution tiff file of the map on climatic variability based on 18 669 climate stations (*Ecological Archives* A022-025-S1).