

Cattle dynamics in African grazing systems under variable climates

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Abstract

Researchers and managers debate the relevance of non-equilibrium dynamics in rangelands, where ungulate populations are more closely associated with abiotic events than forage availability, and density independence is common. Rules-of-thumb state that precipitation below 300–400 mm per year or an annual coefficient of variation above 30% makes non-equilibrium dynamics likely. These have not been well tested. Three applications of an integrative model to African ecosystems were modified so that each modeled twenty 50 km² parcels and a single population, cattle. Precipitation histories were altered so that annual rainfall varied from 100 to 1000 mm and coefficients of variation from 0% to 60%, and simulations run. For populations that did not collapse, density dependence was quantified. In two sites under their average rainfall, the frequency of density independence increased as rainfall variation increased, but in the most forested of the three sites, the pattern was opposite. There, a transition sometimes occurred where tree cover increased, increasing competition for grasses and density dependence in cattle. Overall, results were heterogeneous, with dynamics sensitive to traits in parcels and subtle climate changes. The rules-of-thumb should not be applied indiscriminately. Simulations suggest annual precipitation and its variability cannot be directly linked to likely dynamics of ungulates within arid and semi-arid African systems.

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Keywords: Coefficient of variation; Density dependence; Ecosystem modeling; Non-equilibrium; Precipitation; SAVANNA

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1. Introduction

In recent years range science has been buffeted by ideas so influential as to be considered by some a paradigm shift (Behnke and Scoones, 1993; Briske et al., 2003; Ellis and Swift, 1988; Sullivan, 1996 judge it not to be a shift). Prior to the 1980s, the science was dominated by Clementsian ideas of equilibriums between plants and herbivores around predictable stable states (Clements, 1916)—the ‘balance of nature’ was the dominant paradigm and biotic relationships were emphasized (Egerton, 1973). In that view, herbivore populations compete for forage with their rate of energy intake reflected in their rates of reproduction and mortality, so that the populations fluctuate around some equilibrium or stable state. Managers of semi-arid and arid rangelands adjusted grazing pressure to maintain animal populations near that calculated stable state (Caughley, 1979; Peel et al., 1999) or some other desired level. Authors working in arid and semi-arid lands noted that the areas have more variable precipitation and more frequent droughts than more mesic rangelands (Conrad, 1941; Ellis and Galvin, 1994; Nicholson, 1980). In such systems, herbivore populations can vary markedly. Caughley et al. (1987) cited only a centripetality in herbivore populations in New South Wales, as the animals were buffeted by variable rainfall. In the Turkana District of northern Kenya, Ellis and Swift (1988) recorded large variations in livestock numbers in response to low and extremely variable precipitation, but emphasized that the system was persistent. Ellis and Swift (1988) hypothesized a non-equilibrium (Wiens, 1984), disequilibrium (Behnke et al., 1993), or density-vague (DeAngelis and Waterhouse, 1987; DeAngelis, 1995) system in which livestock populations increased during years of ample rainfall, then crashed during droughts, with populations at other times rarely becoming high enough to be limited by primary production, or in turn to have significant affects upon vegetation. Vegetation and livestock dynamics were only weakly linked, competition for forage was low, and the system was dominated by abiotic factors. In semi-arid systems, attempts to maintain herbivores at carrying capacity have caused overgrazing and inefficient livestock production (Briske et al., 2003; Ellis and Swift, 1988; Ellis, 1994; Oba et al., 2003; Sullivan and Rohde, 2002; Vetter, 2005; Westoby et al., 1989).

The hypothesis that secondary production is in some cases only weakly related to primary production was labeled non-equilibrium dynamics, to contrast it with equilibrium dynamics (Ellis, 1994). Both terms have been misunderstood. Those immersed in the debate now recognize that the terms do not refer to an absolute disassociation or complete association between primary and secondary production through time (Briske et al., 2003; Bayer and Waters-Bayer, 2004; Ellis et al., 1993; Illius and O'Connor, 1999; Vetter, 2005); all systems are in disequilibrium to some degree (Illius and O'Connor, 1999). That said, terminology is helpful that labels systems where disequilibrium is low to moderate as distinct from those where disequilibrium is high. We therefore use the established terms equilibrium and non-equilibrium dynamics, recognizing them as useful caricatures of reality. However, there remain many who see the terms as absolutes. For example, many in rangeland management and the social sciences believe stocking on arid rangelands cannot affect primary production, except in limited areas (Sullivan and Rohde, 2002; reviewed in Vetter, 2005) and that there is continued overemphasis on equilibrium dynamics in ecology and some social sciences (Sullivan, 1996; Scoones, 1999). Others see evidence for non-equilibrium dynamics as unconvincing (Cowling, 2000), that it risks being applied too broadly (Fernandez-Gimenez and Allen-Diaz, 1999), or that apparent non-equilibrium

dynamics in rangeland populations are artifacts due to comparing weakly associated ecosystem attributes, and systems would appear in equilibrium if appropriate resources, such as key resource areas, were used in comparisons (Illius and O'Connor, 1999, 2000).

In addition, researchers have defined rules-of-thumb for a cutoff in the coefficient of variation (CV) in annual precipitation or in precipitation amounts that delimits equilibrium from non-equilibrium ecosystems. Shepherd and Caughley (1987) used their observations on sheep and kangaroo ecology to estimate that areas with CVs in interannual rainfall approaching 30% or greater would tend to be non-equilibrium. Ellis et al. (1993) used 30% and Ellis and Galvin (1994) used 33% as the cutoffs past which systems tend to be non-equilibrium. Coppock (1993) predicted that areas below 400 mm annual rainfall would tend to be non-equilibrium, and Briske et al. (2003) cite 300 mm or below as the cut-off. Ellis (1994) described hypotheses of rangeland dynamics in Africa based upon these rules-of-thumb. These rules are based on field work in sites with CVs greater than 40% (e.g., Ellis and Swift, 1988), plus more general experience within rangelands, and have not been thoroughly assessed (Fernandez-Gimenez and Allen-Diaz (1999) did an assessment at three Mongolian sites). The dichotomous nature of the rules-of-thumb may be contributing to the strict but erroneous interpretation of equilibrium and non-equilibrium dynamics in herbivores.

Three related aspects of rangeland dynamics have been focused upon in the equilibrium/non-equilibrium debate: (1) the dynamics of herbivore populations on semi-arid and arid lands (Ellis and Swift, 1988; Illius and O'Connor, 1999; Sullivan and Rohde, 2002), (2) the likelihood of rangeland degradation (Boone, 2005; Oba et al., 2003; Vetter, 2005), and (3) the states and transitions of those lands (Friedel, 1991; Scheffer et al., 2001; Westoby et al., 1989; reviewed in Briske et al., 2005). We address each here, but herbivore dynamics are our focus. Under non-equilibrium dynamics, herbivore populations are limited by abiotic factors such as precipitation and the frequency of drought, so that their populations in a given year are not closely related to their populations in the previous year—they are density independent. In situations tending toward equilibrium, the herbivore population grows to be limited by forage availability (or some other constraint, such as disease), and intraspecific competition dominates. In these density dependent systems, the population in a succeeding year is closely related to that in the previous year. Researchers have devised rigorous methods of quantifying density dependence within populations (e.g., Ricker, 1954; Royama, 1992; Wang et al., 2006). Characterizing populations in this way allowed us to place simulated responses along a continuum of disequilibrium.

In past assessments we have successfully applied an integrative ecosystem model to three areas in East and South Africa. The applications are spatially explicit and process-based, so that variations in precipitation will cause variations in forage quality and quantify, in turn in herbivore condition indices, and potentially variation in populations. Land cover in each of the sites is semi-arid African savanna and mixed classes, but the sites vary in such things as their precipitation history, seasonality, topographic diversity, and land use histories. Aspects of the applications were standardized to ease interpretation. We modified the 30+ year precipitation histories for each of the sites to vary rainfall across a range from very arid to almost non-arid (Ellis and Galvin, 1994), and from zero interannual variability to extreme variability, and conducted simulations. Measures of density dependence quantified the association between simulated population sizes from year to year, a reflection of equilibrium or non-equilibrium dynamics.

2. Methods

2.1. Ecosystem model

We use a model that includes the important processes and interactions in semi-arid and arid ecosystems called SAVANNA. Development of the SAVANNA ecosystem model began 20 years ago (Coughenour, 1985), with the model updated and applied widely since (e.g., Boone et al., 2002, 2005; Coughenour, 1992; Christensen et al., 2004; Eastman et al., 2001; Ludwig et al., 2001; Thornton et al., 2003). SAVANNA divides landscapes into a series of square cells, and for each cell, models ecological processes. The model processes spatial data that characterize the cells as to elevation, slope, aspect, and vegetation type. Weather data used include monthly precipitation from a series of stations, plus detailed data for one station that includes minimum and maximum temperature, humidity, wind speed, radiation, and CO₂ concentration. Plants and animals are represented as functional groups, which may be individual species, or groups of species. Each modeled week, plants within SAVANNA compete for soil moisture, light, space, and nutrients. In each time step, plants may produce seed, may be browsed, may outcompete others and gain ground cover, or may die. Animals are distributed on the landscape based on a suitability index derived from forage quality, quantity, elevation, slope, distance to water, woody cover, and temperature. Ungulates feed upon the forage and gain energy from it. Energy is expended through basal metabolism, travel, and lactation. Energy gains and expenditures are reflected in animal condition indices, which influence rates of weight gain, reproduction, and mortality (see Boone, 2000 for more detail; Ellis and Coughenour, 1998).

2.2. Study areas

Three African sites where the SAVANNA model had been successfully applied were used in these analyses. The sites (Fig. 1) were:

Southern Kajiado District, Kenya, where a SAVANNA application merged with the PHEWS pastoral household welfare simulator was used to explore effects of land tenure changes on Maasai (Boone, 2005; Boone et al., 2005; Thornton et al., 2006). The site is 10 746 km², which includes Amboseli National Park and the slopes of Mount Kilimanjaro and the Chyulu Hills. Rainfall ranges from about 400 to 800 mm in the study area, with more rainfall on the mountain slopes, and gradating higher to the north. Annual rainfall from 1969 to 1998 averaged 550 mm, with a coefficient of variation (CV) in annual year-to-year precipitation of 27.6%. Grasslands, wooded grasslands, and brushlands dominate the landscape. Wildlife disperse from Amboseli in the wet season, and graze alongside livestock owned by Maasai and others. Seven plant functional groups were included in the SAVANNA application, representing palatable grasses, palatable forbs, unpalatable grasses and forbs, swamps represented by papyrus (*Cyperus papyrus* L), palatable and unpalatable shrubs, and deciduous woodlands, which were mostly acacias (*Acacia* sp.). Nine animal types were modeled, wildebeest (*Connochaetes taurinus* Lichtenstein), zebra (*Equus quagga* Boddaerti), African buffalo (*Syncerus caffer* Sparrman), grazing antelope, browsing antelope, elephants (*Loxodonta africana* Blumenback), plus three livestock species, cattle, goats, and sheep. For more detail, such as antelope species in the grazing and browsing functional groups, see Boone et al. (2005).

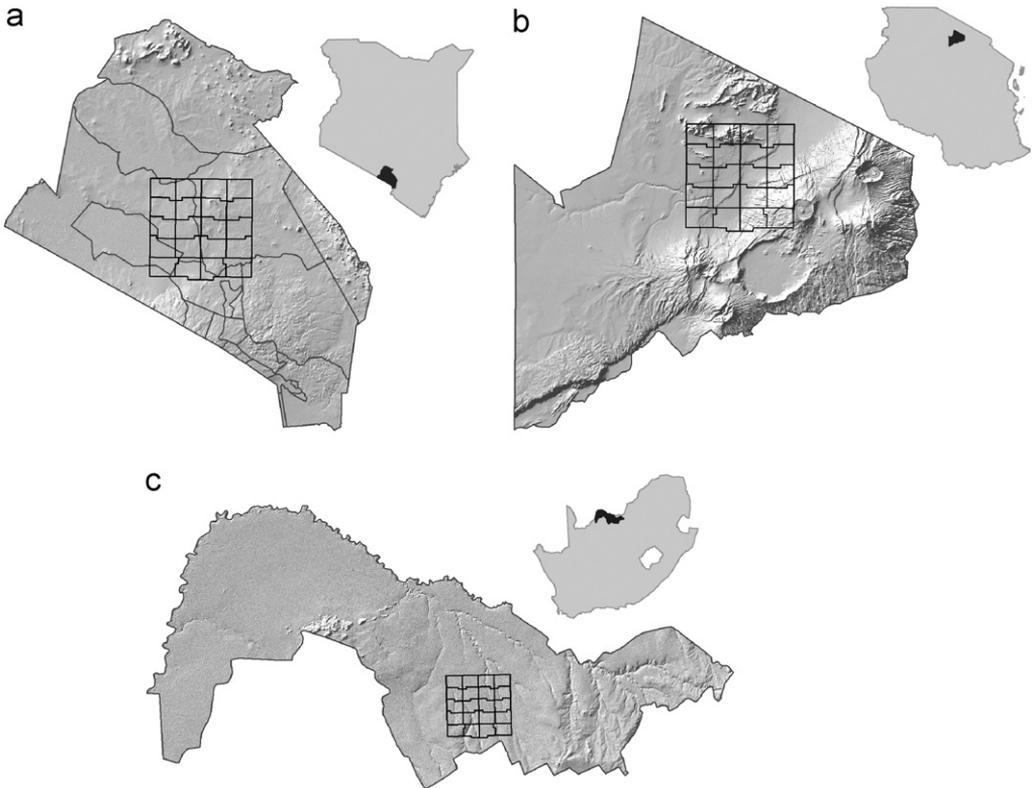


Fig. 1. Simulations were conducted in (a) southern Kajiado District, Kenya, (b) Ngorongoro Conservation Area, Tanzania, and the (c) North-West Province, South Africa. The boundary of Amboseli National Park and group ranches are shown in Kajiado (a) and Vryburg District in the North-West Province (c). In each case, the 1000 km² area modeled, composed of twenty parcels 50 km² each, is shown in black, topography is shaded, and areas are shown within their countries in insets. For scale, in each case the 1000 km² areas modeled are 32 km across.

Ngorongoro Conservation Area, Tanzania, was our first application of the PHEWS model joined with SAVANNA. The conservation area (8288 km²) is unique in its long history of multiple-use management, with land use needs by wildlife, Maasai, and their livestock considered in decision making. An integrated assessment was conducted that explored potential effects of cultivation, human population growth, improved veterinary care, changes in water availability, and changes in ungulate access to grazing lands (Boone et al., 2002, 2006; Galvin et al. 2004; Thornton et al., 2003). The site is topographically diverse, spanning from mountain tops of volcanic origin to the Serengeti Plains, and includes world-famous Ngorongoro Crater, an important wildlife viewing area, and Olduvai Gorge, where remains of early man were found. Climate is diverse as well, with more than 1000 mm of rainfall annually within the Highlands Forest Reserve, and less than 450 mm rainfall in the southern Serengeti Plains, in the shadow of the Ngorongoro mountains. Across the entire area, from 1963 to 1992, an average of 800 mm of rain fell each year, with a CV of 20%. More than 60 000 Maasai move their livestock seasonally from the highlands to the plains and back again, and practice small scale cultivation. In the SAVANNA application, we included seven plant functional groups: palatable grasses, palatable forbs,

unpalatable grasses and forbs, palatable and unpalatable shrubs, evergreen trees of the highland forests, and deciduous woodlands mostly of acacia. Eleven animal groups were modeled: migratory wildebeest, zebra, and grazing antelope, plus resident zebra and grazing antelope (resident wildebeest live mostly in Ngorongoro Crater, which was not included in this model), browsing antelope, African buffalo, elephants, plus three livestock species, cattle, goats, and sheep. Boone et al. (2006) provides more detail about the model application.

North-West Province, South Africa, where the SAVANNA model was linked with a mathematical programming model to judge the usefulness of climate forecasts produced by the national weather bureau to livestock producers (Boone et al., 2004; Thornton et al., 2004). The study area included five districts, two used for commercial livestock production (Vryburg 1 and 2), and three used communally by pastoralists (Kudamane, Ganyesa, and Taung). A gentle gradient in rainfall spans from an average of 500 mm yr⁻¹ on the eastern edge to 300 mm yr⁻¹ along the Orange River and the Kalahari Desert. Across the site, rainfall averages 400 mm yr⁻¹, and is extremely patchy and variable, with a CV from 1960 to 1995 of 37.4%. The area is thornveld and shrub bushveld. Some areas are in agriculture, but most of the area is used for livestock grazing. The SAVANNA application had seven plant functional groups, including perennial grasses of high, moderate, and low palatability, annual grasses, acacia shrubs, camphorbush shrubs (*Tarchonanthus camporatus*) and acacia trees. Five animal species were modeled, cattle, goats, sheep, horses, and donkeys.

2.3. Model modifications

The model applications as described represented their ecosystems reasonably (the cited works include assessments, for example), ecosystems that span in annual rainfall from 400 to 800 mm, and CVs of annual rainfall from 20% to 37.4%. We sought to retain the multiple representations of African grazing systems, but to standardize the applications somewhat to ease interpretation of the results. Household economics (e.g., from PHEWS) were not represented in these simulations. A 1000 km² subset of each study area was modeled at 1 km² resolution (i.e., a 32 × 32 km² landscape, with 24 cells in the most southern row not modeled). The locations of the 1000 km² areas were (Fig. 1): Kajiado: north of the slopes of Mount Kilimanjaro, centered on the border of Imbirikani and Olgululi/Lolorashi Group Ranches, and including the southern third of Amboseli National Park (37.309 decimal degrees latitude, -2.470 longitude to 37.597 latitude, -2.759 longitude); Ngorongoro: from the Gol Mountains to the slopes north of Ngorongoro Crater, including the Salai Plains (35.339, -2.785 to 35.627, -3.074); North-West Province: within Vryburg 1 District, north of the northeast extension of Ganyesa District (24.140, -26.357 to 24.464, -26.071).

Interpreting population responses of up to 11 animal functional groups as they change in compensatory ways can be confusing. In each application, plants were modeled as in their original applications, but we reduced the animals modeled to a single species, cattle (following Boone and Hobbs, 2004; Boone et al., 2005). The densities of cattle were set as in the original applications (Kajiado: 19 cattle/km²; Ngorongoro: 35 cattle/km²; North-West Province: 14.3 cattle/km²). Small changes were made to the energy requirements of the cattle until their populations remained relatively constant across a 40 year simulation, although the populations continued to change in response to wet and dry years. As part of a larger analysis, the landscape was fragmented into successively smaller parcels, and

populations modeled. The analyses reported here used the landscape divided into 20 parcels, each 50 km², to provide replication across space.

2.4. Weather data

Each of the applications had precipitation data from 30 or more years (Kajiado: 1969–1998, 47 stations; Ngorongoro: 1963–1992, 55 stations; North-West Province: 1960–1995, 166 stations), and temperature data for the same periods for a focal station. In our 40 year simulations, if simulations reached the end of the weather data, the model read again from the beginning of the set. We sought to alter the rainfall amount and interannual CV in rainfall for each study area. To decrease CV in annual rainfall, for example, it is intuitive to decrease precipitation from a year of high rainfall and increase rain to a year of low rainfall. That alters CV, but such a change may remove the seasonality and spatial patterning in the rainfall. Instead, we used a coefficient applied to the deviation from the mean and an offset value applied to the mean to essentially stretch or compress rainfall for each station, yielding appropriate CVs and annual rainfall amounts, while retaining seasonality and the spatial patterning of relative rainfall amounts. The following formula was applied to each monthly weather station rainfall record,

$$R_1 = (R_o - \bar{R}) * C + O,$$

where \bar{R} is the long-term annual average in total rainfall (mm) across the site, R_o is the rainfall (mm) at a given place in a given month, C is a coefficient that increases (> 1) or decreases (< 1) variation around the mean rainfall, O is an offset to ensure the end result has the long-term annual average that is desired, and R_1 is the new monthly rainfall value (in mm and ≥ 0) for the given place. The parameters C and O were adjusted incrementally until the desired annual rainfall and CV was achieved. We used a custom program to modify the average rainfall across years to span from 100 to 1000 mm (100 mm, 200, 300, ..., 900, 1000 mm) and the CV across years to span from 0% to 60% (0%, 5%, 10%, ..., 55%, 60%). It was not possible using our methods to generate CVs equal to 0%; in practice, the minimum CV we could attain was about 0.3%.

2.5. Analysis

A goal was to quantify density dependence in population responses, related to equilibrium and non-equilibrium dynamics. In simulated populations, there were three general trends. In responses we will label type I, the population tended to stay bounded, and are related to typical conditions or sites. Type II responses characterized populations that declined rapidly, approaching zero and are related to very poor conditions. Type III populations increased rapidly, then declined rapidly as the site was overstocked, and are related to very good conditions. Methods used to calculate density dependence would be misleading for type II and III responses, so these were segregated. We used the statistical package R (The R Foundation for Statistical Computing, Vienna, Austria) to calculate a series of statistics to aid in defining types I–III responses, and to quantify density dependence. Each simulated 40 year time series was fitted with a broken line regression of the natural log of the population against year, a linear regression of the logged population on year, and the Ricker model (see below) yielding an estimate of density dependence.

Specifically, the broken line regression is given by the equations:

$$\begin{cases} \ln N_t = a_1 + b_1 \text{ year}_{t1}, & \text{year}_{t1} \leq bp, \\ \ln N_t = a_2 + b_2 \text{ year}_{t2}, & \text{year}_{t2} > bp, \end{cases}$$

where bp is the breaking point in the broken line regression. The breaking point within each 40 year simulation, if present, was found by an iterative search from year 5 to year 35, with AIC calculate for each candidate year. The year with the lowest AIC, and a difference between minimum and maximum AIC ≥ 2.0 , was chosen as the breaking point bp . If the AIC for the broken line regression was lower than the AIC from the typical linear regression (i.e., $\ln N_t = a + b * \text{year}$) by 2.0, we chose the broken line regression as the best approximating model. If regression results were significant ($P \leq 0.05$), slopes representing annual rates of increase were reported for b_1 and b_2 , the two parts of the broken line, or for b , the entire line. Otherwise the slopes were reported as zero.

The Ricker model (Ricker, 1954) fitted population growth:

$$r_t = a + bN_t,$$

where r_t is population growth rate at year t and is calculated as differences in the natural logs of population sizes of two successive years, i.e., $r_t = \ln N_{t+1} - \ln N_t$, N_t is the difference in population size at time t , a is the population growth rate in absence of density dependence, and b is the parameter reflecting the strength of density dependence in the population response. Density independent responses received a b of 0. In addition to these analyses, our programs calculated mean population size and its coefficient of variation through simulations, mean growth rate and its variation, plus measures reflecting rangeland status, such as tree cover, shrub cover, mean leaf biomass, root biomass, and leaf biomass for individual herbaceous functional groups.

Prior to labeling simulations as type I, II, or III, we calculated a *ratio* of the population in the last 10 years of simulation to the initial population. We then labeled simulations as type I unless $b_1 < -0.1$ and the *ratio* < 0.2 , which were labeled type II, and if $b_1 > 0.005$ and $b_2 < -0.005$ and *ratio* < 0.2 , the response was a type III. That is, we labeled simulation responses as type I unless their initial populations declined rapidly and stayed below 20% of the initial population (type II), or if they increased initially then decreased, and ultimately were below 20% of the initial population (type III).

Results are presented graphically, with tests to quantify the significance of some differences. We used tree classification to relate annual rainfall and annual CV in rainfall to the frequency of density dependence in responses, not for purposes of prediction, but as alternative views of results of our simulations.

3. Results

For each area, 130 precipitation records were created, spanning from 100 to 1000 mm annual rainfall, and CV from 0% to 60% (Fig. 2), and simulations done. The proportions of types I, II, and III responses for the 20 parcels simulated with each precipitation record are shown in Fig. 3. Mean annual rainfall of 100 mm led to a large proportion of type II responses in each site, with few animals able to be supported. Otherwise, the proportions varied markedly between sites. In Kajiado and the North-West Province, very low rainfall (200–300 mm) and low annual CV led to more type II responses than at higher CVs

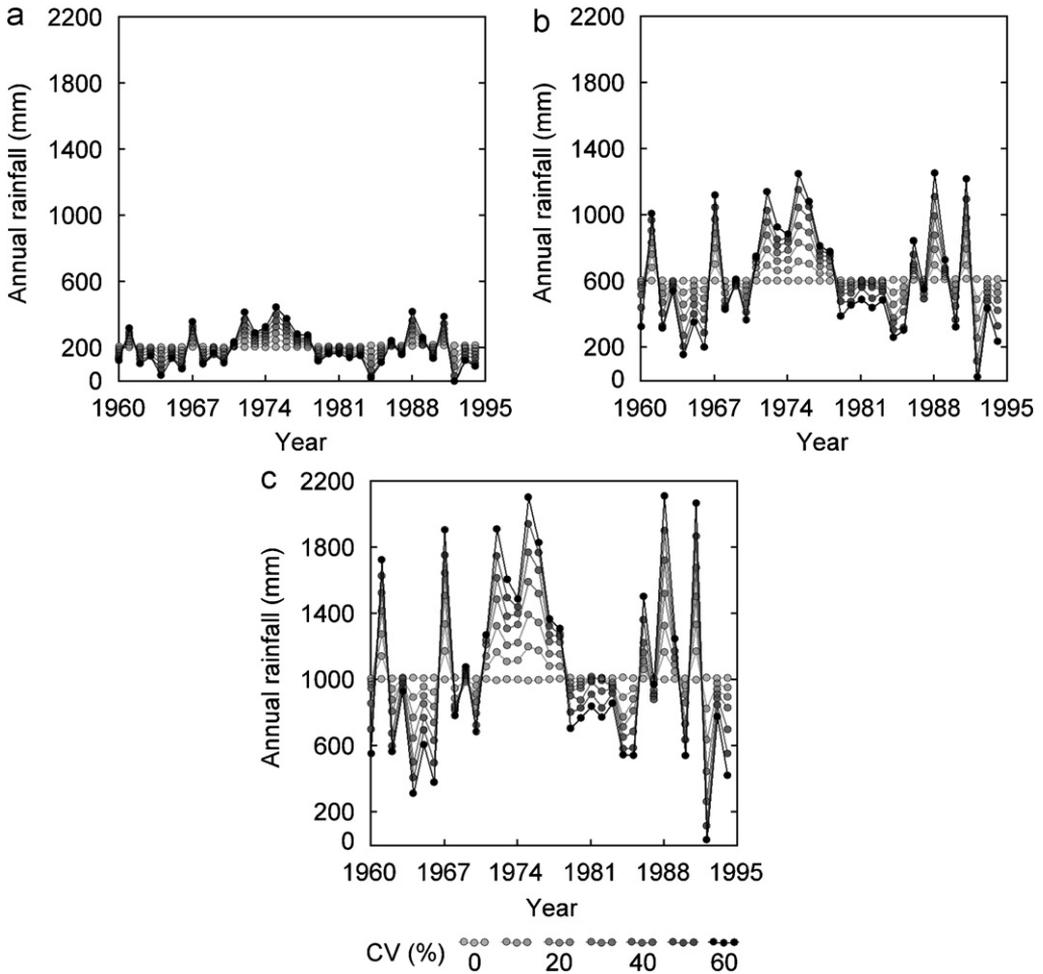


Fig. 2. The precipitation record from 1960 to 1995 from the North-West Province, South Africa, adjusted to yield annual rainfall from (a) 200 mm, (b) 600 mm, and (c) 1000 mm, and interannual coefficients of variation (CV) from 0% to 60%. In practice, rainfall for each area was incremented by 100 mm from 100 to 1000 mm, and CV by 5% from 0% to 60%.

(Fig. 3). The low CVs led to subtle increases in populations (below the threshold used to label a response type III), then declines, yielding a type II classification. High CVs led to increasing type II responses in Kajiado and Ngorongoro, but not in the North-West Province, perhaps because of the already high observed CV in rainfall in the North-West Province. Type III responses were seen at higher levels of rainfall (600 mm or above) in Kajiado District only (Fig. 3). Type III responses may not have occurred in Ngorongoro because the relatively high initial densities of cattle may have prevented them from increasing dramatically then declining. In Fig. 3c, the North-West Province, in the region that is of 600–800 mm rainfall and $CV < 30\%$, type I population trends have higher populations (paired t -test, $df = 18$, $P < 0.001$) and lower interannual variation ($P < 0.001$) than those that were type II. There was less highly palatable grass in the parcels that

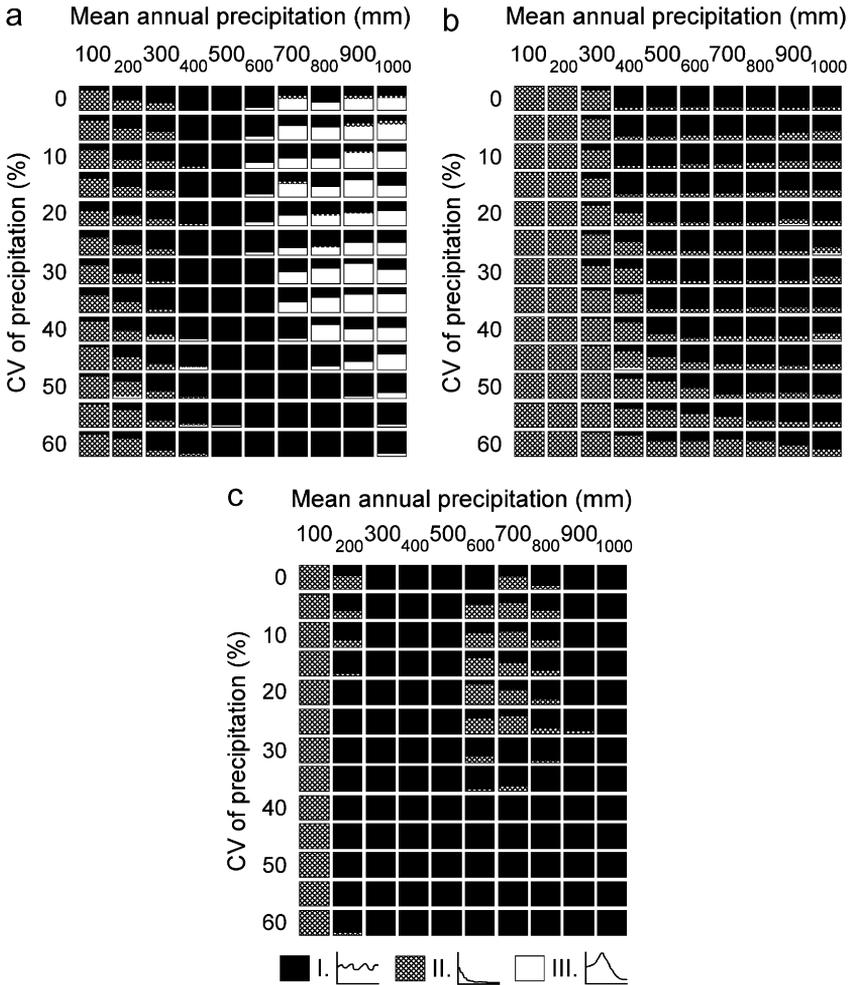


Fig. 3. General population responses for all combinations of annual rainfall and interannual coefficients of variation (CV), for (a) Kajiado, (b) Ngorongoro, and the (c) North-West Province. Each box depicts the proportions from 20 parcels that were type I (relatively bounded), type II (declining rapidly), and type III (increasing rapidly, then declining rapidly).

showed a type I response (14 g/m^2 on across seasons, versus 17 g/m^2 for type II responses, $P < 0.001$) and livestock populations with density dependent dynamics were lower (mean population = 1660) than those that were density independent (mean = 2610; ANOVA, $P < 0.01$), but whether that was a cause for the different responses or an effect from them is not clear. Differences in other ecological responses (e.g., leaf biomass, tree cover, shrub cover) were small, suggesting a biocomplex threshold in the North-West Province, where properties of the ecosystem make cattle dynamics particularly sensitive to climatic patterns at the thresholds seen (Fig. 3c), and ecosystem states can shift dependent on whether populations increase or decrease by small amounts.

We then focused on rainfall amounts closest to those observed for the sites and for which simulations were made (600 mm for Kajiado, 800 mm for Ngorongoro, and 400 mm

for North-West Province), and looked only at type I responses. For two of our sites (Kajiado and North-West Province), population dynamics were as expected, with increasing CVs leading to a higher proportion of density independent responses (Figs. 4ia–ic)—a weaker link between forage availability and animal population as interannual rainfall variability increased. The pattern was opposite but weaker in Ngorongoro (Fig. 4ib). Populations with density dependent responses had much higher tree cover in Ngorongoro, compared to density independent responses (Fig. 4iib), whereas the values were similar across density categories in Kajiado and the North-West Province (Figs. 4iia and iic). The differences seen are due to tree encroachment in Ngorongoro.

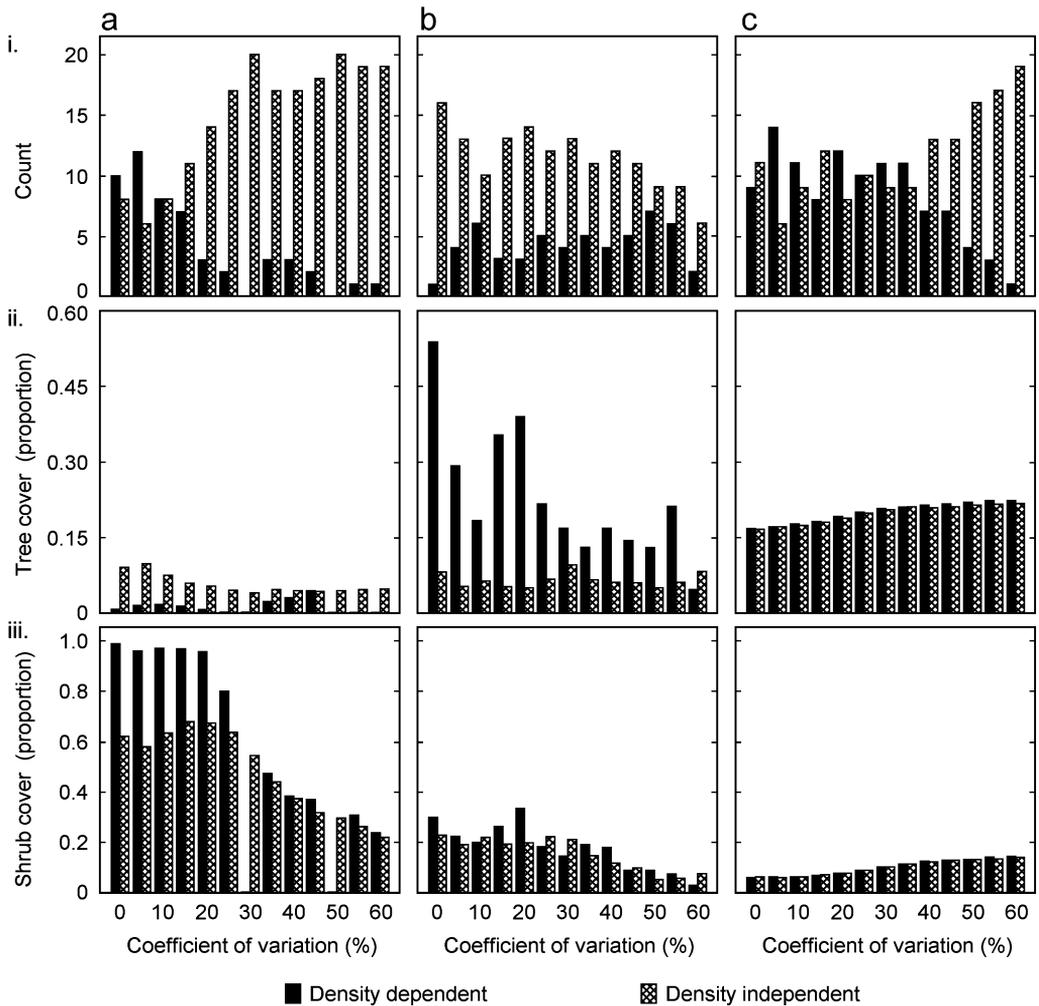


Fig. 4. Considering type I responses only and rainfall amounts on-par with those observed, the (i) count of density dependent (solid) and density independent (hatched) responses are compared for (a) Kajiado at 600 mm annual rainfall, (b) Ngorongoro at 800 mm, and the (c) North-West Province at 400 mm. The (ii) average tree cover and (iii) shrub cover for parcels with density dependent and independent responses are shown.

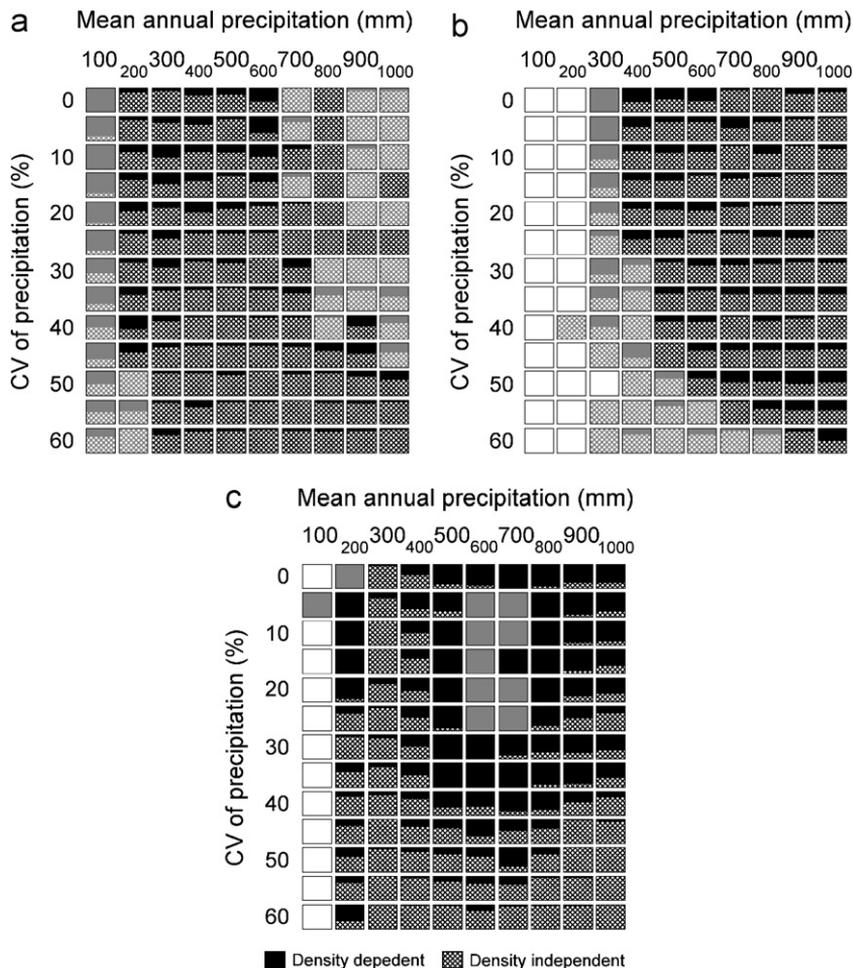


Fig. 5. Considering type I responses only, the portion of parcels that exhibited density dependent and density independent responses across all annual rainfall and interannual coefficient of variation (CV) combinations, for (a) Kajiado, (b) Ngorongoro, and the (c) North-West Province. Each box represents a maximum of 20 parcels; proportions calculated from 10 or fewer parcels with type I responses (see Fig. 2) are shown in gray, and combinations with no type I responses are shown empty.

Differences in shrub cover, for example, appear not to be important in the relationship (Fig. 4iii).

Returning to the full range of rainfall and using type I responses only, Fig. 5 depicts for each area the proportion of the 20 parcels simulated for each rainfall/CV combination that were density dependent or density independent. The pattern of responses is complex, but in general, simulations with low CV yielded more density dependent responses. Density dependence was more likely in the lowest rainfall (e.g., ≤ 200 mm, except in Ngorongoro where type I responses were rare under those climatic patterns), less likely with somewhat more rainfall, more likely at intermediate rainfall levels (e.g., 500–700 mm) and less likely at the highest levels simulated (900 and 1000 mm). Responses are shifted to higher rainfall

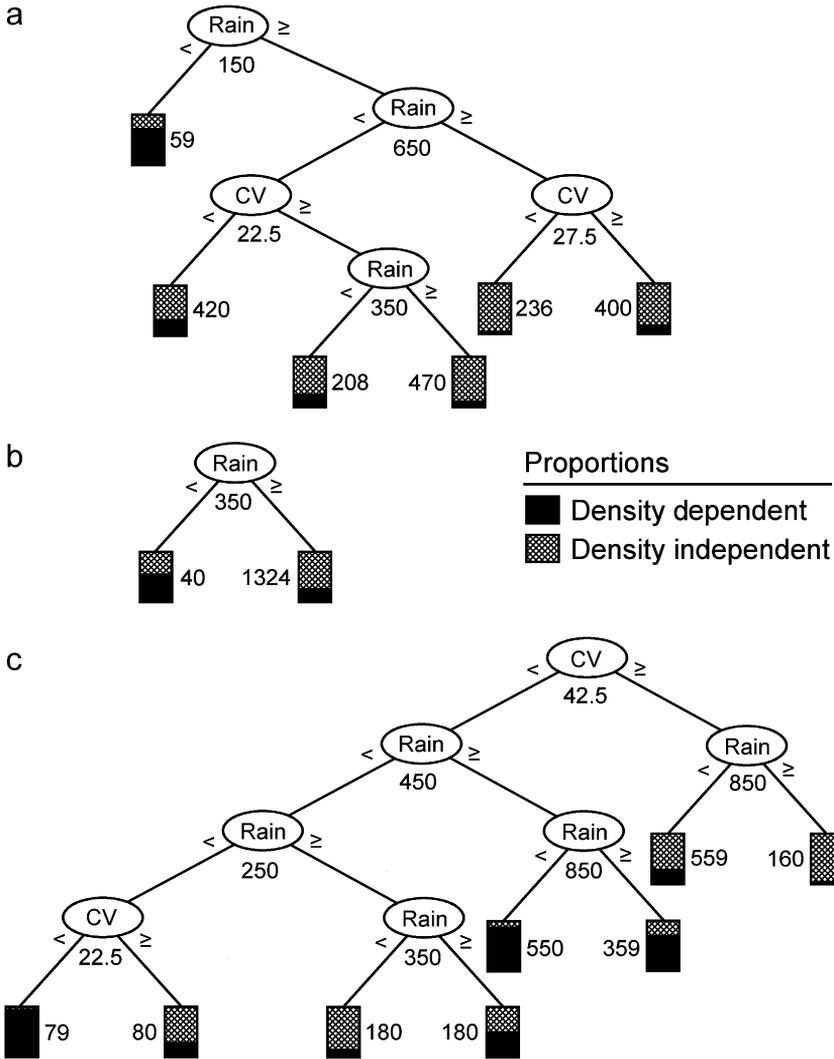


Fig. 6. Tree classifications discriminating proportions of density dependent and independent responses (Fig. 4) for (a) Kajiado, (b) Ngorongoro, and the (c) North-West Province. Variables that best discriminated groups or subgroups are labeled in the nodes, values at those splits are shown, and the number of cases in each leaf are labeled. Note that the values shown for splits are between values used in modeling, so that for Kajiado, a split with rainfall at 150 mm (not tested) denotes that rainfall at 100 mm (tested) would follow the left branch, and 200 mm (tested) would follow the right branch.

amounts in Ngorongoro, because of its greater annual rainfall. Tree classification discriminated proportions of density dependent and density independent responses (Fig. 6). In southern Kajiado, simulations with rainfall at 100 mm (i.e., <150 mm in Fig. 6a) yielded few type I responses ($n = 59$), but those were most often density dependent. Simulations with rainfall between 200 and 600 mm (i.e., <650 mm in Fig. 6a) had a higher proportion of density dependent responses than those 700 mm or above. In Ngorongoro, the tree that best discriminated responses had only one node; simulations

with 300 mm rainfall or less ($n = 40$; Fig. 6b) were more likely to be density dependent than those with higher rainfall. The tree for the North-West Province was more complex, with simulations with CVs of 45% and above splitting from the remainder first, then splitting again based on rainfall (Fig. 6c). For simulations with CVs 40% or less, those with rainfall between 500 and 800 mm ($n = 550$) were almost wholly density dependent. Simulations with rainfall 200 mm or less, and CVs 20% ($n = 79$) or less were nearly entirely density dependent.

4. Discussion

The overarching message from these analyses is that livestock population dynamics are complex, cautioning against a simplistic view of equilibrium and non-equilibrium dynamics, and the uncritical use of rules-of-thumb. Simulated livestock population responses showed very different dynamics in the three study areas (Fig. 3). Looking at rainfall levels similar to those in reality, the frequency of density dependences declined as interannual variability in rainfall increased in Kajiado and the North-West Province, but not in the other site (Fig. 4). In Kajiado and the North-West Province, increased variability in inter-annual rainfall caused enough variability in secondary production (e.g., die-offs related to droughts) that cattle dynamics were more often density independent. In Ngorongoro, which is the most forested of the three sites, a state-and-transition threshold (Friedel, 1991; Westoby et al., 1989) appears to have been identified, where tree cover can increase markedly with increasing frequency as the CV in rainfall declined. This transition increases competition for forage and makes a density dependent response in the livestock populations more likely (Fig. 4bii).

The original model applications were parameterized to represent the range of naturally occurring rainfall in the areas, with a given level of variation. Kajiado District and Ngorongoro include areas with rainfall near 400 mm annually and other areas where rainfall is 1000 mm. In contrast, the North-West Province site spans rainfall from about 300 to 500 mm. Our analyses using rainfall spanning from 100 to 1000 mm extrapolates beyond the original applications. The coefficients of variation in interannual rainfall, spanning from near 0% to 60% extrapolate beyond the original applications, and reality, as well. For example, no semi-arid site would have a CV of 0%, with rainfall amounts repeated perfectly from year-to-year. Our method of dividing population responses into three general categories, isolating those where populations remained bounded from those where transitions had occurred (Figs. 3, 5, 6), and focusing on modeled rainfall amounts similar to those observed (Fig. 4) helped isolate the effects of extrapolation.

Our results focused upon cattle in three pastoral areas, but the results should be qualitatively similar for wild and domestic ungulates of similar body mass. Intrinsic rates of population increase are associated with body mass, with large-bodied animals such as elephants (6000 kg) having low intrinsic rates of increase ($r = 0.022$; Moss, 2001), and small bodied animals such as blue duiker (*Cephalophus monticola* Thunberg; 5 kg) having high intrinsic rates of increase ($r = 0.490$; Fa et al., 1995). Density dependence is more common in rapidly increasing species, with populations able to recover from perturbations quickly (Caughley and Krebs, 1983; Ellis, 1994), although this has not been shown definitively.

Simulations were replicated spatially, with 20 parcels each 50 km² (5000 ha) in area modeled with each rainfall and CV combination. Fine scale differences in habitat affect

population responses (Fynn and O'Connor, 2000; Oba et al., 2003). Some parcels contained key resource areas (Illius and O'Connor, 1999, 2000; Scoones, 1992), some contained shrubs, some steep slopes. Had the animals had more area from which to select foraging areas, relatively bounded type I responses would have been more common (Ash et al., 2004; Boone and Hobbs, 2004; Boone et al., 2005). That said, a 5000 ha parcel is larger than the average commercial farm in the North-West Province, South Africa (4100 ha, Thornton et al., 2004), and 50 times larger than parcels group ranch members in southern Kajiado District typically receive during subdivision (Boone et al., 2005).

The generalized simulations are based on applications used in integrated assessment, and many of the caveats cited in Boone et al. (2004, 2005, 2006) apply here. We are comparing population dynamics within single systems, where the only feature altered between simulations for any given parcel is rainfall and its variability. If any parameters were incorrect, the ratio of density dependent to density independent population responses would presumably be reasonably robust. We altered precipitation amount and its variability. SAVANNA correctly models many relationships that follow from that, such as changes in storm frequency and cloud shading. However, temperature is modeled from observations, and these were not altered. Temperatures are correlated with precipitation (Trenberth and Shea, 2005). However, in East Africa, temperatures vary remarkably little throughout the year or across years (e.g., in southern Kajiado, intra-annual CV in maximum temperature averaged 4.5%, inter-annual CV is 0.3%). Any effect from this simplification would be greatest in the North-West Province of South Africa (intra-annual CV averaged 17.8%; inter-annual CV is 2.9%). Although beyond the scope of this effort, using multiple randomizations of the observed climate records in simulations would be helpful in generating standard errors around mean responses (e.g., Boone et al., 2005; Illius et al., 1998, 2000). Methods to classify population responses as density dependent or independent use relatively long trends, 30 years or more (Dennis and Tapper, 1994). Populations may be responding in a density dependent way in some years and a density independent way in other years (Vetter, 2005). Lastly, we considered other approaches to quantify the strength of relationships between primary and secondary production. Principally, we explored using multivariate correlation to relate climate, plants, and cattle. However, thousands of correlations of direct and indirect effects across multiple temporal scales of the changes in biomass in seven plant functional groups to changes in livestock populations would be overly complex and difficult to interpret.

Much has been written about the management of lands where non-equilibrium dynamics, or in our context where density independent responses, dominate (reviewed in Behnke et al., 1993). In summary, the emphasis shifts from tracking an ever-changing capacity of the landscape to support ungulates, to a system that is flexible across space and time, allowing pastoralist to take advantage of ephemeral or external resources (Ellis et al., 1993). Our results highlight the fine spatial and temporal scales at which ungulate dynamics may vary. In any simulation, cattle in one 50 km² parcel may exhibit density independent dynamics, whereas in another parcel, they may be density dependent, decrease rapidly (type II), or increase dramatically then crash (type III). Further, fairly subtle changes in precipitation amounts and variation sometimes altered livestock dynamics markedly. The rules-of-thumb authors have provided, such as 30% or 33% CV and rainfall below 400 mm (Coppock, 1993; Ellis et al., 1993; Ellis and Galvin, 1994) are clearly not intended as thresholds where dynamics shift dramatically (Coughenour, 2004), but our results suggest that changes across systems from those dominated by biotic to abiotic

interactions is even more heterogeneous than we had anticipated. System dynamics are influenced by a myriad of things, such as drought frequency, properties of soils, human population, annual versus perennial forage plants, and woody cover. Total annual precipitation and its variability cannot be directly linked to the likelihood of different dynamics of ungulates within arid and semi-arid systems.

We certainly are not the first to alter rainfall variability in analyses. For example, [Caughley et al. \(1987\)](#) used simulations to explore dynamics of sheep and kangaroos. However, these analyses are the first to explore population responses across a multiple African systems using a spatially explicit, process-based ecosystem model. [Owen-Smith \(2002\)](#) reminds us that exploring population dynamics alone, quantifying the rate of density dependence for example, would ideally be made more revealing by exploring the underlying relationships. Our analyses of climatic variation, ecosystem attributes, and livestock dynamics (e.g., [Fig. 4](#)) move us closer to that ideal.

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References

- Ash, A., Gross, J., Stafford-Smith, M., 2004. Scale, heterogeneity and secondary production in tropical rangelands. *African Journal of Range and Forage Science* 21, 137–145.
- Bayer, W., Waters-Bayer, A., 2004. Why is it so difficult to translate rangeland non-equilibrium theory into pastoral development practice? In: Vetter, S. (Ed.), *Rangelands at Equilibrium and Non-equilibrium: Recent Developments in the Debate Around Rangeland Ecology and Management*. Programme for Land and Agrarian Studies, University of the Western Cape, The Rhodes University Botany Department, and the Leslie Hill Institute for Plant Conservation, Cape Town, South Africa, pp. 68–70.
- Behnke, R., Scoones, I., 1993. Rethinking range ecology: implications for range management in Africa. In: Behnke, R., Scoones, I., Kerven, C. (Eds.), *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas*. Overseas Development Institute, London, UK, pp. 1–30.
- Behnke, R., Scoones, I., Kerven, C. (Eds.), 1993. *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas*. Overseas Development Institute, London, UK.
- Boone, R.B., 2000. Integrated management and assessment system training manual. Manual for IMAS, Global Livestock Collaborative Research Support Program, US Agency for International Development, University of California, Davis, California, USA.
- Boone, R.B., 2005. Quantifying changes in vegetation in shrinking grazing areas. *Conservation and Society* 3, 150–173.
- Boone, R.B., Hobbs, N.T., 2004. Lines around fragments: effects of fragmentation on large herbivores. *African Journal of Range and Forage Science* 21, 147–158.
- Boone, R.B., Coughenour, M.B., Galvin, K.A., Ellis, J.E., 2002. Addressing management questions for Ngorongoro Conservation Area using the Savanna Modeling System. *African Journal of Ecology* 40, 138–150.
- Boone, R.B., Galvin, K.A., Coughenour, M.B., Hudson, J.W., Weisberg, P.J., Vogel, C.H., Ellis, J.E., 2004. Ecosystem modeling adds value to a South African climate forecast. *Climatic Change* 64, 317–340.
- Boone, R.B., BurnSilver, S.B., Thornton, P.K., Worden, J.S., Galvin, K.A., 2005. Quantifying declines in livestock due to land subdivision in Kajiado District, Kenya. *Rangeland Ecology and Management* 58, 523–532.
- Boone, R.B., Galvin, K.A., Thornton, P.K., Swift, D.M., Coughenour, M.B., 2006. Cultivation and conservation in Ngorongoro Conservation Area, Tanzania. *Human Ecology* 34, 809–828.

- Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2003. Vegetation dynamics on rangelands: a critique of the current paradigm. *Journal of Applied Ecology* 40, 601–614.
- Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management* 58, 1–10.
- Caughley, C., 1979. What is this thing called carrying capacity? In: Boyce, M.S., Hayden-Wing, L.D. (Eds.), *North American Elk: Ecology, Behavior and Management*. The University of Wyoming, Laramie, Wyoming, pp. 2–8.
- Caughley, G., Krebs, C.J., 1983. Are big mammals simply little mammals writ large? *Oecologia* 59, 7–17.
- Caughley, G., Shepherd, N., Short, S.J., 1987. *Kangaroos, Their Ecology and Management in the Sheep Rangelands of Australia*. Cambridge University Press, Cambridge.
- Christensen, L., Coughenour, M.B., Ellis, J.E., Chen, Z.Z., 2004. Vulnerability of the Asian typical steppe to grazing and climate change. *Climatic Change* 63, 351–368.
- Clements, F.E., 1916. *Plant Succession and Indicators*. Carnegie Institute, Washington DC, USA.
- Conrad, V., 1941. The variability of precipitation. *Monthly Weather Review* 69, 5–11.
- Coppock, D.L., 1993. Vegetation and pastoral dynamics in the southern Ethiopian rangelands: implications for theory and management. In: Behnke, R., Scoone, I., Kerven, C. (Eds.), *Range Ecology at Disequilibrium: New Models of Natural Variability And Pastoral Adaptation in African Savannas*. Overseas Development Institute, London, UK, pp. 42–61.
- Coughenour, M., 2004. The Ellis paradigm—humans, herbivores and rangeland systems. *African Journal of Range and Forage Science* 21, 191–200.
- Coughenour, M.B., 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* 72, 852–863.
- Coughenour, M.B., 1992. Spatial modelling and landscape characterization of an African pastoral ecosystem: a prototype model and its potential use for monitoring drought. In: McKenzie, D.H., Hyatt, D.E., McDonald, V.J. (Eds.), *Ecological Indicators*, vol. 1. Elsevier Applied Science, New York, USA, pp. 787–810.
- Cowling, R.M., 2000. Challenges to the ‘new’ rangeland science. *Tree* 15, 303–304.
- DeAngelis, D.L., 1995. Equilibrium and nonequilibrium concepts in ecological models. *Encyclopaedia of Environmental Biology* 1, 687–695.
- DeAngelis, D.L., Waterhouse, J.C., 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* 57, 1–21.
- Dennis, B., Tapper, M.L., 1994. Density-dependence in time-series observations of natural-populations-estimation and testing. *Ecological Monographs* 64, 205–224.
- Eastman, J.L., Coughenour, M.B., Pielke Sr., R.A., 2001. The regional effects of CO₂ and landscape change using a coupled plant and meteorological model. *Global Change Biology* 7, 797–815.
- Egerton, F.N., 1973. Changing concepts of the balance of nature. *Quarterly Review of Biology* 48, 322–350.
- Ellis, J., Coughenour, M.B., 1998. The SAVANNA integrated modelling system. In: Squires, V., Sidahmed, A. (Eds.), *Drylands: Sustainable use of Rangelands in the Twenty-First Century*. IFAD Technical Reports, Rome, pp. 97–106.
- Ellis, J., Galvin, K.A., 1994. Climate patterns and land-use practices in the dry zones of Africa. *Bioscience* 44, 340–349.
- Ellis, J.E., 1994. Climate variability and complex ecosystem dynamics: implications for pastoral development. In: Scoones, I. (Ed.), *Living with Uncertainty: New Directions in Pastoral Development in Africa*. Intermediate Technology Publications, Northern Yorkshire, UK, pp. 37–46.
- Ellis, J.E., Swift, D.M., 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management* 41, 450–459.
- Ellis, J.E., Coughenour, M.B., Swift, D.M., 1993. Climate variability, ecosystem stability, and the implications for range and livestock development. *Rethinking range ecology: implications for rangeland management in Africa*. In: Behnke, R., Scoone, I., Kerven, C. (Eds.), *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas*. Overseas Development Institute, London, UK, pp. 31–41.
- Fa, J.E., Juste, J., del Val, J.P., Castroviejo, J., 1995. Impact of market hunting on mammal species in equatorial Guinea. *Conservation Biology* 9, 1107–1115.
- Fernandez-Gimenez, M.E., Allen-Diaz, R., 1999. Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology* 36, 871–885.
- Friedel, M.H., 1991. Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management* 44, 422–426.

- Fynn, R.W.S., O'Connor, T.G., 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology* 37, 491–507.
- Galvin, K.A., Thornton, P.K., Boone, R.B., Sunderland, J., 2004. Climate variability and impacts on East African livestock herders: the Maasai of Ngorongoro Conservation Area, Tanzania. *African Journal of Range and Forage Science* 21, 183–189.
- Illius, A.W., O'Connor, T.G., 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* 9, 798–813.
- Illius, A.W., O'Connor, T.G., 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* 89, 283–294.
- Illius, A.W., Derry, J.F., Gordon, I.J., 1998. Evaluation of strategies for tracking climatic variation in semi-arid grazing systems. *Agricultural Systems* 57, 381–398.
- Illius, A.W., Derry, J.F., Gordon, I.J., 2000. Corrigendum—evaluation of strategies for tracking climatic variation in semi-arid grazing systems. *Agricultural Systems* 63, 73–74.
- Ludwig, J.A., Coughenour, M.B., Liedloff, A.C., Dyer, R., 2001. Modelling the resilience of Australian savanna systems to grazing impacts. *Environment International* 27, 167–172.
- Moss, C.J., 2001. The demography of an African elephant (*Loxodonta Africana*) population in Amboseli, Kenya. *Journal of Zoology* 255, 145–156.
- Nicholson, S.E., 1980. The nature of rainfall fluctuations in sub-tropical West Africa. *Monthly Weather Review* 108, 473–487.
- Oba, G., Weladji, R.B., Lusigi, W.J., Stenseth, N.C., 2003. Scale-dependent effects of grazing on rangeland degradation in northern Kenya: a test of equilibrium and non-equilibrium hypotheses. *Land Degradation & Development* 14, 83–94.
- Owen-Smith, R.N., 2002. *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments*. Cambridge University Press, Cambridge, MA, USA.
- Peel, M.J.S., Biggs, H., Zacharias, P.J.K., 1999. The evolving use of stocking rate indices currently based on animal number and type in semi-arid heterogeneous landscapes and complex land-use systems. *African Journal of Range and Forage Science* 15, 117–127.
- Ricker, W., 1954. Stock and recruitment. *Journal of Fisheries Research Board of Canada* 11, 559–623.
- Royama, T., 1992. *Analytical Population Dynamics*. Chapman & Hall, London, UK.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Scoones, I., 1992. Coping with drought: responses of herders and livestock in contrasting savanna environments in southern Zimbabwe. *Human Ecology* 20, 31–52.
- Scoones, I., 1999. New ecology and the social sciences: what prospects for a fruitful engagement. *Annual Review of Anthropology* 28, 479–507.
- Shepherd, N., Caughley, G., 1987. Options for management of kangaroos. In: Caughley, G., Shepherd, N., Short, S.J. (Eds.), *Kangaroos, Their Ecology and Management in the Sheep Rangelands of Australia*. Cambridge University Press, Cambridge, MA, USA, pp. 188–219.
- Sullivan, S., 1996. Guest editorial: towards a non-equilibrium ecology: perspectives from an arid land. *Journal of Biogeography* 23, 1–5.
- Sullivan, S., Rohde, R., 2002. On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography* 29, 1595–1618.
- Thornton, P.K., Galvin, K.A., Boone, R.B., 2003. An agro-pastoral household model for the rangelands of East Africa. *Agricultural Systems* 76, 601–622.
- Thornton, P.K., Fawcett, R.H., Galvin, K.A., Boone, R.B., Hudson, J.W., Vogel, C.H., 2004. Evaluating management options that use climate forecasts: modeling livestock production systems in the semi-arid zone of South Africa. *Climate Research* 26, 33–42.
- Thornton, P.K., BurnSilver, S.B., Boone, R.B., Galvin, K.A., 2006. Modelling the impacts of group ranch subdivision on agro-pastoral households in Kajjido, Kenya. *Agricultural Systems* 87, 331–356.
- Trenberth, K.E., Shea, D.J., 2005. Relationships between precipitation and surface temperature. *Geophysical Research Letters* 32, L14703.
- Vetter, S., 2005. Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments* 62, 321–341.
- Wang, G.W., Hobbs, N.T., Boone, R.B., Illius, A.W., Gordon, I.J., Gross, J.E., Hamlin, K.L., 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. *Ecology* 87, 95–102.

- Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42, 266–274.
- Wiens, J., 1984. On understanding a nonequilibrium world: myth and reality in community patterns and processes. In: Strong, D.R., Simberloff, D., Abele, L.G., Thistle, A.B. (Eds.), *Ecological Communities: Conceptual Issues and Evidences*. Princeton University Press, Princeton, New Jersey, pp. 439–457.