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# Long-term changes in the plant ecology of an African savanna landscape and the implications for ecosystem theory and conservation management



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**Abstract: Background:** Studies of the African savannas have used national parks to test ecological theories of natural ecosystems, including equilibrium, non-equilibrium, complex adaptive systems, and the role of top-down and bottom-up physical and biotic forces. Most such studies have excluded the impact of pastoralists in shaping grassland ecosystems and, over the last half century, the growing human impact on the world's rangelands. The mounting human impact calls for selecting indicators and integrated monitoring methods able to track ecosystem changes and the role of natural and human agencies. Our study draws on five decades of monitoring the Amboseli landscape in southern Kenya to document the declining role of natural agencies in shaping plant ecology with rising human impact.

**Results:** We show that plant diversity and productivity have declined, biomass turnover has increased in response to a downsizing of mean plant size, and that ecological resilience has declined with the rising probability of extreme shortfalls in pasture production. The signature of rainfall and physical agencies in driving ecosystem properties has decreased sharply with growing human impact.

We compare the Amboseli findings to the long-term studies of Kruger and Serengeti national parks to show that the human influence, whether by design or default, is increasingly shaping the ecology of savanna ecosystems. We look at the findings in the larger perspective of human impact on African grasslands and the world rangelands, in general, and discuss the implications for ecosystem theory and conservation policy and management.

**Conclusions:** The Amboseli study shows the value of using long-term integrated ecological monitoring to track the spatial and temporal changes in the species composition, structure, and function of rangeland ecosystems and the role of natural and human agencies in the process of change. The study echoes the widespread changes underway across African savannas and world's rangelands, concluding that some level of ecosystem management is needed to prevent land degradation and the erosion of ecological function, services, and resilience. Despite the weak application of ecological theory to conservation management, a plant trait-based approach is shown to be useful in explaining the macroecological changes underway.

**Keywords:** Savannas, Plants, Human dominance, Macroecology, Conservation

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## Background

Research over the last five decades has shown the plant structure and composition of African savanna communities to be shaped by physical and biotic factors. Protected areas have been widely used as inferential models to pose and test ecological theories of natural ecosystem (Sinclair and Norton-Griffiths 1979). The theoretical models include equilibrium, non-equilibrium, multi-state equilibria, and complex adaptive systems (Caughley 1976; Walker and Noy-Meir 1982; Dublin et al. 1990; Gillson 2004), and the role of top-down and bottom-up driving forces and their interactions (Power 1992).

Despite hunter-gatherers shaping the African savannas since the late Pleistocene (Redman 1999; Archibald et al. 2012) and the growing impact of farming and pastoralism through the Neolithic (Nentwig 2007; Wright 2017), human activity has been largely ignored in ecological studies. Pastoralism spread into eastern Africa at the end of the African Humid Period 4000 BP (Marshall and Hildebrand 2002), and livestock has since become numerically dominant to wild herbivores across African woodland and grassland ecosystems (Bourn 1978; Fritz and Duncan 1994). As a result, wildlife populations have declined steeply over the last half century due to rapid human population and economic growth (Craigie et al. 2010; Ogutu et al. 2016).

Whereas early studies of savannas ecosystems used national parks as baselines for inferring the ecology of naturally functioning systems (Sinclair, 1998), recent studies have shown the indirect impact of human activities to modify vegetation composition in even the largest parks (du Toit et al. 2003; Sinclair et al. 2015). Collectively, the segregation of formerly interlinked ecologies of wildlife and pastoralism can cause ecological knock-on effects independent of park size (Western and Gichohi 1993).

The ubiquity of the human imprint calls for monitoring ecosystems with sufficient resolution to detect the ecological changes and the role of natural and human agencies, and assess the implications for ecological theory and ecosystem conservation. The adequacy of a monitoring program to detect and decipher ecological changes hinges on the selection of indicators and protocols able to track the complexity and interconnectedness of ecosystem processes (Dale and Beyeler 2001). Other considerations include the choice of sampling procedures, consistency of monitoring, and its long-term sustainability (Hinds 1984). Poor spatial coverage and infrequent sampling, in particular, complicate the task of untangling oscillations from directional trends and, consequently, make it hard to distinguish human-induced from natural fluctuations, test ecological theories, and offer guidelines for conservation policy and management.

Here, we draw on a long-term monitoring study of a savanna landscape in southern Kenya to track the changes in vegetation and the declining responsiveness to natural processes. Conducted by the Amboseli Conservation Program (ACP), the study monitored human activity, including farming, livestock numbers, human settlement, and poaching, as well as wildlife populations, habitat changes, and plant composition and ecological properties (Western and Nightingale 2004; Western and Behrensmeier 2009; Mose et al. 2012).

Our main aim is to document the changing structure and ecological characteristics of a savanna ecosystem over the last half century. We use habitat type, tree, shrub, herb and grass biomass, and species composition to measure changes in plant structure, composition, production, size frequency, richness, diversity, and resilience to measure the changes in the Amboseli ecosystem. We show that the changes are commensurate with human-induced changes across the African savannas and rangelands of the world. The study underscores the importance and feasibility of long-term monitoring programs in tracking natural and human-induced changes, and highlights the use of a trait-based ecological approach in deciphering and explaining the interlocking changes.

## Study area

The greater Amboseli ecosystem covers the 8500 km<sup>2</sup> migratory range of the wild herbivore and pastoral livestock populations which move seasonally between wet and dry season pastures and portions of adjacent ecosystems. The ecosystem lies between latitudes 2°–3°S and longitudes 36.5°–38°E ranging in elevation from 1200 to 1500 m located north of Mt. Kilimanjaro along the Kenya-Tanzania border (Western et al., 2009). Both wild herbivores and Maasai herds spread widely during the rains and aggregate in the dry season around the permanent swamps of the Amboseli basin (Western 1973).

The ecosystem has been described in detail in several publications (Western 1973; Western and Dunne 1979; Western and Nightingale 2004; Western and Behrensmeier 2009; Moss et al. 2011; Mose et al. 2012). Maximum temperatures vary between 26 and 44 °C and minimum temperatures between 6 and 14 °C (Western, 1973, Altmann et al., 2002). Rainfall averages 350 mm annually with rains during October to December and March to May. The dominant vegetation is bushed grassland classified as ecological Zone V (Pratt et al. 1966). Aquifers from the northern forests of Kilimanjaro filter into the Amboseli basin and sustain a series of permanent swamps and hydrophilic woodlands dominated by *Acacia xanthophloea*.

The Amboseli ecosystem has been occupied by Maasai pastoralists for over half a millennium. The Maasai traditionally subsisted largely on the milk and meat of cattle,

supplemented by sheep and goats (Jacobs 1965; Home-wood 2008). Starting in the 1960s, the higher rainfall areas on the slopes of Kilimanjaro were partitioned into private farms which, over the following decades, spread downslope to the permanent swamps and rivers of Namelog and Kimana. The Ilkisongo section of the Maa-sai continued to track the wildlife migrations seasonally across the ecosystem until 1977 when livestock was excluded from the 388 km<sup>2</sup> Amboseli National Park, which aimed at protecting wildlife and promoting tourism. Starting in the 1970s, communally owned lands in the Amboseli ecosystem were divided into seven group ranches held under joint title deed by the customary pas-toral occupants (Kimani and Pickard 1998; Ntiati 2002; BurnSilver and Mwangi 2007). Seasonal herding practices nonetheless continued until the late 1980s when pastoral families began setting up permanent settlements to gain access to social services (Western and Nightingale 2004; Muchiru et al. 2008; Western et al. 2009).

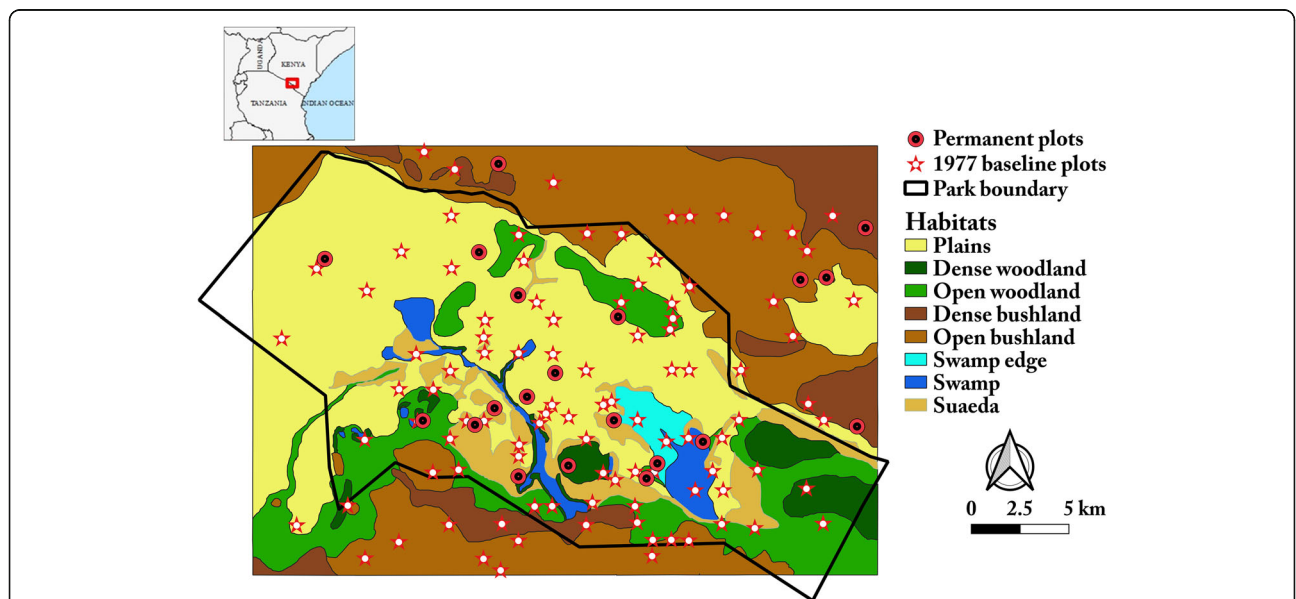
**Methods**

The habitat composition of the 700 km<sup>2</sup> Amboseli basin was described and mapped in 1967, transposed onto 1950 aerial photos and updated every 5 years through to 2002 (Western 2007). Twenty-five vegetation zones were initially described using Poore’s (1962) successive ap-proximation technique. Several zones too small to war-rant distinction were later amalgamated into larger zones, and three new zones were added as the vegetation composition changed over the ensuing decades. The vegetation zones were lumped into eight major habitats:

grasslands, dense woodlands, open woodlands, dense bush, open bush, swamp edge, permanent swamp, and *Suaeda* scrub for ease of interpretation and analysis (Western, 2007). The major habitats are shown in Fig. 1.

The structure and composition of Amboseli habitats was initially sampled quantitatively in 1977 using 101 circular plots 10 m in radius, giving an area of 314 m<sup>2</sup> (Fig. 1). The plots were randomly distributed across the 700 km<sup>2</sup> dry season range of the wild and domestic her-bivores. Vegetation cover was measured using the point intercept method (Jonasson 1988). For each frame, ten pins were dropped through a slanting pin frame angle of 67°, and each plant hit recorded. Plant cover was estimated as a percentage of total hits over the total number of pins (Western et al. 2015). Grass height was recorded in centimeters. Percentage grazing pressure was estimated from the proportion of grazed and non-grazed hits. The biomass for each species was derived from the equation  $\log_{10}D = \log_{10}(HC) - 0.38$  (Western and Lind-say 1984), where *D* is plant dry mass, *H* is the mean plant height in cm, and *C* is the percentage ground cover.

Bush and tree cover was sampled using the exclusion quadrant method (Cottam and Curtis 1956). Twenty plots were selected from the randomized set for continu-ous monthly monitoring of herb layer biomass and sea-sonal species composition (Western et al. 2015). To detect trends in plant characteristics, 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



**Fig. 1** Major habitats amalgamated into eight habitats from 29 vegetation zones defined in the 1967 baseline and subsequent surveys. The distribution of the 101 randomized plots in the 1977 species composition survey and the 20 subplots monitored every 4 to 6 weeks are shown. The permanent vegetation plots selected from the randomized set and measured monthly are distinguished by circles

possible autocorrelation in time series data, recognizing that vegetation biomass levels depend significantly on the previous month's biomass stock.

The changes in species composition in each habitat were based on relative abundance using a detrended correspondence analysis (DCA) and ordination technique of Hill and Gauch (1980). Change point analysis was used to identify significant fluctuations in plant biomass, diversity, dominance, richness, size frequency, and production. We used the Behavioral Change Point Analysis (BCPA) in R (R Core Team 2020) to detect the likelihood of significant changes in long-term datasets (Gurarie 2014).

The macroecological changes in the vegetation structure and composition of the Amboseli plant community were quantified using measures of plant size frequency, turnover rate, species richness, diversity, dominance, and productivity. The size frequency of woody plants was calculated using the following formula:

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

At time  $t$ ,  $\bar{w}_t$  is the size frequency for all plants (mean biomass weight of all species combined),  $N_t$  is the total number of species sampled,  $n_{it}$  is the number of species  $i$  observed during the survey, and  $\bar{x}_i$  is taken as the mean weight of species  $i$ . Changes in plant production were calculated for tree, shrub, and herb biomass for individual species, based on the average weights and specific gravity for each species in Amboseli. The total production for all species combined was calculated using the equation

$$P_t = \sum_i n_{it} \bar{x}_i^{0.763} \quad (2)$$

At time  $t$ ,  $P_t$  is estimated as the production for all plants,  $n_{it}$  is the number of species  $i$  observed during the survey, and  $\bar{x}_i$  is the mean weight of species  $i$ .

## Results

### Habitat changes

Habitat changes over the five decades from 1950 to 1997 have been detailed in a previous publication (Western 2007). Here, we have extended the analysis to 2017. Of the 25 vegetation zones mapped in 1967 (Western 1973) and tracked since 1950 from aerial photo coverage, dense and open *Acacia xanthophloea* habitat was replaced by *Suaeda monoica* shrubland. Dense *Acacia tortilis* woodlands and *Acacia mellifera* bushlands were replaced by open scrub and herbaceous habitats. The mixed *Acacia xanthophloea* and *Phoenix reclinata* zone lost most of its *Acacia* trees before being replaced by open grasslands. Classifying the vegetation zones into

woodland (open and dense woodland), bushland (open and dense bushland), scrubland (*Suaeda*), grassland (plains), swamp, and swamp-edge habitats (Fig. 2) shows woodlands have shrunk from 25% cover in 1950 to 5% in 2017, and grassland has expanded from 28 to 40% cover. Swamp and swamp-edge habitats, which expanded with the loss of woodlands, have shown minor changes since the 1990s, corresponding to fluctuations in water discharge from Kilimanjaro.

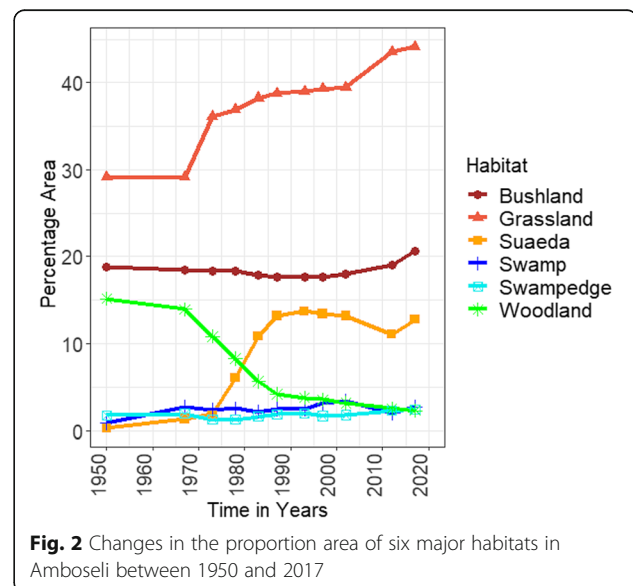
The reduction in habitat diversity based on the 25 vegetation zones mapped in 1967 is striking. The highly significant decline ( $r = -0.91$ ,  $r^2 = 0.82$ ,  $P < 0.0001$ ) measured by the Shannon-Wiener's diversity (Peet 1974) index is shown in Fig. 3.

### Plant biomass

Total biomass declined steeply from over 600  $\text{gm}^{-2}$  in the 1970s to 200  $\text{gm}^{-2}$  in 2017 ( $\tau = -0.66$ ,  $P < 0.001$ ). The decline in vegetation biomass was significant for all habitats except the plains (Table S1). The largest contributors to the biomass decline were the woodland (30%), swamp (20%), and swamp edge habitats (14%).

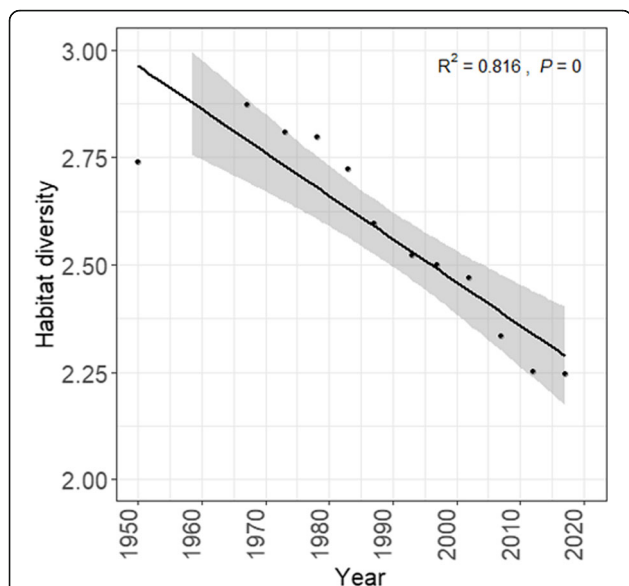
### Biomass composition

Figure 4 illustrates the changes in tree, shrub, herb, and grass biomass for all habitats combined. A modified Mann-Kendall trend test (Hamed and Rao 1998) shows a significant decline in tree ( $\tau = -0.409$ ,  $P < 0.001$ ), shrub ( $\tau = -0.609$ ,  $P < 0.001$ ), and grass biomass ( $\tau = -0.355$ ,  $P = 0.007$ ), but not in herb biomass ( $\tau = 0.118$ ,  $P = 0.378$ ). Herb biomass did, however, decline significantly after 1994 ( $\tau = -0.412$ ,  $P = 0.018$ ). The largest contributor to the overall decline was the loss of grass and tree biomass. Tree and shrub biomass declined significantly



**Fig. 2** Changes in the proportion area of six major habitats in Amboseli between 1950 and 2017

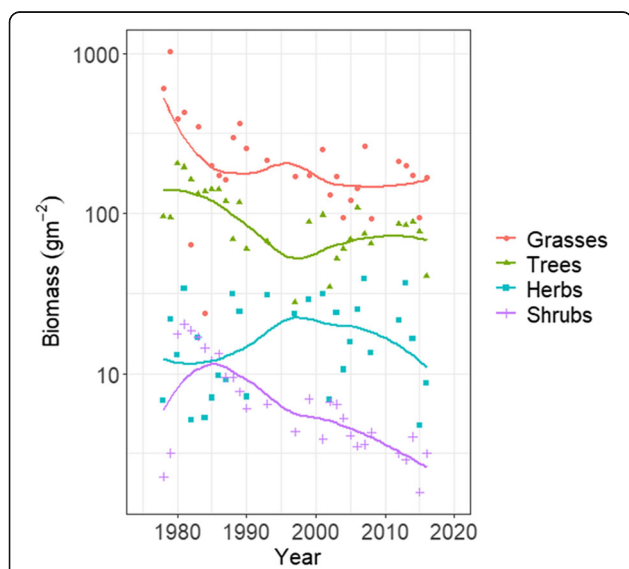




**Fig. 3** Shannon-Wiener's index of diversity based on the 25 vegetation zones originally mapped in Amboseli in 1967 and transposed onto 1950 aerial photos

in all habitats; grass biomass declined in woodland, swamp, and swamp-edge habitats; and herbs only declined in woodland habitats.

The decline in tree and shrub species in all habitats resulted in a convergence in biomass heterogeneity between habitats. A dissimilarity index based on biomass differences between the twenty permanent plots distributed across all habitats decreased over time ( $\tau = -0.326, P = 0.02$ ). The convergence was largely due to the reduction of tree, shrub, and sedges in the high biomass



**Fig. 4** Average biomass density changes in trees, shrubs, herbs, and grasses between 1977 and 2017

woodland, swamp-edge, and swamp habitats in favor of low biomass grasslands, *Suaeda*, and bushland habitats.

**Species similarity and turnover**

Species richness in the 20 permanent plots declined between 1977 and 2017 ( $\tau = -0.326, P = 0.02$ ) based on species comprising 4% or more of the 101 randomly selected plots in the 1977. The list of 73 plant species included in the analysis is given in Table S2.

A Sorensen's similarity index (Sorensen 1948) of species composition showed no significant change in the bushland ( $\tau = 0.027, P = 0.87$ ) and plain habitats ( $\tau = -0.071, P = 0.62$ ), but a significant increase in the woodlands ( $\tau = 0.32, P = 0.027$ ) and swamp-edge habitats ( $\tau = 0.30, P = 0.041$ ).

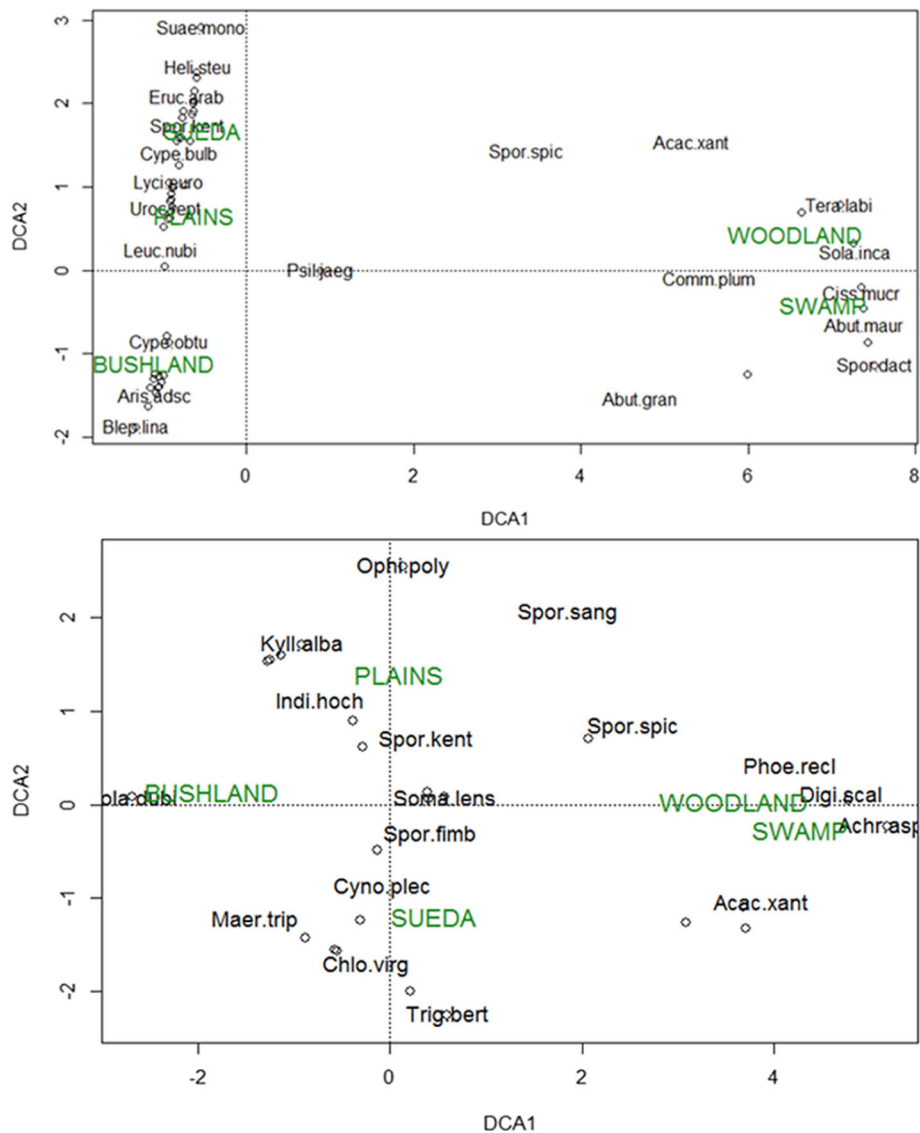
**Changes in species composition**

The changes in species composition in each habitat are shown in Fig. 5. The analysis includes the most abundant species which have cumulatively contributed 95% of the total plant biomass. The clustering was pronounced in the 1970s, with the woodland and swamp habitats showing close similarity and the plains, *Suaeda*, and bushland habitats a clearer delineation along axis 1 (DCA1). *Suaeda* and plain habitats were closely clustered on axis 2 (DCA2) and distinct from the bushlands. By the 2010s, the distinctions between habitats declined sharply, pointing to a narrowing species composition.

**Macroecological changes**

The temporal changes in total production of trees, shrubs, and herbs combined are given in Fig. 7. Production declined sharply from 1977 ( $\tau = -0.758, P < 0.001$ ) to the change point in 1997, followed by a small recovery. The decline in production corresponds to changes in size frequency ( $\tau = -0.354, P = 0.012$ ), pointing to the loss of trees and large shrubs as the main cause of decline (Fig. 6). Given the functional relationship between species size ( $M$ ) and growth rate ( $G$ ) in  $G\alpha M^{0.75}$  (Niklas and Enquist 2001), it follows that annual turnover rate in plant biomass averaged for all habitats is directly correlated with changes in production shown in Fig. 7.

Changes in herb layer biomass aggregated for the 20 permanent plots are shown in Fig. 8. The graph expands the 1982 to 2010 coverage cited in Western et al. (2015) to 2018. Herb layer biomass declined significantly over the last five decades ( $\tau = -0.223, P < 0.001$ ). The change point at 1998 closely matches the change point in size frequency and production of woody vegetation (Figs. 6 and 7), again showing an upturn with the exceptionally heavy El Niño rains of 1998.



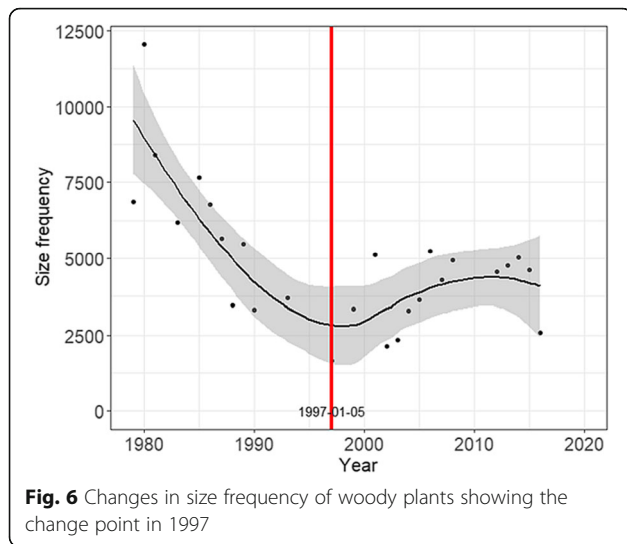
**Fig. 5** Detrended correspondence analysis ordination shows the increasing similarity in species composition among habitats between the 1970s (top) and 2010s (below). The names shown in the figures are the first four letters of the genus and species names. The complete species list is provided in Table S2

Changes in the resilience of vegetation (Walker and Noy-Meir 1982) can be gauged by a reduced production response to rainfall and in seasonal production normalized for rainfall. Western et al. (2015) used the declining response of pasture production to rainfall in Amboseli to show a loss of resilience due to intensified herbivory from 1982 to 2010. Figure 9 shows the data extended to 2018. The diminished response of production to rainfall is highly significant ( $\tau = -0.256, P < 0.001$ ), giving a direct measure of the decline in the resilience of the herb layer community.

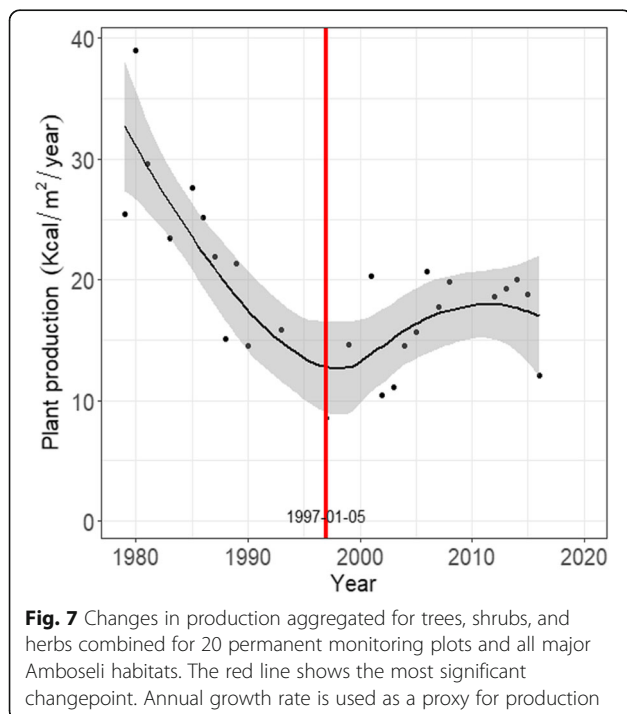
We found a similar loss of woody plant resilience using the same method to measure the decline in production (Fig. 7) per unit of rainfall ( $\tau = -0.169,$

$P = 0.012$ ). We also found a decrease in resilience measured by an increase in plant seasonality. We used the likelihood ratio test to determine the probability of increased forage and rainfall seasonality by comparing a null regression model with a model including time in years for rainfall and forage seasonality. The model yielded a significant fit for forage shortfalls ( $\chi^2_{(1)} = 24.04, P < 0.0001$ ), signaling a rising likelihood of extreme deficits, despite showing no significant rise in the probability of rainfall deficits ( $\chi^2_{(1)} = 1.98, P = 0.1592$ ).

Changes in species diversity (Simpson 1949; Peet 1974), richness, and dominance (McNaughton and Wolf



1970) used as measures of macroecological change in all plots combined are shown in Fig. 10. Diversity ( $\tau = -0.573$ ,  $P < 0.0001$ ) and dominance ( $\tau = 0.317$ ,  $P = 0.025$ ) declined steadily over the study period but most strongly after the change point in the late 1990s. Species richness over the study period showed no significant change ( $\tau = -0.197$ ,  $P = 0.17$ ) but did show a significant decline after the 1990 change point ( $\tau = -0.402$ ,  $P = 0.044$ ). The change point in each case is similar, showing a decline in species richness and diversity and an increase in dominance to have accelerated after the 1990s. The decline corresponds to the replacement of the woodlands by



*Suaeda* (Fig. 2) and the decline in size frequency with the loss of large trees (Fig. 6).

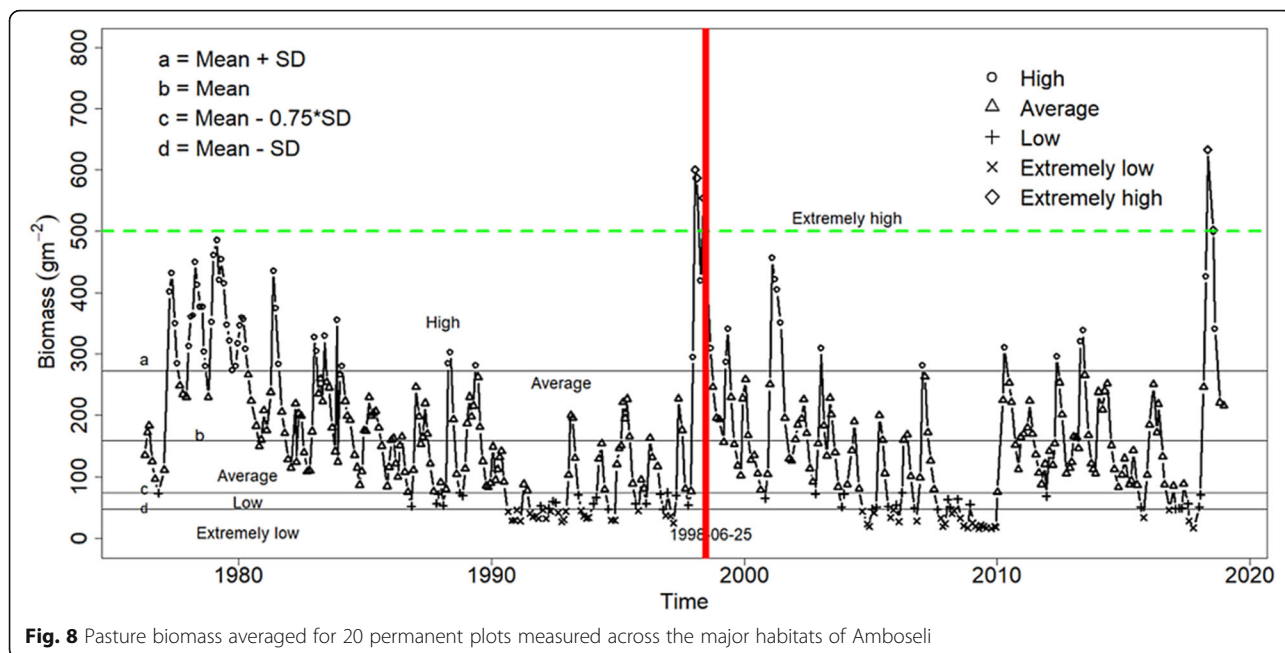
## Discussion

The Amboseli monitoring program shows the value of long-term ecological research sites (Franklin et al. 1990) in tracking a wide range of plant properties in an ecosystem in response to natural and human agencies. The study also points to the need to view protected areas within a larger landscape context in order to capture the external causes of vegetation changes. The results also illustrate the variety of information which can be gathered for documenting and exploring the interconnected ecosystem changes.

In the case of Amboseli, the results track the declines in habitats, tree, shrub, herb and grass biomass, species diversity, and mean plant size since the 1970s. Species dominance has risen as species diversity has fallen, and annual biomass turnover has grown inversely with diminishing plant size. Plant productivity has declined, seasonality has increased, and the probability of extreme shortfalls has risen. Taken together, the results show that the production, diversity, ecological function, and resilience of the plant community have all declined sharply over the last five decades.

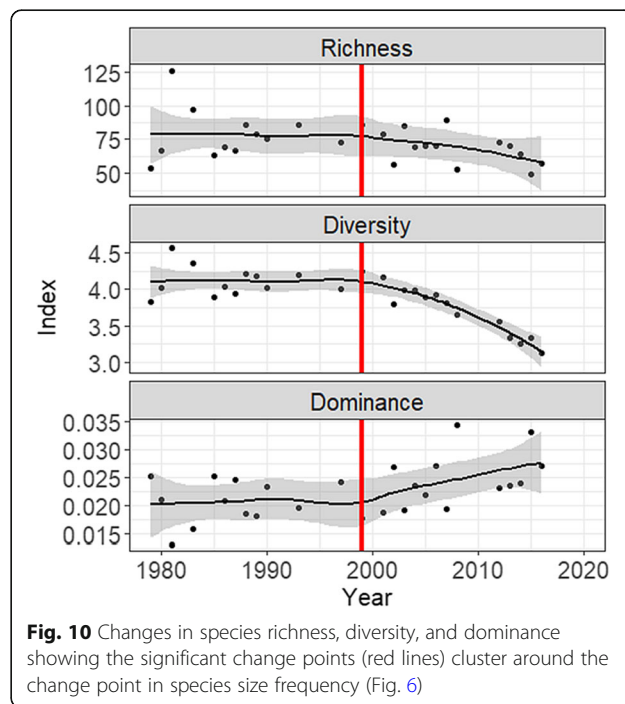
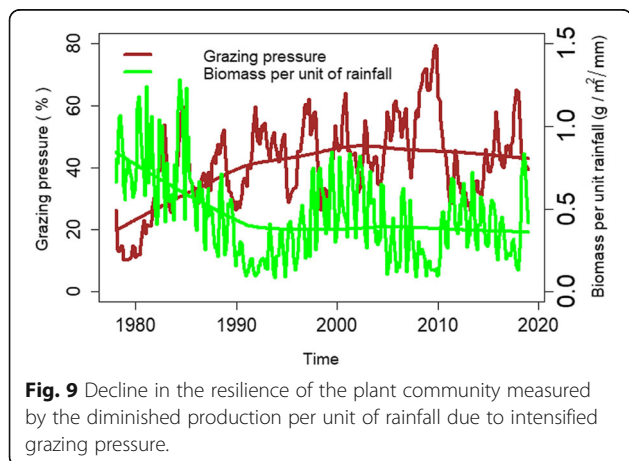
Prior to the 1990s change point, a simple regression model shows rainfall to significantly predict total plant biomass ( $r^2 = 0.45$ ,  $P = 0.012$ ), grass biomass ( $r^2 = 0.56$ ,  $P = 0.003$ ), tree biomass ( $r^2 = 0.32$ ,  $P = 0.046$ ), and shrub biomass ( $r^2 = 0.43$ ,  $P = 0.014$ ) and marginally herb biomass ( $r^2 = 0.43$ ,  $P = 0.082$ ). After 1990, rainfall falls to insignificance in predicting total biomass ( $r^2 = 0.21$ ,  $P = 0.071$ ), tree biomass ( $r^2 = 0.03$ ,  $P = 0.514$ ), shrub biomass ( $r^2 = 0.07$ ,  $P = 0.336$ ), and herb biomass ( $r^2 = 0.05$ ,  $P = 0.386$ ) and becomes a weak predictor of grass biomass ( $r^2 = 0.25$ ,  $P = 0.049$ ).

The declining significance of rainfall corresponds to an increase in browsing and grazing pressure in recent decades. So, for example, the loss of *Acacia* woodlands and woody vegetation (Western and Van Praet 1973; Western and Maitumo 2004) was shown in a 20-year elephant exclusion experiment (Western 2007). The heavy browsing resulted from the recovery of elephant populations throughout East and Central Africa after the decline of the 19th century ivory trade (Parker and Amin 1983; Cumming et al. 1997; Håkansson 2004). In Amboseli, the growth in elephant numbers was coupled with a concentration of herds into the safety of Amboseli National Park in the 1970s (Western and Lindsay 1984; Moss 2012) during a surge in poaching across Africa (Douglas-Hamilton 1987). A meta-analysis of many studies shows that high densities of elephants reduce woody vegetation in dry savannas (Guldmond and Van Aarde 2008).



The 30% decline in herbaceous productivity has been attributed to a three-fold increase in grazing pressure due to intensified pastoralism, land use changes, sedentarization, and reduced livestock mobility (Worden et al. 2003; Groom and Western 2013; Western et al. 2015; Okello et al. 2016), coupled with the compression of wildlife into the late season pastures (Sarkar 2006; Western et al. 2015). The impact of intensified herbivory was anticipated by earlier studies in the Amboseli area. Casady (1973), for example, showed that repeated grazing through the year reduced plant production by 22 to 60% relative to controls, whereas heavy defoliation once each dry season sustained production. Georgiadis et al. (1989) further demonstrated in potted plant experiments which manipulated water, nutrient, and defoliation treatments

that frequent repeated offtake deletes resilience far more than short-intensive defoliation. Studies by Dunne et al. (2011) experimentally manipulating trampling and grazing showed both factors to depress pasture production per unit of rainfall. The results match similar findings in South America where Toft et al. (1987) showed trampling coupled with heavy grazing reduced plant biomass





and caused a convergence in stand floristics across plant communities.

The reduction in plant biomass and productivity in Amboseli applies widely across African grassland ecosystems. Le Houerou (1989), for example, found cultivation and heavy grazing to have reduced grassland and woody vegetation across 3 million km<sup>2</sup> of northern Africa since World War II. Dodd (1994) documented similar widespread rangeland degradation in Sub-Saharan Africa. Angerer et al. (2016) have shown similar human-induced changes across the rangelands which cover 40% of the earth's terrestrial surface. Although the proximate causes of degradation have commonly been attributed to intensified herbivory in each case, the ultimate causes are often complex, including human and livestock population growth, land subdivision and expropriation, social dislocation, a breakdown in governance institutions, and climate change (Palmer and Bennett 2013; Boles et al. 2019)

Most research on African savanna ecosystems in recent decades has focused on changes in large mammals. Widespread declines in wildlife populations have been documented inside as well as outside protected areas across east and southern Africa (Caro and Scholte 2007; Craigie et al. 2010; Ogotu et al. 2016). The causes include loss of range, land transformation, habitat fragmentation, population growth, livestock impact, poaching, lack of local engagement, human-wildlife conflict, insufficient conservation funding, and climate change (Craigie et al. 2010; Ogotu et al. 2016).

In contrast to the large mammal studies of the African savannas, few studies apart from Amboseli have systematically monitored changes in plant communities and their causes and their applications to ecosystem management. The two exceptions include Africa's largest protected areas, the 22,000 km<sup>2</sup> Kruger National Park in South Africa, and the 25,000 km<sup>2</sup> Serengeti-Mara complex in East Africa. Both parks cover a large and diverse landscape and include almost all the plant and animals that occurred in historical times. The studies underscore the importance of large open landscapes in sustaining natural ecological process, yet also highlight the weakening influence of natural agencies and rising impact of human activity in determining the ecology of animal and plant communities.

In Kruger National Park, which was established in 1926, the vegetation was, until the 1990s, actively managed to prevent the destruction of woodlands by a rising elephant population fenced within the park. Water points, fire, elephant numbers, populations of other large herbivores, and diseases were controlled within defined limits to maintain the park in a relative constant state (Mabunda et al. 2003). Recognizing over-management had created vegetation homogeneity, park policy changed in the 1990s to restore heterogeneity by allowing

natural processes to prevail, intervening only to avoid extreme disruptions (du Toit et al. 2003). So, for example, the fence bordering Mozambique was removed to allow greater freedom of elephant movement and reduce the compression effects on vegetation. Further, the long-term studies have shown that a hierarchy of factors and non-linear processes govern ecosystem heterogeneity and shaped the new management policies which recognize Kruger as a complex adaptive system continually responding to new influences (Mills et al. 2003). In short, both management and policy have been guided by a close link between scientific research and conservation goals.

Serengeti, established in 1952, brought together disparate threads of research in the 1960s to describe the processes and patterns governing the Serengeti ecosystem and provide information for management (Sinclair 1973). The research program found tree cover giving way to grasslands due to the recovery of migratory wildebeest populations after the rinderpest epidemic of the late 1900s, and to increased fire, elephant ingress, and changes in rainfall regime (Sinclair 1973). Unlike Kruger, Serengeti management and policy has not been closely guided by research but used to test alternative ecosystem theories, including the stable limit cycles proposed by Caughley (1976) and multiple stable states proposed by Dublin et al. (1990). The studies concluded that neither theory is upheld by data from Serengeti. Rather, the plant community is changing continuously, though with no monotonic trend toward a different compositional state (Woodroffe and Ginsberg 1998).

Later studies that expanded to include surrounding lands dominated by farming and pastoralism, found Serengeti's ecology intertwined with human impact (Sinclair et al. 2015). A recent study of the changes in the spatial distribution of large herbivores and vegetation responses found livestock and farming to have compressed wildlife within the park. The compression caused lower primary production, a loss of favored herbivore grass species, an increase in unpalatable herbs, lower carbon storage, and decreased resistance to rainfall deficits (Veldhuis et al. 2019). The impact of human activity surrounding Serengeti National Park, though muted, mirrors the impact of intensified herbivory in Amboseli, a national park less than 2% its size.

The long-term research in Amboseli, Kruger, and Serengeti shows the importance of long-term landscape-level monitoring to the conservation of protected areas. The ecology of parks, even the largest of them, has been shown to be influenced by edge effects (Woodroffe and Ginsberg 1998), insularization (Soule et al. 1979), invasive species (Crowl et al. 2008), and disruptions due to ecological dislocations across park boundaries (Western and Gichohi 1993).

The long-term studies of African landscapes reflect universal changes underway. On a global scale, for example, Tucker et al. (2018) found that a wide range of species in the Anthropocene show reduced movements and constricted ranges. The findings demonstrate human impact to be so widespread and pervasive as to call for a reclassification of natural biomes as anthromes (Ellis and Ramankutty 2008). The pervasiveness raises the question of whether ecosystem theories have validity or utility in conservation management, whether baseline reference points are useful given millennial changes (Foster and Aber 2004; Briske et al. 2020), and whether species diversity as a measure of ecosystem functionality is useful. Boles et al. (2019), for example, found in all major ecosystems and climatic zones worldwide that, despite no systematic change in species richness, composition had changed extensively. The biodiversity crisis, they concluded, is more of a case of large-scale reorganization than species loss.

Janzen (1998) and Kareiva et al. (2011) assert that human modification is so great and irreversible as to justify “gardening” nature rather than management based on historical templates. Sinclair and Dobson (2015) argue that protected areas can serve as a control to test whether human-dominated ecosystems are sustainable and robust. Based on the continued growth in protected areas worldwide (McNeely and Miller 1983), and the growing conservation efforts in human-dominated landscapes (Berkes 2007), we consider both protected and non-protected areas to play important and complementary roles (Western et al. 2020). We argue that the worldwide biodiversity loss calls for some level of ecosystem management to prevent land degradation and the erosion of ecological function, services, and resilience as documented in detail in Amboseli. Further, the complexity of ecosystems and the multiplicity of human factors call for monitoring human activity as an integral part of research.

## Conclusions

The long-term Amboseli research shows that it is possible to simultaneously monitor the spatial and temporal changes of a wide range of compositional, structural, and functional plant variables, and to detect the changing role of natural and human agencies.

The Amboseli study in encompassing human activity also points to the weaknesses of using parks as referential models of natural ecosystems and the importance of human dimensions in accounting for ecological changes within parks. Further, although ecosystem theories are proving of limited value in conservation policy and management, the results of the long-term monitoring in Amboseli support a growing body of ecologists who consider functional traits to offer a useful framework for

drawing ecological generalities and making predictions (Levin 1998). The macroecological synthesis linking organism size, life history traits, and function, already well established in animals (Brown and Maurer 1989; Smith et al. 2014), has also been shown to apply to plants (Díaz et al. 2016; Kunstler et al. 2016), based on universal scaling laws (Enquist et al. 1999; West et al. 1999; Enquist 2002). Levin (1998) concludes that with the likelihood of climate change creating new species and novel assemblages, a trait-based approach may be the only way to predict interactions and outcomes. The Amboseli study bears out the utility of a trait-based approach in explaining the interconnected cascade of changes in plant communities linked to changes in size frequency.

## Declarations

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-021-00286-5>.

**Additional file 1:** Electronic Supplemental Material (ESM)

## Abbreviations

ACP: Amboseli Conservation Program; DCA: Detrended correspondence analysis; BCPA: Behavioral Change Point Analysis

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## Authors' contributions

DW has designed, directed, and funded Amboseli Conservation Program (ACP) since its origins in 1967. DM has served as research field assistant to ACP since 1977 and collected most of the permanent plot data used in the analysis. VNM has overseen the computer database, analytical design, statistical analysis, and modeling used in this article; assisted in the analysis by CM; and is an intern and research associate to the project. All authors read and approved the final manuscript.

## Authors' information

DW (Ph.D.) established the Amboseli Conservation Program (ACP) in 1967 and is a former director of the Kenya Wildlife Service. VNM (Ph.D.) is ACP's Biostatistician and co-director. DM (KCE) is ACP's field researcher since 1977. CM (MSc) is a research associate of ACP.

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## Availability of data and materials

The plant data used in this paper can be requested directly via [www.amboseliconservation.org](http://www.amboseliconservation.org) or from the Database Administrator, Amboseli Conservation Program ([acc@acc.or.ke](mailto:acc@acc.or.ke)).

## Ethics approval and consent to participate

Not applicable.

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**Competing interests**

The authors declare no competing interests.

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