SOCIO-ECOLOGICAL SYSTEMS

The changing role of natural and human agencies shaping the ecology of an African savanna ecosystem

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Abstract. Reconstructing the historical interplay of wildlife and pastoralists in the African savannas is clouded in contemporary studies by the transformation of subsistence societies and land use changes. We draw on five decades of monitoring by the Amboseli Conservation Program to illustrate the rainfall–plant–herbivore linkages in a free-ranging wildlife–livestock system transitioning to contemporary savanna landscapes. In half a century, the coupled interactions of wildlife and livestock in the Amboseli ecosystem driven by rainfall and water sources have been severed and reshaped by farming, land subdivision, sedentism, poaching, and intensified herbivory. Livestock ranges have expanded, wildlife ranges have contracted, and overlapping spatial use has fluctuated with population sizes. In contrast, wildlife and livestock herds have been sustained where the rangelands remain open. A decrease in the mean body size reflecting a shift to small stock among pastoralists has increased species dominance, decreased diversity, and elevated biomass turnover and the probability of extreme shortfalls. In recent droughts, pastoralists have been importing food supplements to reduce drought risk and purchased livestock to restock herds, further uncoupling the rainfall-herbivore link. Our study reinforces the view that biomes worldwide are shaped at an accelerating pace by human agencies rather than endogenous environmental factors. Disputes over models of rangeland systems echo the wider debate over using natural ecosystems as benchmarks for conservation verses "gardening" nature. We argue that models of natural ecosystems fail to account for the dominant role of humans in contemporary ecosystem yet that it is possible to monitor the complex interplay of human and natural systems and interpret the changes in terms of ecological function using macroecological analysis. The key finding for conservation is the importance of space, landscape heterogeneity, social networks, and mobility in sustaining the large herbivore populations.

Key words: conservation; human dominance; livestock; macroecology; pastoralism; savannas; wildlife.

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INTRODUCTION

Early comparative studies of savanna ecosystems showed rainfall to closely predict large herbivore biomass (Coe et al. 1976, Bourn 1978, Fritz and Duncan 1994). Other studies added nutrients (Bell 1982, East 1984) and water distribution (Western 1975) as important factors governing the productivity and structure of large herbivore communities. Long-term research in Kruger National Park in South Africa and Serengeti National Park in East Africa has since shown a complex hierarchy of top-down and bottom-up factors to shape savanna ecosystems, including physical factors, environmental heterogeneity, herbivory, predation, disease, fire, competition,

and keystone species (du Toit et al. 2003, Hatton et al. 2015).

Missing from studies of herbivore-dominated communities has been the role of humans, despite the emergence of pastoralism in Sub-Saharan Africa 4000 BC (Marshall 1990, Smith 1992) and the preponderance of livestock over wildlife across Africa (Bourn 1978, Fritz and Duncan 1994). The persistence of the pre-historical complement of large herbivores in the East African savannas and the abundance of wildlife alongside livestock raises the question of how they traditionally coexisted (Reid 2012, Tyrrell et al. 2017). Protected areas have often been used as baselines to document the ecology of savannas and infer the impact of human activity in disrupting natural ecosystem processes (Arcese and Sinclair 1997, Sinclair 1998). There are several shortcomings in using parks as ecological baselines though, including site selection, typically centered on dry season concentration areas (Western and Ssemakula 1981), the ecological reverberations of earlier human occupation, insularization (Soule et al. 1979), disease transmission, poaching, fire, range fragmentation, compressed herbivore populations, and the persistence of coupled human-natural system across park boundaries (Mabunda et al. 2003, Fryxell et al. 2014). The segregation of formerly interlinked ecologies of wildlife and pastoralists continues to redound in the ecology of protected areas independent of size (Western and Gichohi 1993, Veldhuis et al. 2019).

Human impacts have accelerated with population growth, land transformation, and intensified use in the last few decades, causing a decline of wildlife in parks across Africa (Craigie et al. 2010, Western et al. 2015). The cumulative changes and impacts on savanna ecosystems make it difficult to reconstruct the ecology of free-ranging pastoral livestock and wildlife populations from contemporary studies, whether in parks or livestock-dominated ecosystems.

A long-term study of the Amboseli ecosystem on the Kenya-Tanzania border by the Amboseli Conservation Program (ACP) provides an insight into ecosystem processes of interlinked livestock and wildlife ecologies before the disruption of traditional herding practices and land transformation. The ecosystem study, begun in the 1960s (Western 1973), has monitored the interactions through the transition in pastoral practices, the creation of Amboseli National Park, the subdivision of communal lands and changing land uses (Western and Nightingale 2005).

We use the results of the ACP ecological monitoring to document the changes in the Amboseli ecosystem over the five decades of transition from the free-ranging interactions of pastoral livestock and wildlife, through the transformation in land uses to permanent settlement. Our main aim is to quantify the changing role of natural and human agencies in shaping the ecology of a savanna ecosystem. We track the changes in herbivore for wildlife, livestock, feeding guilds, and individual species responses to rainfall, land uses, sedentarization, intensified herbivory, and poaching. We then discuss the implications of the findings for ecosystem theory and conservation management in human-dominated ecosystems.

METHODS

Area description

The physical, biotic, and human characteristics of the Amboseli region in southern Kenya have been described in detail in several publications, including (Western 1973, 1975, Western and Nightingale 2004, Moss et al. 2011). The ecosystem is defined by the wet season range of the migratory herbivores using the Amboseli Basin during the dry season (Fig. 1). The Basin, an infilled Pleistocene lakebed, is fed by underground aquifers draining the Kilimanjaro rainforests. The aquifers supply large permanents swamps and extensive acacia woodlands which support the migratory populations of wildlife and livestock through the dry seasons (Western 1973).

During the rains, the migratory herbivores, principally wildebeest, zebra, elephant, and pastoral livestock, which collectively make up more than 90% of the large mammal biomass, spread widely into the lands surrounding the Amboseli Basin. In the 1960s, the wet season range of the migrants overlapped adjacent wildlife populations spanning an area of 10,000 km^2 of eastern Kajiado District north of Kilimanjaro lying between latitudes 2°–3° S and longitudes 36.5°–38° E (Western and Behrensmeyer 2009).

Maximum temperatures in Amboseli National Park, located at the foot of Kilimanjaro, range
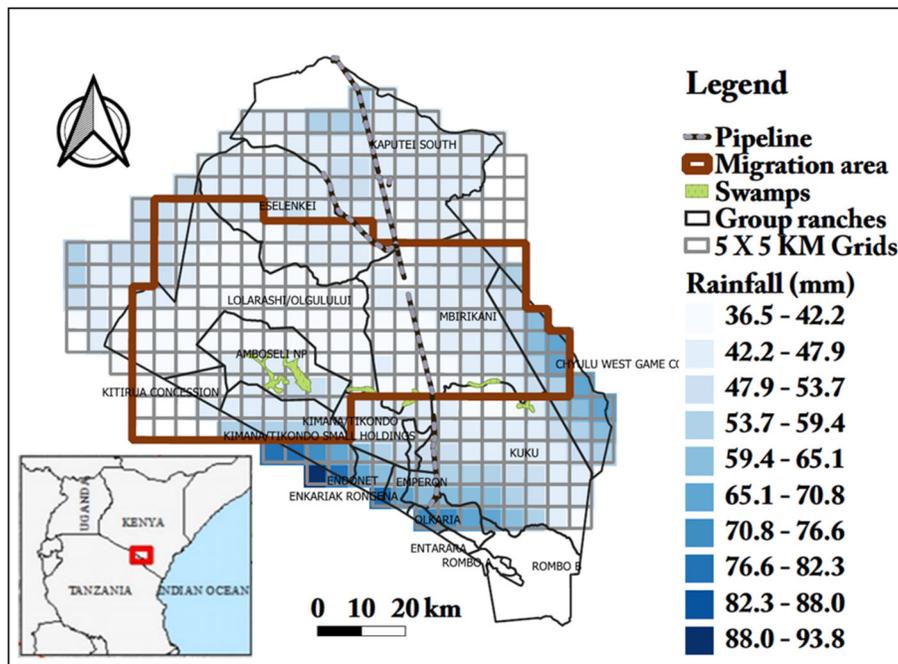
Fig. 1. A map of the area monitored by aerial counts since 1974 showing Amboseli National Park, surrounding group ranches, rainfall isopleths and the 5 × 5 km grid overlay used in flying flight lines and spatially plotting wildlife and livestock. The area defined by the red box defines the migratory range used by wildlife and livestock centered on the Amboseli Basin and permanent swamps. Adjacent migratory populations occupied areas to the north and southeast of the Amboseli ecosystem.

between 26°C and 44°C and minimum temperatures between 6°C and 24°C (Western 1973, Altmann et al. 2002). The mean annual rainfall approximates 350 mm, falling between March to May and October to December. The vegetation, dominated by bushed grassland Ecological Zone V of Pratt, Greenway, and Gwynne, has been described in detail elsewhere (Western 2007).

The Maasai pastoralists dominating southern Kenya for half a millennium traditionally subsisted on the milk and meat production of zebu cattle and the consumption of sheep and goats (Jacobs 1965, Galaty 1982). The enduring impact on the landscape is evident from the altered mineralogical and structural composition of soils detectable on settlement sites occupied over 2500 yr ago (Marshall et al. 2018). Contemporary settlements create extensive clearings in bushed savannas and play a large role in structuring the composition of vegetation and spatial dynamics of the large herbivore community (Augustine 2003, Muchiru et al. 2009).

Starting in the 1970s the communally owned lands of the 21,300 km^2 Kajiado District were divided into group ranches under title deeds jointly held by the customary pastoral occupants (Grandin 1991, Kimani and Pickard 1998). Group ranches in the 8500 km^2 of eastern Kajiado District covered by ACP's aerial monitoring (Fig. 1) range in size from Kuku at 25,120 ha to Ogulului at 147,959 ha.

By the 1980s immigrant farmers and Maasai holding individual land titles had spread down the arable slopes of Kilimanjaro and developed irrigated plots in the swamps east of Amboseli National Park (BurnSilver et al. 2008). Land privatization policies of the Kenya government and internal pressures for securing land against outside interests led to the subdivision of several group ranches, including Kaputei, Matupato, and Kimana to individual allotments ranging from 100 to 1000 ha (Ntiati 2002, BurnSilver and Mwangi 2007). Traditional dung huts built by pastoralist in temporary settlements gave way to

permanent thatch and tin-roofed houses as pastoralists became more sedentary. The sedentism began with the subdivision of the Kaputei group ranches (Groom and Western 2013) and the spread of farms in the early to mid-1970s. In late 1980s, and accelerating through the 1990s, the seasonal movements among the Maasai using the Amboseli Basin dwindled as families set up permanent settlements close to water sources and social services centers prior to land privatization.

The 388 km^2 Amboseli National Park was set aside by presidential decree in 1974 to protect the swamps and woodlands of the basin from settlement and farming. Herders were excluded from the park after 1977 when watering points were supplied to displaced members of Ol-lolorashi Ogulului Group Ranch. Although the park reduced livestock access to the Amboseli Basin, herders continued entering the park in dry years when forage on the group ranches ran short. Wildlife still moves freely across the group ranches in return for a grazing offset fee paid from the national park revenues (Western 1994).

Study design

Our study draws on 52 aerial sample counts of the 8500 km^2 eastern Kajiado county covering the Amboseli ecosystem of 3700 km^2 and bordering areas flown regularly between 1974 and 2020. The area was divided on a UTM map projection into 5 × 5 km grids (Fig. 1). The aerial counts were established in 1973 to cover the migratory range of the Amboseli migrants. The Amboseli zebra, wildebeest, and elephant herds were found to overlap populations on Kaputei Group Ranches to the north, Chyulu Hills and Tsavo West National Park to the east, Kilimanjaro and Ngaserai in Tanzania to the south, and Namanga to the west. The count area was expanded to 8500 km^2 over two subsequent counts to encompass the metapopulations. The spatial coverage was continued from 1974 onward despite the land use changes, aimed at capturing the impact of development on pastoralism and wildlife in eastern Kajiado and the Amboseli migratory ecosystem.

Transect lines were flown through the center of each grid in a north south-direction 90 m above ground with two back-seat observers counting all wild and domestic herbivores Thomson gazelle size (25 kg) and upwards within 150–200-m strip. The strip was corrected for deviations in height and width (Pennycuick and Western 1972). Due to the mixing of sheep and goat herds by Maasai pastoralists, we lumped both as "shoats." Herds too large to count by eye were photographed and later counted under a binocular microscope. Population estimates were derived from the 8% to 10% sample counts using the Jolly II equation (Jolly 1969). Eighteen counts conducted by the Department of Regional Surveys and Remote Sensing for the Amboseli ecosystem (Ogutu et al. 2014) were added to the 34 ACP counts after finding no significant differences in any species population estimates except for donkeys.

Human activities, including livestock corrals, the number and type of huts, and presence of farms in a grid, were also scored. The numbers and distribution of livestock corrals and homesteads, rather than human population per se, have been shown to displace wildlife through disturbance and pasture depletion (Groom and Western 2013). Homes were logged as traditional temporary dung huts (*ngajijik*), and permanent thatch-roofed or other structures.

We used herbivore production derived from allometric equations specific for African mammals (Western 1983) to track the aggregated and individual species changes in energy output over time. The equation for herbivore production is given by:

$$P_s = 13.8 N_s M_s^{\frac{2}{3}}$$

where P_s is the production estimation, N_s and M_s are density and average body mass for species s, respectively. We used production in preference to the biomass density as the basis of calculating energy flow through the ecosystem (Phillipson 1966). Details on the estimation and derivation of annual herbivore production (P) are provided in Appendix S1.

Pasture biomass and grazing pressure were measured in twenty 300 m^2 permanent plots across the wet and dry season range every 4–6 weeks. The methodology is described in detail elsewhere (Western et al. 2015). The biomass of vegetation in the herb layer is given by $\log_{10}D = \log_{10}(HC) - 0.38$ (Western and Lindsay 1984), where D is plant dry mass, H is the mean plant

height in cm and C is the ground cover as a percentage. No endangered plant species were involved. Grazing pressure was calculated as the percentage of grazed to non-grazed hits using the point intercept method (Western et al. 2015). We used grazing pressure as a direct measure of herbivore offtake and depletion of pastures rather than inferential methods based on calculated consumption. The direct measure of grazing pressure and differences in standing crop biomass between measuring intervals includes changes due to growth, and depletion due to decay, trampling, fire, and other factors.

Pasture production as a function of rainfall was derived from the biomass increment in a growing season divided by the cumulative seasonal rainfall to give biomass growth per unit of rainfall (Western et al. 2015).

Species were divided into grazing and browsing feeding guilds using the gut anatomical classification of Hofmann (1989). The dominant mixed feeder, elephant, is largely a grazer feeding on the Amboseli swamp sedges in the dry season (Western and Lindsay 1984) but has such a large ecological impact that we treat it as a distinctive feeding guild. The scientific names, guild, and mean body weight of each species included in the monitoring program are given in Appendix S1: Table S1.

Statistical modeling

We used changepoint analysis to identify significant fluctuations in total herbivore production and human settlements in the ecosystem. A changepoint for the herbivore production and human settlements data, where the parameters changes occurred, were identified by simply sweeping all possible breaks and finding the most likely changepoints according to the likelihood estimation and a neighborhood kernel density clustering technique (Gurarie et al. 2009, Gurarie 2014). The Behavioral Change Point Analysis (BCPA) identified significant changes in movement parameter values across the long-term datasets. We utilized the BCPA package in R for the analysis (R Core Team 2020).

To detect monotonic trends in herbivore production across species and guilds, we used a modified non-parametric Mann-Kendall trend test (τ) analysis (Hamed and Rao 1998). The advantage of the modified Mann-Kendall

analysis is its ability to incorporate autocorrelation in timeseries data.

Robust data smoothing was conducted by fitting penalized regression splines that are based on generalized additive models (Lee and Oh 2007, Wood 2017). A beta regression analysis (Cribari-Neto and Zeileis 2010) was used to model how the proportion of area utilized by wildlife is affected by the proportion of area utilized by livestock and total herbivore production over time. Pearson's correlation (r) was used to test the association of production between different species.

To investigate the interaction of rainfall and grazing pressure in determining grass biomass, we fitted an autoregressive integrated moving average (ARIMA) regression (Miswan et al. 2016, Paolella 2018) model given by:

$$y_t = \beta_o + \beta_1 x_t + \eta_t \qquad (1)$$

where η_t is an ARIMA (1, 0, 0) error term that accounts for possible autocorrelation in the grass biomass, y_t sampled monthly since 1976, x_t is a matrix whose columns are predictor variables, in this case, rainfall (mm), herbivore offtake (grazing pressure percentages) and their interaction, and β_1 is a vector of parameters associated with the predictor variables while β_o is the model intercept.

To examine the ecological changes resulting from the changes in the size-frequency composition, we used the formula given by

$$\bar{w}_t = \frac{1}{N_t} \sum_i n_{it} \bar{x}_i \qquad (2)$$

For each survey conducted at time t, $\overline{w}_t$ is the size frequency for all herbivores counted (mean body weight of all species combined), N_t is the total number of herbivores counted, n_{it} is the number of species i observed during the survey, and $\bar{x}_i$ is the mean body weight of species i. The same formulation was also applied for livestock and wildlife separately. The mean body weight of each species is given in Appendix S1: Table S1.

RESULTS

Changes in herbivore production

Fig. 2 graphs the long-term changes in the large herbivore production of the Amboseli
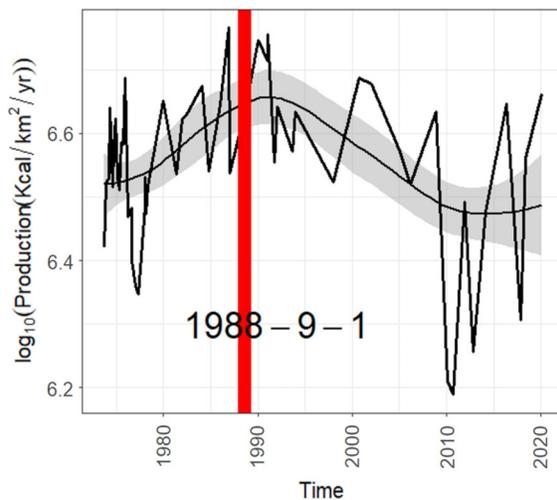
Fig. 2. Temporal trends in total species production in the Amboseli ecosystem between 1974 and 2020. The shaded bands are the pointwise 95% confidence limits derived from a generalized additive model (gam) smoothing function. The red line shows the most significant changepoint (1988-09-01) based on a likelihood function.
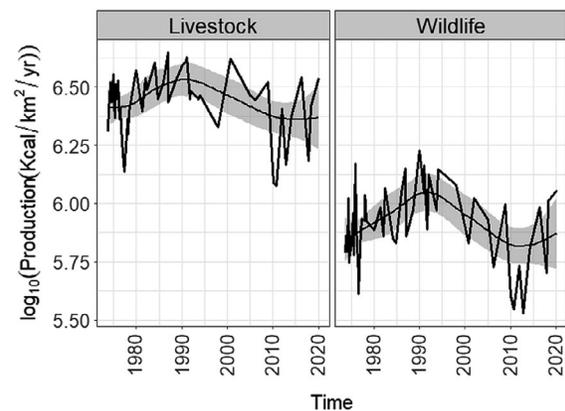

Fig. 3. Trends in livestock and wildlife production in the Amboseli ecosystem from 1974 to 2020. The shaded bands are the pointwise 95% confidence bounds derived from a generalized additive model (gam) smoothing function.

ecosystem for all species combined between 1974 and 2020. Production shows a non-linear trend, with a significant increase to a changepoint in 1988 ($\tau = 0.258$, $P = 0.036$) followed by a significant decline through the 1990s into the 2000s ($\tau = -0.314$, $P = 0.049$). Variance in species production increased significantly after the changepoint ($F_{13,21} = 3.38$, $P = 0.0064$). Production dropped sharply below the 95% confidence limits during two severest droughts, the first in the mid-1970s, the second in the late 2000s. The 2000s drop in production was far greater and significantly higher than the 1970s drought ($\chi^2_{(1)} = 6.37$, $P = 0.012$).

Livestock and wildlife production (Fig. 3) were both highly correlated with total herbivore production ($r = 0.97$, $P < 0.0001$) and ($r = 0.73$, $P < 0.0001$), respectively, and with each other ($r = 0.53$, $P < 0.0001$). Livestock, which accounts for 77% of total production, explained most of the fluctuations in total production. The two largest deviations in both livestock and wildlife production occurred during the droughts of the 1970s and 2000s. The other large deviation for livestock occurred during the 2000 dry spell when pastoralists moved their herds into Tanzania in response to good rains across the border.

The close correspondence in the fluctuations of livestock and wildlife production is illustrated in Fig. 4. The Johansen cointegration test (Naser 2017) shows the fluctuations to be highly correlated over the last five decades ($t_{\text{trace}} = 28.61$, $P < 0.01$) but with livestock having far higher oscillations than wildlife ($t = 5.034$, $P < 0.0001$).

Broken down by feeding guilds (Fig. 5), grazers, which account for 79% of total production, closely match the combined herbivore production ($r = 0.97$, $P < 0.0001$) with a significant increase ($\tau = 0.258$, $P = 0.0328$) to a changepoint around 1986, and significant subsequent decline ($\tau = -0.438$, $P = 0.006$). Browser production, which accounts for 19% of total production and is also significantly correlated with total production ($r = 0.43$, $P < 0.001$), increased significantly over the study period ($\tau = 0.379$, $P = 0.002$). Elephant production, which accounts for 2% of total production, is not correlated with total production ($r = 0.43$, $P = 0.267$) and shows a significant monotonic increase ($\tau = 0.26$, $P = 0.006$) after a sharp decline prior to the 1980s. Elephant production is, however, significantly correlated with total browser production ($r = 0.3$, $P = 0.029$). Grazer production dropped sharply in the mid-1970s and 2000s. Browsers show no such drop in the 1970s but did fall below the 95% percentile
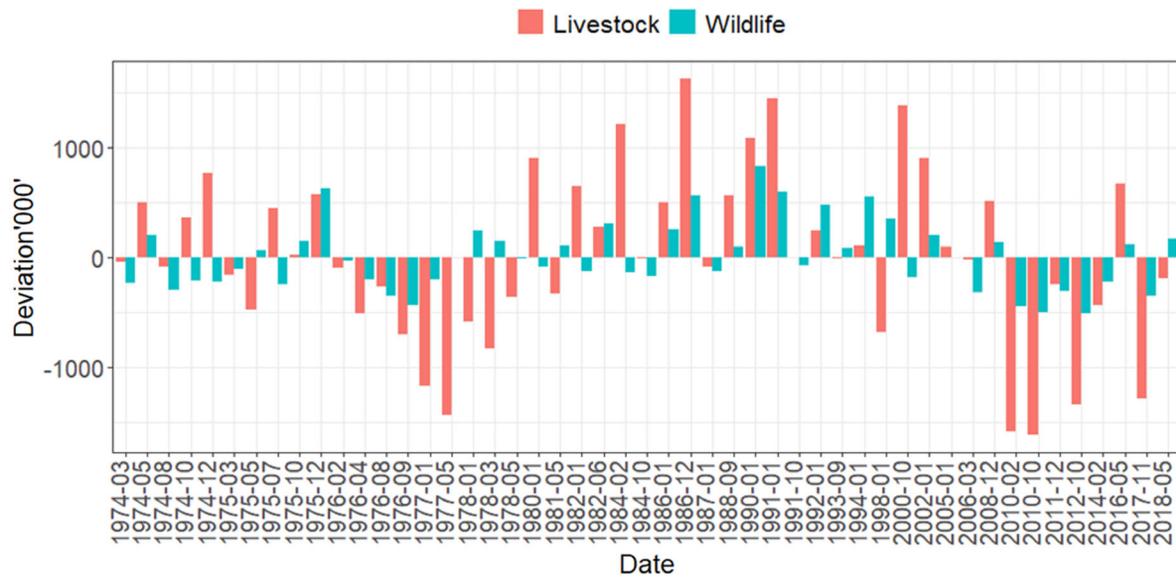
Fig. 4. Fluctuations in livestock and wildlife production based on deviations from the mean production for counts between 1974 and 2018. The negative deviations have proportionately become larger than positive deviations after the 2000s by 17% ($\chi^2_{(1)}$ = 2.92, P = 0.088).
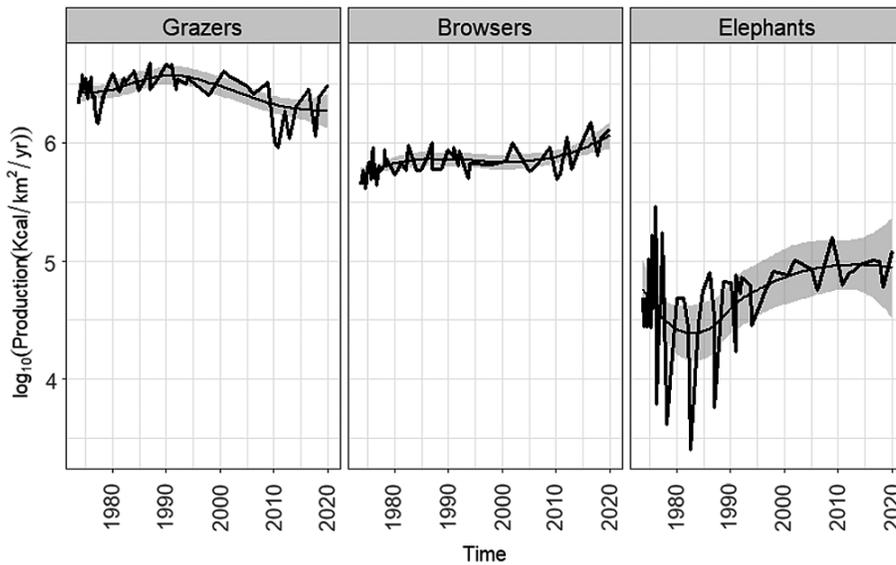

Fig. 5. Trends and the pointwise 95% confidence limits for browsers, grazers, and elephants in the Amboseli ecosystem between 1974 and 2020. The shaded confidence bands are derived from a generalized additive model (gam) smoothing function.

point in the 2009 drought. The large inter-count variance in elephant production (Fig. 5) is attributed to the clumped distributions of herds, disguising any clear drought signal.

The change in livestock production is shown in Fig. 6. Cattle, the dominant herbivore in the Amboseli ecosystem, closely corresponds to the overall production (r = 0.93, P < 0.001), and to
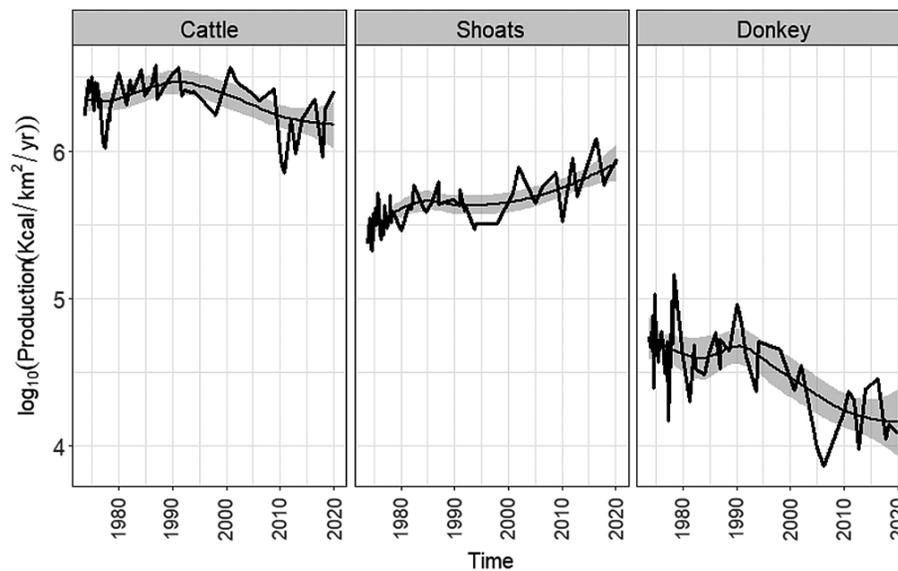
Fig. 6. Trends in cattle, sheep and goats (shoats), and donkey production from 1974 to 2020. The shaded point-wise 95% confidence limit bands are derived from a generalized additive model (gam) smoothing function.

total livestock production ($r = 0.98$, $P < 0.001$). Cattle increased significantly after the 1970s drought ($\tau = 0.56$, $P = 0.0015$), peaked by 1990, then declined significantly ($\tau = -0.39$, $P = 0.0144$), to the lowest recorded level during the 2009 drought when over two thirds of the population died of starvation. Sheep and goats, which showed no significant correlation with overall production ($r = 0.27$, $P = 0.06$), increased significantly ($\tau = 0.521$, $P < 0.0001$) throughout the four decades, broken only by a downturn in the 1990s. Although sheep and goats suffered losses in the 1973 drought, the larger losses in the 2009 drought reached 30%. Donkey production oscillated until 1990 with noticeable losses in the 1970s and 2000s drought. A prolonged and significant decline set in during the 2000s ($\tau = -0.467$, $P = 0.0034$).

The production responses in individual species of wildlife in time is shown in Fig. 7. Zebra ($r = 0.68$, $P < 0.0001$) and wildebeest ($r = 0.68$, $P < 0.0001$) are closely correlated to the overall herbivore production changes and to each other ($r = 0.46$, $P < 0.001$). Neither zebra nor wildebeest showed a strong decline in the 1970s droughts but did suffer large losses in the 2000s drought. The loss and eventual near-extinction of the Amboseli rhino population due to

poaching has been well documented (Western 1982*a*). A small remnant population of 8 or so rhinos under close protection survives in the dense thickets of the Chyulu Hills in the eastern boundary of the ecosystem. Giraffe ($r = 0.39$, $P < 0.001$), Grant's gazelle ($r = 0.4$, $P = 0.003$), impala ($r = 0.27$, $P = 0.05$), ostrich ($r = 0.47$, $P = 0.0004$), hartebeest also known as Kongoni ($r = 0.29$, $P = 0.03$), eland ($r = 0.28$, $P = 0.04$), and oryx ($r = 0.33$, $P = 0.0155$), each show production changes significantly correlated with the total production. Buffalo, Thomson's gazelle, waterbuck, gerenuk, warthog, and lesser kudu show no correlation to the overall production changes at the 5% significance level. The numbers in each case are low and collectively account for less than 3.6% of the total production. The high inter-count population variance in each case masks any clear population trends except for a slow decline in each species after 2000s.

The correspondence in production among species in Fig. 8 shows a marked similarity among the three migratory grazers, cattle, zebra, and wildebeest. The correspondence suggests similar temporal fluctuations in response to ecosystem changes. Browsers and non-migratory species show less temporal correspondence.
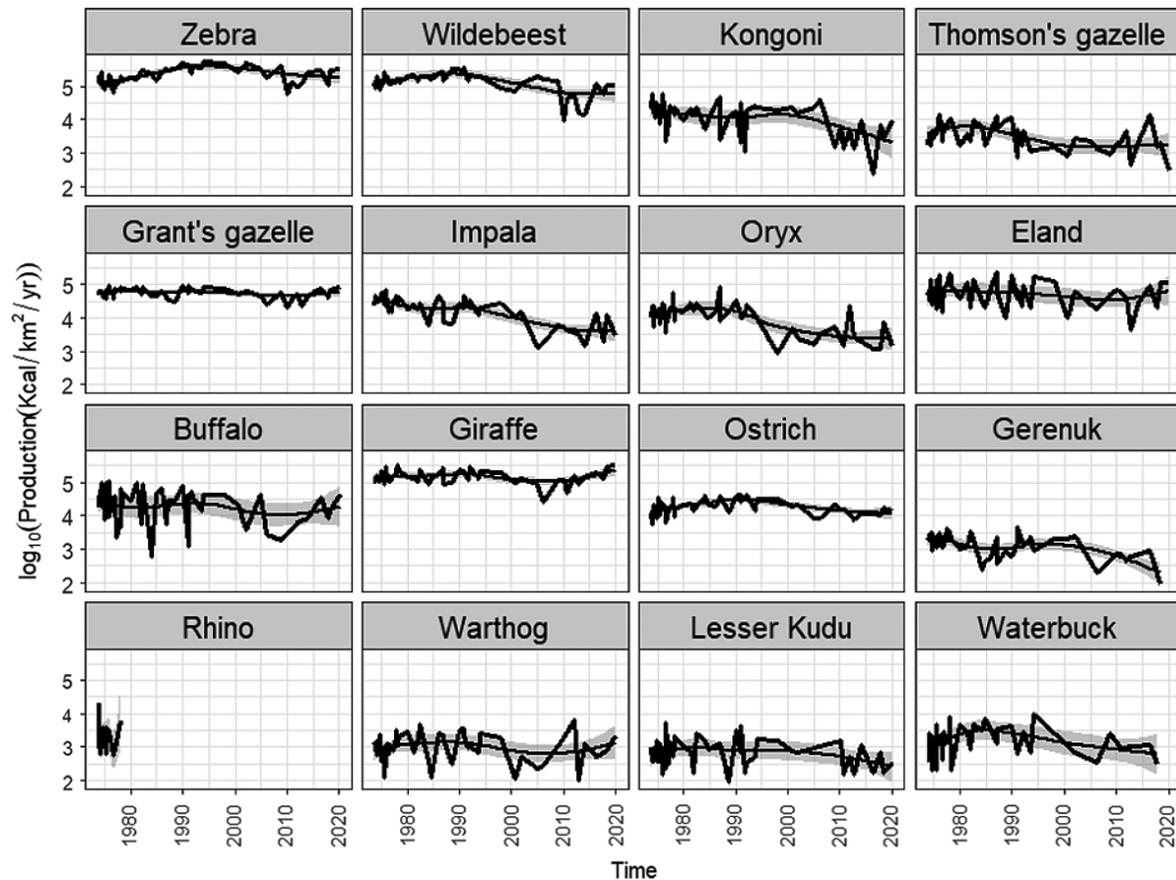
Fig. 7. Wildlife species production trends in the Amboseli ecosystem from 1974 to 2020. The shaded pointwise 95% confidence limit bands are derived from a generalized additive model (gam) smoothing function.

The strong upward trend in total production prior to the 1988 changepoint and steady downward trend after 1990 (Fig. 2) is mirrored in the individual species trajectories over four decades (Fig. 7). Prior to 1988, all species showed a significant upward trend at the 5% level, except for Grant's gazelle, oryx, eland, buffalo, hartebeest, and warthog, which showed no significant change. The only species which declined significantly were impala ($\tau = -0.28$, $P = 0.025$) and gerenuk ($\tau = -0.27$, $P = 0.03$). After 1988 all species showed a significant decline at the 5% level, with the exception of Thompson's gazelle, Grant's gazelle, eland, buffalo, gerenuk, warthog, lesser kudu, and waterbuck, all species with a high inter-count variance due to low population numbers. The only two species showing a significant increase were elephant ($\tau = 0.43$, $P = 0.0065$) and sheep and goats ($\tau = 0.46$, $P = 0.004$).

Changes in human activity

The number of occupied Maasai huts used seasonally is given in Fig. 9. Thatched and tin-roofed huts denote permanent settlements. The number of occupied traditional huts increased from 6000 to 7000 in the early 1970s to a peak of 15,000 in 1990, before falling steeply to under 2000 in the 2000s. Thatch and tin-roofed huts increased from 3000 in the early 1970s to a peak of 20,000 in the 2000s. The numbers of both traditional mobile and permanent huts fell in the 1970s and 2000s droughts, with an additional decline in the mid-1990s when many families moved temporarily across the border into Tanzania to take advantage of good grazing when the rains were poor in Amboseli.

Based on the Hopkins–Skellam test of complete spatial randomness (Ebner et al. 2018), a density-based point pattern analysis (Wiegand
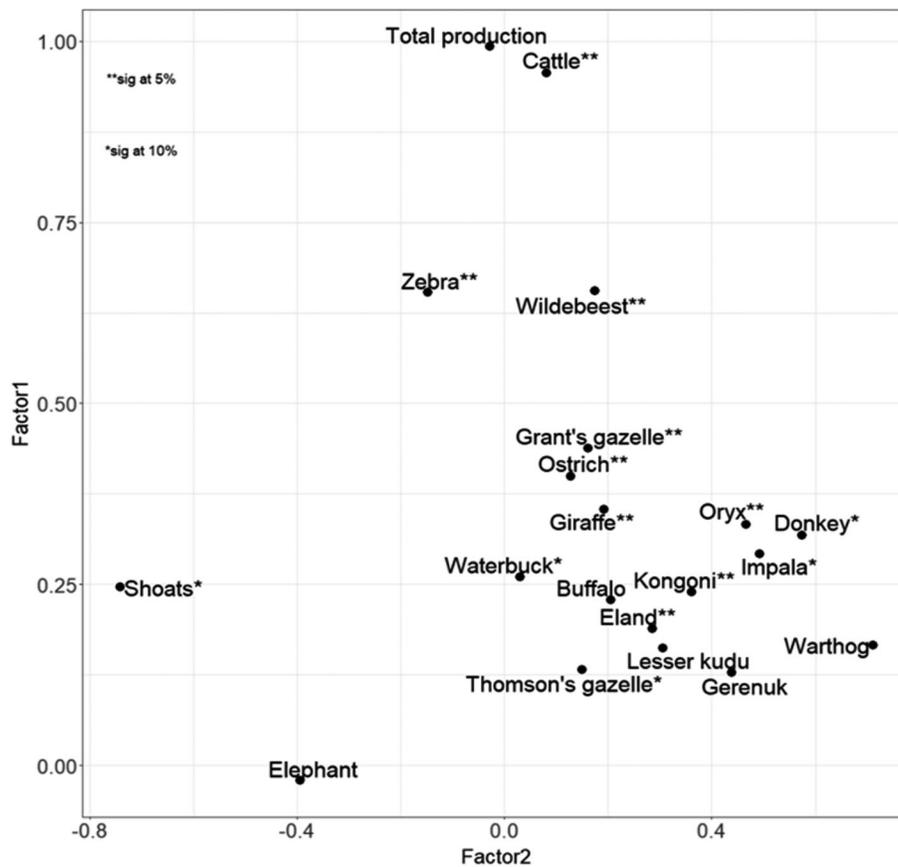
Fig. 8. Factor analysis of Amboseli's all-time species correlation patterns in relation to each other and the total production. The migratory grazers, wildebeest, zebra, and cattle are highly correlated with total production and each other. The non-migratory species and browsers are weakly correlated with total production and each other. Elephants show the weakest correspondence to other species.

and Moloney 2013) shows recent increased clustering of human settlements in the Amboseli ecosystem ($A = 0.455$, $P = 0.001$), related to sedentism as families settle around permanent water points and social facilities.

The growth and spread of small farms across the Amboseli ecosystem are captured in Fig. 10. Farms, which covered 12% of the ecosystem in the 1970s, were largely confined to grids in the wetter uplands north of Kaputei section north of Amboseli, and to the slopes of Kilimanjaro to the south. Farms covering 10% or more of a grid grew threefold from 925 km^2 in the 1970s to 3025 km^2 in the 2000s. The spread then slowed as farms reached the limits of rainfed growth and irrigated farms east of Amboseli National Park used up available spring-fed water.

Causes of change

Farming, land subdivision, and sedentism.—The causes of large herbivore changes in eastern Kajiado have been attributed to several factors, including land subdivision, sedentism, pasture degradation, farming, poaching, human–wildlife conflict, and drought (Western et al. 2009a, Ogutu et al. 2014, Okello et al. 2016).

The continuous five decades of ACP monitoring shows farming to have by far the greatest impact on free-ranging pastoral herds and wildlife in the 8500 km^2 eastern Kajiado region (Fig. 10). Fencing and active defense of crops by farmers displaces all large herbivores except for livestock in areas of continuous farm cover in the moister rainfall areas of eastern Kajiado. So, for example, no wildlife has been counted on the
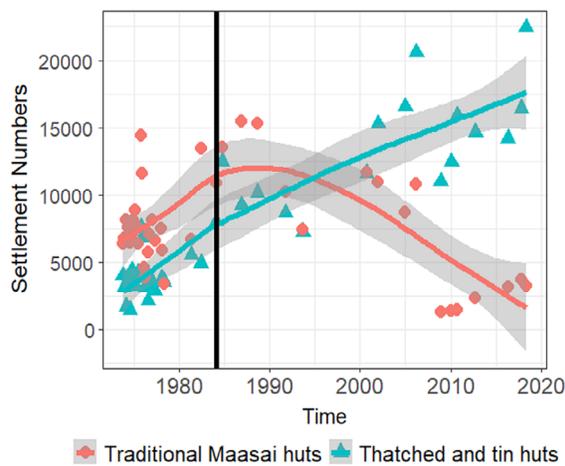
Fig. 9. Changes in human settlements in the Amboseli ecosystem from 1974 to 2020. The shaded bands are the pointwise 95% confidence limits derived from a generalized additive model (gam) smoothing function. The traditional Maasai huts used as temporary settlements by mobile pastoralists are replaced by thatch and tin huts of resident families after the mid-1980s changepoint (black line).

farms spreading down the slopes of Kilimanjaro since the 1970s when the land was subdivided and privatized. Similarly, the spread of farms in northern Kaputei, and in the Simba region of Ukambani north of the Mombasa-Nairobi road in the mid-1970s, blocked the seasonal migrations of zebra and wildebeest from the Kaputei ranches. The farming areas north of the Mombasa Road were dropped from the ACP monitoring area when the last wildlife herds disappeared in the late 1970s.

The area occupied by irrigated farms around the permanent rivers and swamps east of Amboseli National Park (Fig. 10) are less continuous than the rainfed farms. Substantial areas between the rivers and swamps remain pasture lands too fragmented to sustain other than small numbers of impala, waterbuck, and zebra. Kimana Group Ranch illustrates the reduction in large herbivore populations following the development of extensive irrigated farming in the late 1970s and early 1980s (Fig. 11). Mean wildlife production fell sharply from 22,692.35 kcal·km^{-2}·yr^{-1} before 1980 to 9063.21 kcal·km^{-2}·yr^{-1} after the year 2000 ($\tau = -0.287$, $P = 0.0024$). Livestock production also declined after 2000, though not

significantly ($\tau = -0.21$, $P = 0.3244$). The results affirm the findings that farms have displaced wildlife through habitat conversion and fencing (Worden et al. 2003).

The impact of land subdivision of group ranches in sub-arable areas has also been shown to displace and depress wildlife populations. The subdivision of the Kaputei Group Ranches led to a sharp decline in wildlife between the mid-1970s and 2005 (Western et al. 2009*a*). In contrast, wildlife increased on the adjacent Mbirikani Group Ranch which remained open to movements. The decline was attributed to the direct displacement by closely spaced settlements on private allotments, and the loss of pasture production due to continuous heavy grazing (Groom and Western 2013). Counts continued since 2005 (Fig. 12) show wildlife production declining further on Kaputei subdivided ranches ($\tau = -0.18$, $P = 0.05$), and increasing significantly on the adjacent Mbirikani Group Ranch where free movements continued ($\tau = 0.217$, $P = 0.0207$).

The impact of human activity in depressing wildlife in the wetter and higher elevations north of Amboseli contrasts sharply with the migratory wildlife populations centered on the Amboseli Basin. The migratory range covering 3700 km^2 (Fig. 1) within the rain shadow of Kilimanjaro too dry to farm and has yet to be subdivided. The free-ranging wildlife populations here show a significant increase in production between 1974 and 2020, livestock a non-significant decline, and total herbivore production no significant change (Appendix S1: Tables S2, S3).

We conclude that farming and subdivision, coupled with the sedentism and aggregation of family settlements, displaces free-ranging wildlife and pastoral herds. The combined displacement effects are captured by changes in the spatial coverage of wildlife and livestock since the 1970s (Fig. 13). The spatial distribution of livestock was far more restricted than wildlife in the 1970s. Livestock in the absence of wildlife used an average of 14% of grids per count, wildlife in the absence of livestock used 59% of grids, and overlapping uses by both used 27% of grids. The restricted distribution of livestock was due to their limited foraging from permanent water sources in the 1970s, and the widespread distribution of wildlife due to the unrestricted range
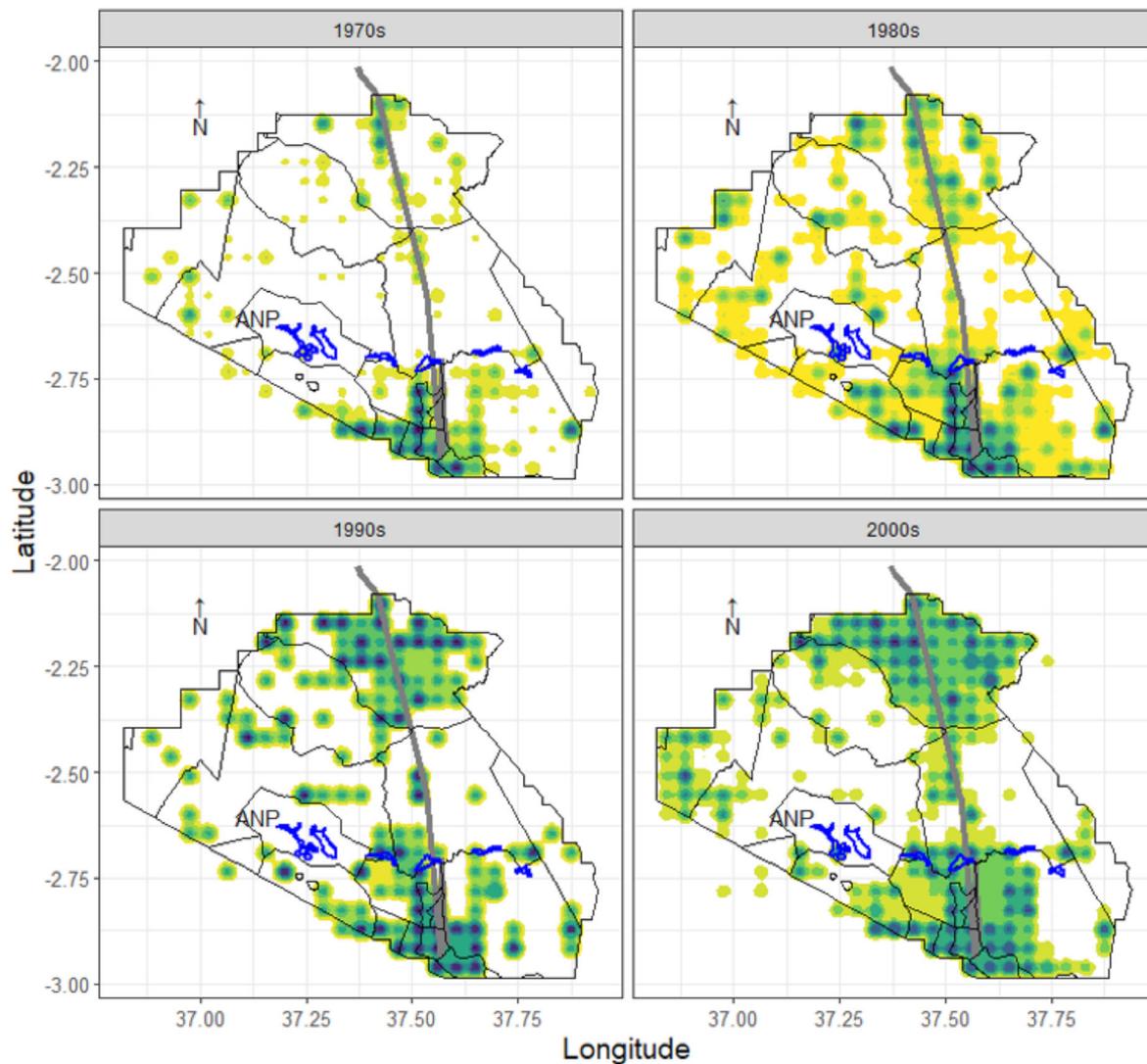
Fig. 10. Concentration and spread of small farms over time, shown in green, from the higher elevations and rainfall areas to the north and south of Amboseli National Park (ANP), extending to the lowland swamps shown in blue, and along the pipeline (gray line) using extraction points. Extent of human settlement spread is also shown by the yellow contours.

of browsing species (Western 1975). The areas occupied by livestock grew steadily in the following decades due to the expansion of boreholes, dams, and the Loitokitok pipeline running north to south through the ecosystem (Fig. 10). Wildlife ranges contracted in the higher elevations due to farming and settlements rupturing the migrations between wet and dry season areas, a pattern consistent with the loss of functional ecological gradients described by Hopcraft et al. (2010). This was not the case in the southern farming areas which were not part of the migratory herbivore range. Here, the sharp decline in herbivore populations resulted from irrigated farming in the lowland areas displacing wildlife from their dry season range centered on the Namelok and Kimana swamps east of the Amboseli National Park (Worden et al. 2003). Across eastern Kajiado, changes in the co-occurrence of wildlife and livestock correlates strongly
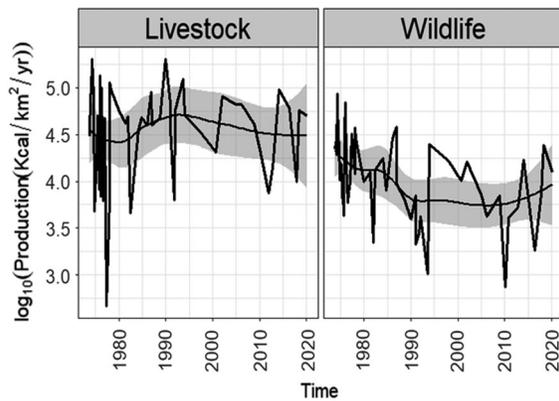
Fig. 11. Changes in large herbivore production in Kimana Group Ranch following irrigated settlement. Wildlife production declined sharply due to exclusion from farming areas. Livestock, which feed on crop residues, showed only a slight and insignificant decline ($\tau = -0.035$, $P = 0.7208$).
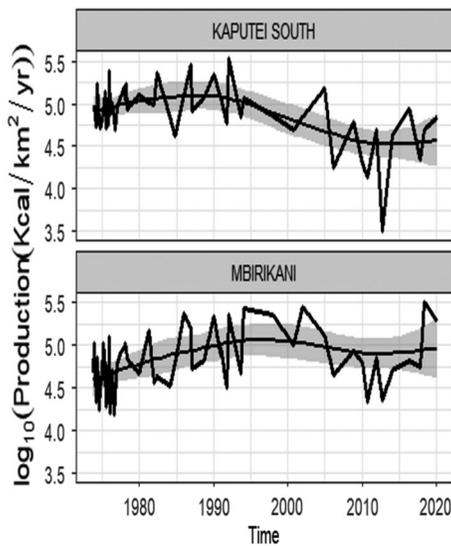

Fig. 12. Wildlife production declined sharply on the Kaputei ranches following subdivision, whereas production increased on neighboring Mbirikani Group Ranch which remained open to free-ranging pastoral livestock and wildlife herds.

($r = 0.56$, $P < 0.0001$) with total herbivore production (Fig. 2), pointing to population sizes as driving overlapping spatial use.

We next look at factors causing changes in herbivore production in the semiarid rangelands which remain open to large herbivore movements.

Rainfall, plant production, and herbivore interactions.—Rainfall has been shown to explain most of the variation in herbivore biomass and production in the African savannas (Coe et al. 1976, Bourn 1978, Fritz and Duncan 1994). The underlying assumption is that rainfall governs herbivore production indirectly by regulating primary production (Phillipson 1975, Le Houérou et al. 1988).

To test whether rainfall variation explains the fluctuations in herbivore production in Amboseli, we used the daily records for the dry season range (Fig. 14) which regulates migratory herbivore populations (Western 1975). We tested cumulative antecedent rainfall at monthly intervals up to 1 yr, and yearly intervals up to 5 yr for the best fit. The best linear association occurred over the preceding year lagged by six months ($r = 0.32$, $P = 0.022$), an interval corresponding to the bi-annual rainfall seasonality. The correlation shows herbivore production in Amboseli closely tracks rainfall, much as it does across ecosystems (Coe et al. 1976, Western 1989). However, although strongly correlated before the 1988 changepoint (pre-1988, $r = 0.4$, $P = 0.026$), herbivore production is no longer correlated with antecedent rainfall afterward (post-1988, $r = 0.24$, $P = 0.286$).

We found no significant changes in annual rainfall ($\tau = -0.0025$, $P = 0.9287$), the number of months with rainfall ($\tau = -0.058$, $P = 0.5881$), or in rainfall seasonality ($F_{11,11} = 0.767$, $P = 0.6708$) that might explain the weaker relationship.

Rather than use rainfall as a proxy for plant production, we draw on the 21 permanent vegetation plots monitored plant biomass since 1975 (Western et al. 2015) to explain the changes in large herbivore production. Fig. 15 shows a strong downward trend in total plant biomass, broken by periods of reversal corresponding to exceptionally heavy rains. So, for example, biomass was low at the start of the monitoring during the 1970s drought, rose to a peak in the late 1980s, and declined through to 1998 when the exceptionally heavy El Niňo event reversed the decline. Biomass fell once more after 2000 to a low point in 2009 when herbivore production dropped by over 60% due to severe forage deprivation (Fig. 2). Despite a resurgence in 2010,
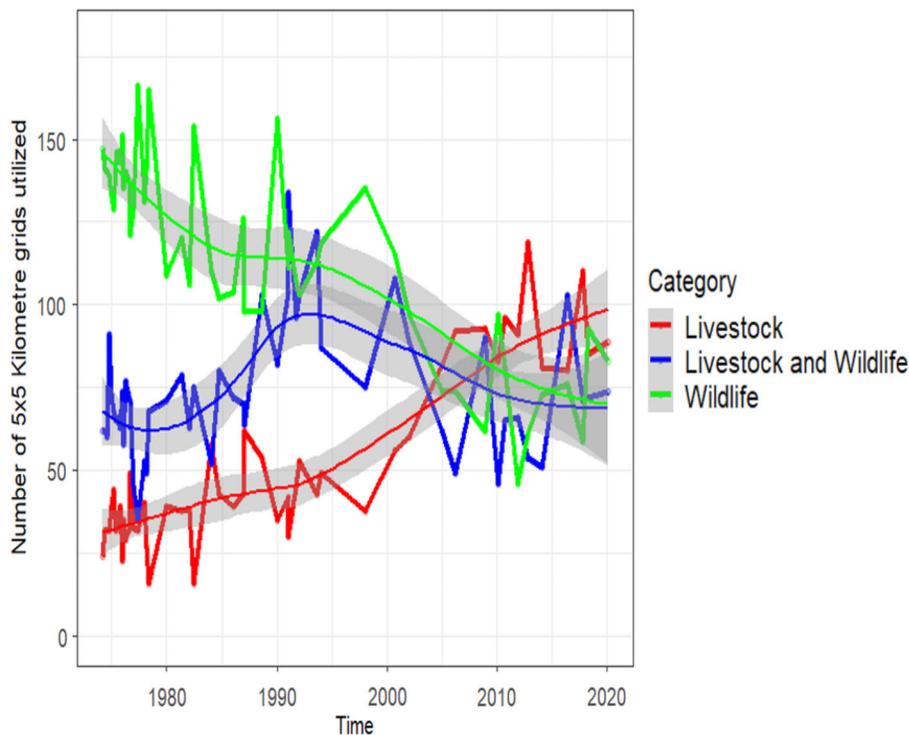
Fig. 13. Number of grids and concurrent use by livestock and wildlife in the study area between 1974 and 2020. Areas used by wildlife decreased and livestock increased until 2010 when they stabilized. Joint grid use increased to a peak in the early 1990s, declined to 2010 and then began increasing once more.
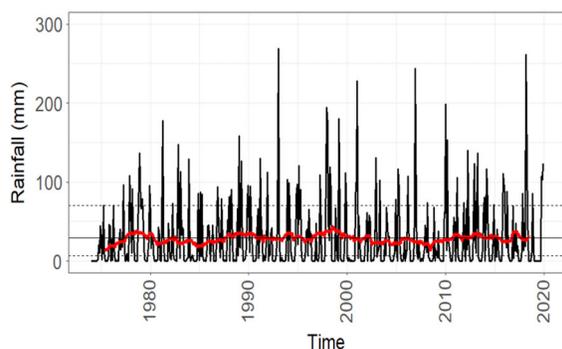

Fig. 14. Monthly rainfall figures for the Amboseli basin showing the mean and standard deviations from the mean. Red line shows one-year running means.

plant biomass resumed a downward trend after 2009 until reversed by the heavy rains of 2018 and late 2019–2020, which matched the intensity of the 1998 El Niňo event.

We found there to be a sharp fall in plant biomass as a function of rainfall after the change point analysis in herbivore production (Fig. 16). An analysis of the pre- and post-1988 change point shows a highly significant decline (ANCOVA, $F = 4.688$, $P = 0.0311$).

The decline in biomass as a function of rainfall is captured by measuring the change in biomass as a function of seasonal rainfall to derive biomass production per unit of rainfall (Western et al. 2015). Fig. 17 shows a strong drop in biomass production from 1975 to the late 1990, a resurgence with the 1998 El Niño event, and a further steep decline to a trough in the 2009 drought. There followed a short-lived recovery due to the large herbivore decline (Fig. 2), followed by yet another decline after 2014 and another brief recovery with the exceptional rains of 2018.

The decline in plant biomass production per unit of rainfall corresponds to a commensurate increase in grazing pressure measured simultaneously with plant biomass in the permanent plots (Fig. 17). Plant biomass production
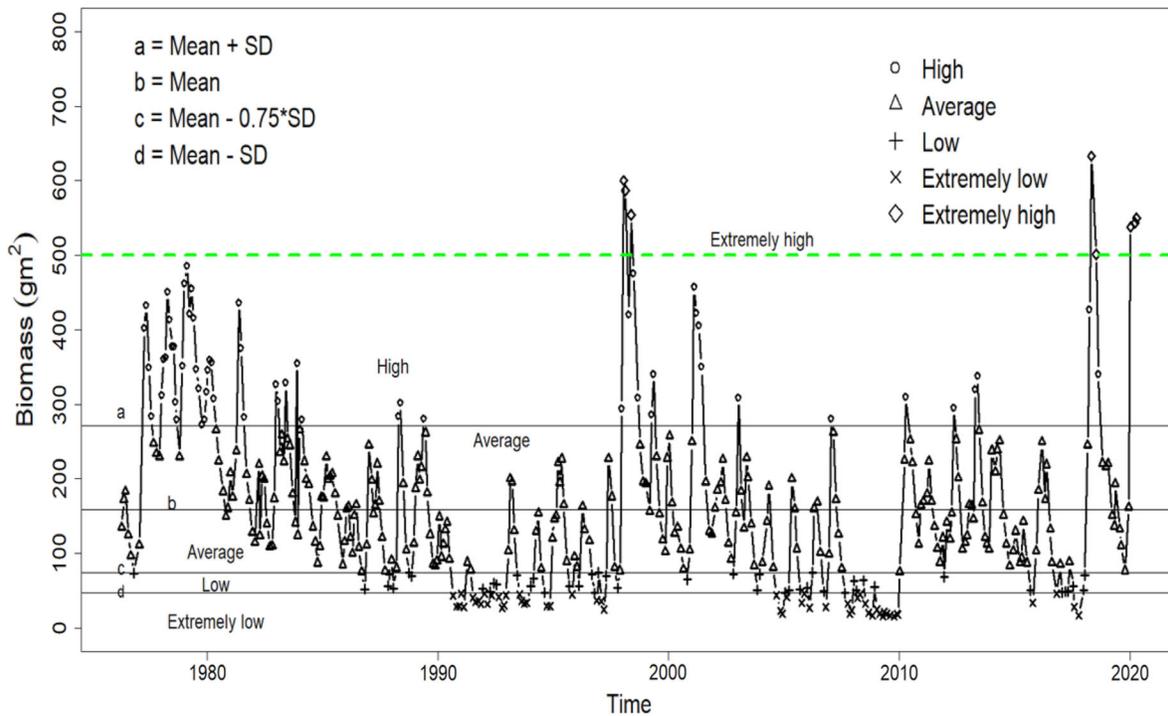
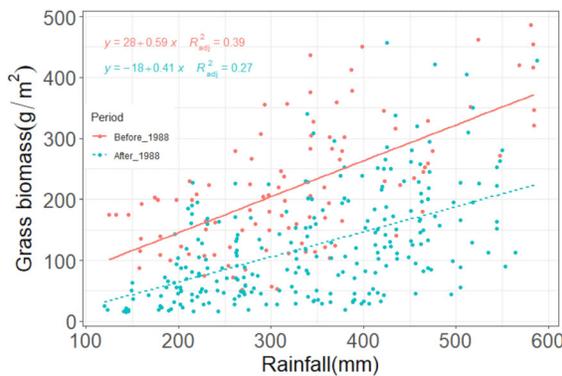Fig. 15. Monthly data for plant biomass averaged for 20 sampling plots.

Fig. 16. Plant biomass as a function of rainfall in the Amboseli basin averaged for pre-1988 (red) and post-1988 changepoint (blue). The linear fits for all periods are significant at 5% level, and the post-1988 period shows a significant decline in pasture biomass to rainfall.

declined inversely proportional to grazing pressure ($r = -0.5$, $P = 0.0032$), which tripled from 20% in the 1980s to over 60% in the 2000s ($t = 5.319$, $P < 0.0001$).

Trends in total herbivore production (Fig. 2) inversely track changes in pasture biomass production per unit of rainfall ($r = -0.41$, $P = 0.035$).

Fig. 18 shows the seasonality in rainfall and pasture biomass measured by the deviations from the means over the period 1975 to 2018. The seasonality in plant biomass shows an increasing negative deviation from the mean and larger cyclical oscillations from the 1990s onwards. Rainfall deviations show no similar trends.

We used the likelihood ratio test to determine the probability of increased forage and rainfall seasonality (Fig. 19) by comparing the null model with a model including time in years. The model yielded a significant fit for forage shortfalls ($\chi^2_{(1)} = 24.04$, $P < 0.0001$), signaling a rising probability of extreme deficits, despite showing no significant rise in the probability of rainfall deficits ($\chi^2_{(1)} = 1.98$, $P = 0.1592$).

Model 1 shows that grass biomass estimates correspond to grazing pressure and antecedent rainfall. The results show that grazing pressure significantly predicts grass biomass in the Amboseli basin area ($\hat{\beta}_{1g} = -7.44$, $P < 0.0001$). Biomass
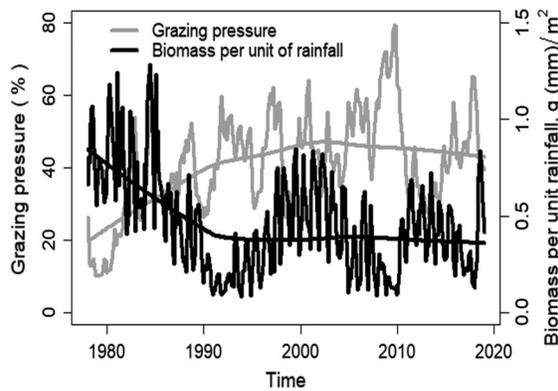
Fig. 17. Averaged annual grazing pressure in Amboseli basin and surrounding areas measured in 20 permanent plots plotted against plant biomass production per unit of rainfall.

levels also depend significantly on previous month's biomass stock ($\rho_{\eta_t} = 0.78$, $P < 0.0001$).

The impact of grazing pressure (g) on variations in grass biomass is significantly larger and reduces the effect of rainfall (r) to insignificant levels ($\hat{\beta}_{1r} = 0.005$, $P = 0.974$). The interaction (i) between rainfall and grazing pressure is also insignificant ($\hat{\beta}_{1i} = 0.004$, $P = 0.204$). The extreme rainfall events of the years 1998, 2019, and early 2020 exceeded an annual total of 600 mm, notably

increasing plant growth and vigor (Fig. 15). Grazing pressure reduced proportionately during these years, pointing to an upward reset of plant biomass in an otherwise declining trend. This accords with the finding that in less productive savannah ecosystems it takes extremely high amounts of rainfall, usually above 600 mm, to counter the effect of grazing pressure on grass biomass (Ondier et al. 2019). Details of the model fit assessment, predictions, and diagnostics are presented in the Appendix S1: Eq. S8, Figs. S1, S2.

Finally, we found an increased variance of pasture biomass over time and in total herbivore production in the 2010s drought relative to the 1970s drought ($F_{10,21} = 3.626$, $P = 0.0062$). The increases in biomass and herbivore variance during droughts occurred without any significant changes in rainfall quantity and seasonality during the study.

Ecological changes

We use six ecological indices to gauge the ecological changes in the large herbivore community: guild composition, species richness, mean body weight, dominance, turnover, and resilience.

The changes in guild composition are given in Fig. 5. The increase in browsers and decrease in
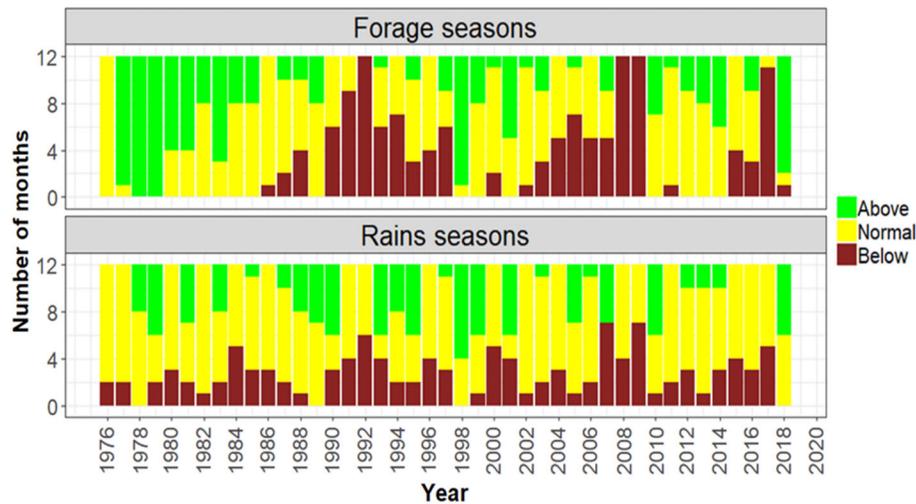
Fig. 18. Plant biomass and rainfall seasonality in the dry season range of Amboseli herbivores derived from deviations from long-term means. Over the five decades, negative (below normal) deviations and cyclicity increased significantly in plant biomass but not in rainfall. Spectral analysis showed a significant peak frequency of 0.0625, $P = 0.042$, corresponding to a 16-yr cycle in plant biomass. See Appendix S1 for details on spectral analysis.
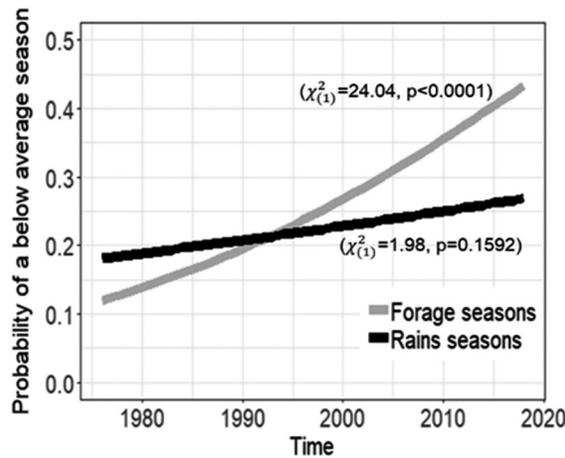
Fig. 19. Probability of extreme seasonality based on rainfall deficit and biomass shortfall from the long-term mean.

Fig. 20. Changes in mean body weights of the large herbivore community for all species combined and livestock and wildlife separately. The mean body weight of all species combined and livestock ($\tau = -0.426$, $P < 0.0001$) has decreased due to rising proportion of shoats, whereas wildlife has increased due to the rising proportion of elephants, giraffe, and zebra ($\tau = 0.402$, $P < 0.0001$).

grazers is explained by the growth in shoats relative to cattle, which collectively account for 77% of the large herbivore production (Fig. 6).

In terms of species richness, there has been no loss of species in the last half century. To the contrary, there has been one addition with the introduction of small numbers of camels into selected pastoral herds since the mid-1990s. In contrast to species richness, there has been extensive change in the species composition of the herbivore assemblage, with large repercussions on the energetics and functional properties of the community stemming from changes in life history traits linked to body size (Western 1979).

The aggregate changes in size-frequency distribution can be measured by the mean body weight of all species combined, and for livestock and wildlife separately (Fig. 20) using formula (2) above.

Fig. 21 shows the changes in dominance (McNaughton and Wolf 1970), Simpson's diversity index (Simpson 1949), and turnover rate (Banse and Mosher 1980). The changes in diversity are inversely related to dominance ($r = -0.95$, $P < 0.0001$) and directly with turnover ($r = 0.7$, $P < 0.0001$).

The interlinked changes in dominance, diversity, and turnover stem from the changes in mean body weight due the large increase of shoats and decrease in cattle production after 2000 (Fig. 6). The increase in mean body weight of wildlife is

due to the population increase in three of the largest species, elephant, giraffe, and zebra (Fig. 5) over the study period (Table 1).

The decrease in resilience in the ecosystem is captured by the rising variance in plant biomass over the study period, the increased seasonality in pasture production independent of rainfall (Fig. 18), the increased probability of biomass shortfalls (Fig. 19), and the increasing vulnerability of herbivore to extreme shortfalls, as noted in the results.

DISCUSSION

The long-term monitoring study shows a rapid shift from rainfall and water as the main drivers of the Amboseli large herbivore community to human activity as the primary force. Prior to the exclusion of pastoralists from Amboseli National Park in 1977 (Western 1994), the seasonal migrations of livestock and wildlife were triggered by and synchronized with the rains, and the return to the Amboseli Basin by the draw of permanent water sources and late season pastures (Western

Fig. 21. Trends in herbivore dominance, diversity, and turnover (production to biomass ratio) in the Amboseli ecosystem 1974–2020.
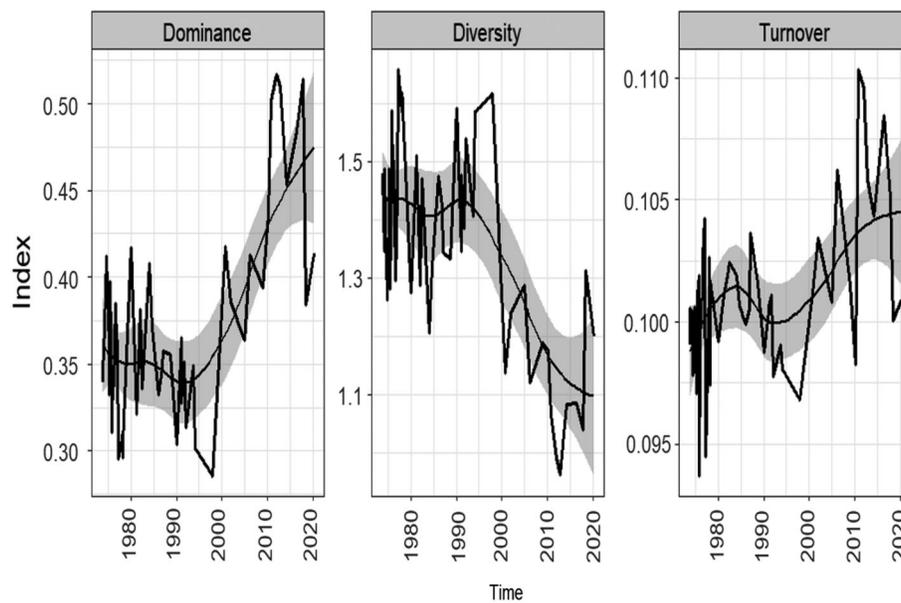
1973). Oscillations in the production of livestock and wildlife were highly correlated with each other (Fig. 4) and tied to antecedent rainfall. The larger livestock than wildlife oscillations reflected the higher drought mortality and faster ensuing recovery due to herder selection to maximize milk production, and lower predation rates due to human protection (Western 1982b).

We attribute the decoupling of livestock and wildlife production to rainfall after the mid-1980s to a combination of farm expansion in the arable areas, water provisioning in the dry season foraging range, and permanent settlements and intensified grazing in depressing pasture production. The expansion and intensification of human developments led to a threefold increase in livestock grid occupancy and a commensurate decrease in wildlife occupancy (Fig. 13). The results show livestock and wildlife grid concurrence to vary inversely in time ($r = -0.91$, $P < 0.0001$). The size of livestock and wildlife populations also influences the extent of overlap. The proportion of concurrence (Fig. 13) correlates strongly with total production ($r = 0.56$, $P < 0.0001$), a measure of combined population sizes. A beta regression analysis (Cribari-Neto and Zeileis 2010) showed the proportion of the

area utilized by wildlife to decline significantly with an increase in the proportion of area utilized by livestock over time. However, the proportional increase with total animal production suggests a significant effect of the combined population sizes (Appendix S1: Table S4).

Wildlife production decreased significantly ($\tau = -0.36$, $P = 0.0207$) after the 1988 change-point in the areas with dense human settlements–mainly the areas north of the main Amboseli migratory range and in the swamps to the east. Wildlife production dropped by 54% on average, pointing to a spatial displacement by farms, subdivision, and sedentism. The spatial displacement of wildlife by human activity bears out the findings of Okello (2005) and Groom and Western (2013).

The increasing grazing pressure and decline in plant biomass (Fig. 17) has been shown to intensify with the sedentism on group ranches (Groom and Western 2013) and, in the Amboseli National Park, due to herbivore compression in the dry season range (Worden et al. 2003, Western and Maitumo 2004, Sarkar 2006, Western et al. 2015). The findings support experimental work on the impact of herbivory on plant production conducted in the Amboseli ecosystem.

Table 1. Changes in the populations of individual species over the period beginning 1974–2020 using the modified non-parametric Mann-Kendall trend test (τ) analysis.

Species	1974–2020 population trend		
	τ	Trend	P
Zebra	0.34	+	0.0003***
Wildebeest	−0.08	−	0.4034
Grant's gazelle	−0.06	−	0.5606
Thomson's gazelle	−0.22	−	0.0184*
Elephant	0.3	+	0.0017**
Buffalo	−0.19	−	0.0447*
Shoats	0.52	+	<0.0001***
Cattle	−0.07	−	0.4378
Donkey	−0.4	−	<0.0001***
Eland	−0.05	−	0.5707
Gerenuk	−0.39	−	<0.0001***
Giraffe	0.05	+	0.5809
Impala	−0.5	−	<0.0001***
Lesser Kudu	−0.11	−	0.2265
Warthog	−0.06	−	0.5308
Waterbuck	−0.2	−	0.0391*
Kongoni	−0.28	−	0.0034**
Oryx	−0.32	−	0.0005***
Ostrich	0.02	+	0.8345
Rhino	−0.56	−	<0.0001***
Total wildlife production	0.08	+	0.3707
Total livestock production	0.04	+	0.6544
Total animal production	0.08	+	0.3787

Notes: Elephant, zebra, and shoats increased significantly. Buffalo, Thomson's gazelle, donkey, gerenuk, impala, waterbuck, hartebeest, and rhino decreased significantly. Other species showed no significant change.

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

Cassady (1973), for example, showed that repeated grazing through the year reduced plant production by 22–60% relative to controls, whereas heavy defoliation once each dry season sustained production. Georgiadis and associates (Georgiadis et al. 1989) showed in potted plant experiment manipulating water, nutrient, and defoliation treatments that frequent repeated off-take depletes resilience more than short-intensive defoliation. Studies by Dunne and colleagues (Dunne et al. 2011) which experimentally manipulated grazing pressure and trampling showed both to heavily depress pasture production per unit of rainfall.

The sustained productivity of the large herbivore system in the Amboseli ecosystem in the face of declining plant production calls for an explanation. We attribute the cause to the transformation of dense swamp vegetation to highly productive grazing lawns (Vesey-FitzGerald 1960, McNaughton 1984) and to the expansion of grasslands with the loss of woodlands (Western and Behrensmeyer 2009) due to the truncation of elephants migrations (Western and Lindsay 1984, Western 2007).

Other human factors than the expansion of farming and settlement have played a role in altering the species composition and abundance of large herbivores in the Amboseli. The most evident and quantifiable is the international wildlife trade. In the 1960s through the 1980s, poaching for the rhino horns eliminated the species in the Amboseli ecosystem (Western 1982*a*), bar a small residual group heavily guarded by rangers in Chyulu Hills. Poaching for ivory reduced the elephant population from over 1000 to under 500 in the 1970s (Western 1994). The remaining animals, concentrating in Amboseli National Park for safety, transformed woodlands to grasslands and increased the ratio of grazers to browsers (Western and Behrensmeyer 2009). Better protection and community conservation initiatives led to a population recovery exceeding its 1970s levels (Fig. 5, Table 1; Moss et al. 2011).

The bush meat trade reduced populations of oryx, giraffe, and kongoni in the 1990 through the early 2000s when reinforced and well-equipped community ranger forces brought poaching under control and saw some recovery (Fig. 7).

Habitat change has also played role, most evidently in the decline of impala populations with the loss of woodlands in and around the Amboseli Basin (Western and Nightingale 2004) and in the decline of waterbuck due to the loss of swamps between Amboseli and Tsavo West National Parks.

The uncoupling of rainfall-plant-herbivore linkages characterizing the pre-subdivision and sedentism period has, since the 2009 drought, broken down further as pastoralists have purchased food supplements in periods of severe pasture shortage and livestock following droughts to restock depleted herds.

General discussion

Evidence from several decades of census data shows widespread wildlife declines in the East African savannas. Ogutu et al. (2016), for

example, found numbers to have declined 68% across the 88% of Kenya covered by rangelands. The declines were attributed to rising human populations, increasing livestock impact, declining rainfall, and institutional and market failures. Western et al. (2009) found wildlife declines in protected areas to match non-protected areas due to surrounding human impacts. Caro and Scholte (2007) and Craigie et al. (2010) showed declines ranging from 59% to 70% for wildlife populations in protected and non-protected areas across Africa since the 1970s.

The African wildlife declines mirror worldwide trends in vertebrate populations. Records for 14,000 populations of 3700 species of mammals, birds, fish, amphibians, and reptiles show and average decline of 58% between 1970 and 2012, with no sign of abatement (WWF 2016). The causes of declines are ascribed to a range of human factors, including over-consumption, intensified land use, range loss, habitat conversion, ecosystem degradation, and climate change.

Recent paleo studies show the human impacts on vertebrates is not unique to modernity. There is evidence of large-scale impacts on vertebrate faunas stretching back 125,000 yr (Smith et al. 2018). The distinctive human imprint is the extermination of mega mammals and faunal downsizing (Martin and Wright 1967, Bartlett et al. 2016, Smith et al. 2018). The downsizing has accelerated in the Anthropocene due to overhunting, displacement by farms and settlements, habitat loss, and human–wildlife conflict (WWF 2016, Tilman et al. 2017).

The decline in plant biomass and productivity in Amboseli also mirrors the impact of human activities in African grassland ecosystems more generally. A similar decline in grassland and woody vegetation and wildfire has occurred across 3 million km^2 of northern Africa since World War II, largely due to cultivation and heavy grazing (Le Houérou et al. 1988). Many studies have documented and reviewed rangeland degradation in Sub-Saharan Africa and worldwide (Dodd 1994, Palmer and Bennett 2013, Angerer et al. 2016). As in Amboseli, the causes of degradation are generally complex, ranging from human and livestock population growth to land subdivision and appropriation, social dislocation, a breakdown in governance

institutions and climate change (Palmer and Bennett 2013, Boles et al. 2019). The paleo, historical, and growing contemporary impact of humans in shaping the macroecology of large herbivore communities has profound implications for ecosystems research, ecological theory, and conservation management.

Among the longest running ecosystem monitoring study, the Amboseli program shows the value of Long-term Ecological Research (Franklin et al. 1990) in detecting ecosystem functions and changes. Foremost, the Amboseli study highlights the need to monitor human activities within and beyond national parks and ecosystems. The results give a rich store of data for exploring the ecological changes and cascading effects of human impact. They also reinforce quantitatively the findings of other studies highlighting human-induced exclusion and displacement as primary causes of wildlife range contraction. Even in the absence of species loss, the Amboseli study shows human-induced exclusion and displacement of wildlife, coupled with intensified herbivory, to cause large ecological changes in the composition, dynamics, and function of savanna ecosystems. Finally, the results point to the value of using size-scaling theory to explore the interlinked ecological changes (Lindstedt and Calder III 1981, Owen-Smith 1988, Smith et al. 2014).

In the 1960s the African savanna parks were studied as models of naturally functioning ecosystems (Sinclair and Norton-Griffiths 1979) and tests of specific ecological theories, including equilibrium, non-equilibrium, multi-state equilibria, (Caughley 1976, Walker and Noy-Meir 1982, Dublin et al. 1990, Gillson 2004). The early research reflected the prevailing ecologist tradition of studying pristine ecosystems, notably protected areas, to understand the workings of nature without the confounding influence of human activity. The tradition only began to change in the 1990s with the recognition that all places on earth fell under humanities shadow (Gallagher and Carpenter 1997).

The broadening scope, scale, and duration of research, coupled with the recognition of the complexity of ecosystems and ubiquity of human impact, features in the changing ecological views and conservation policies stemming from the multi-decadal studies of the 22,000 km^2 Kruger

National Park in South African and the 25,000 km² Serengeti-Mara ecosystem in Tanzania and Kenya. In the case of Kruger, management of the park prior to the 1970s was driven by policies of boundary fencing, orchestrating water distribution and fire regimes, and regulating diseases, predators, large herbivores and elephant populations (du Toit et al. 2003). Recognizing that the intensive management created ecological homogeneity, park policy changed in the 1990s to managing for heterogeneity by minimizing intervention. The policy explicitly recognized non-linear continual changes in response to new impacts as the norm, citing the Levin's view of ecosystems as complex adaptive systems (Levin 1998). In response to the long-term research findings, park policy adopted an adaptive approach using the best available information. The new policy aims at minimizing risks beyond defined thresholds, rather than basing the management of Kruger on specific ecological theories (Mills et al. 2003).

Park policy in Serengeti has taken a more hands-off approach than Kruger. The link between science and management is, consequently, far weaker. The objectives of the Serengeti Research Institute when set up in the late 1960s was to bring together the threads of research to look at the process and patterns defining the ecosystem, the changes in time, and to provide the information for management (Sinclair and Norton-Griffiths 1979). None of the early studies looked at human agencies or at surrounding land uses. The main drivers were attributed to climate, a rebound of wildebeest populations from the 1880s rinderpest epidemic, competition, facilitation, predation, and environmental heterogeneity (Sinclair 1972). Over the ensuing 40 yr researchers began incorporating human studies, resulting in the fourth book in the Serengeti research series stressing the need to sustain biodiversity in a coupled human-natural system (Sinclair et al. 2015). A recent study (Veldhuis et al. 2019) found a compression of wildlife due to surrounding human pressure to reduce grassland productivity and resilience in the center of Serengeti National Park much as it has in Amboseli, a national park 2% its size. The finding points to segregation of formerly coupled human-wildlife ecosystem and the disruption of ecological gradients (Hopcraft et al. 2010) as

having a persistent impact on parks independent of size (Western and Gichohi 1993).

Such human impacts on the largest and most intact large mammal ecosystems in Africa are universal. An example drawing on 239 studies across all major ecosystems and climatic zones, found extensive changes in species composition despite no systematic loss of species (Blowes et al. 2019). They concluded that the global biodiversity crisis is not so much about species declines as large-scale reorganization. Echoing the fragmentation of wildlife ranges in the African savannas, compression, expressed by reduced movement, has been shown among species worldwide (Tucker et al. 2018). A review on the impact of humans on natural biomes (Ellis and Ramankutty 2008), concluded that the extensive transformation calls for a reclassification as human-modified anthromes.

Our study adds to the evidence that human activity has overtaken natural factors in shaping the structure and dynamics of ecosystems over the last half century. The findings apply widely to the world's rangelands where large herbivores assemblages are predominant. A recent review of whether equilibrium or non-equilibrium theories most accurately represent rangelands systems for example, argues that the scale and heterogeneity of coupled herbivore-plant systems were blind spots in the debate, and that the externalities governing livestock and rangeland management in the global community negate the unified model of rangeland ecology (Briske et al. 2020). The Amboseli study reinforces the view that rangelands systems are increasingly driven by human agencies locally and globally rather than endogenous factors, important as they remain.

The debate over models of rangeland systems echoes a yet wider debate over whether conservation should use ecosystems of the past as benchmarks for managing protected areas, or accept the inevitability of "gardening" nature (Janzen 1998, Kareiva and Marvier 2012, Marris 2013, Noss et al. 2013). We suggest that although models of natural ecosystems fail to account for the dominant role of humans in shaping contemporary ecosystem–or in providing suitable benchmarks for conservation policy–macroecology offers a method of tracking the multiplicity of human factors and complex ecosystem responses. McGill et al. (2006) point out that

macroecology calls for linking functional traits and biotic interactions along ecological gradients to predict and maintain ecological interactions. The trait-based approach (Brown and Maurer 1989, Smith et al. 2014) coupled by universal scaling laws (Enquist et al. 1999, West et al. 1999) may be the only way to predict interactions and outcomes, given the complexity of ecosystem responses to human activity, including climate change (Levin 1998).

Recognition of shortcomings of parks in conserving large free-ranging wildlife populations, and the disruptive economic and social impact on communities displaced from their traditional homes, led to a broader conservation paradigm based on Collaborative Natural Resource Management in Africa (Anderson and Grove 1987) and community-based conservation more generally (Western and Wright 1994). Collaborative community-based conservation aims at sustaining the ecological integrity of large open landscapes in order to sustain biodiversity and benefit local communities (Sayer and Cassman 2013).

The ACP study shows the possibility of monitoring the complex interactions of humans and natural systems and interpreting the ecological impacts on ecological functionality using macro ecological analysis. The study was designed and intended to provide ecological information for the conservation of the Amboseli ecosystem. The conservation applications have been detailed elsewhere (Western 1994). More recently the long-term monitoring data formed the basis of the Amboseli Ecosystem Management Plans 2008–2018 and 2020–2030 and the Amboseli National Park Development Plan embedded within the ecosystem plan (KWS 2020). The seven group ranches within the Amboseli ecosystem, the Kenya Wildlife Service and conservation partners drew up the plans collaboratively. The primary goal of the Amboseli ecosystem plan is to secure the migratory space, landscape heterogeneity, and mobility needed to sustain the viability of wildlife populations and pastoral livelihoods. The planning process entailed an ecosystem-wide approach to conserving wildlife populations; land planning and zoning among the landowner and users; government agencies and conservation partners. The plans provide a balance of the various uses of the land, including farming, ranching, settlement, and service areas;

wildlife conservation and nature enterprises; legal provisions to institute and regulate the land use plans, and a mix of funding mechanisms to implement the plans.

The wider implications and applications of integrating livestock and wildlife management in Africa have been detailed by Keesing et al. (2018) and the broader principles of integrating conservation and other forms of land use by Sayer and Cassman (2013), Kremen and Merenlender (2018) and Kiffner et al. (2020). The prospects of conserving wildlife using traditional husbandry and land management practices for sustaining space and winning a place for wildlife among pastoral societies without protected areas have been documented by Western et al. (2020).

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DATA AVAILABILITY

The herbivore and plant data used in this paper can be requested directly via www.amboseliconservation.org or from the Database Administrator, Amboseli Conservation Program (acc@acc.or.ke).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3536/full