

# Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines

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## Summary

1. Large mammalian herbivores (LMH) exert strong effects on plants in tropical savannas, and many wild LMH populations are declining. However, predicting the impacts of these declines on vegetation structure remains challenging.

2. Experiments suggest that tree cover can increase rapidly following LMH exclusion. Yet it is unclear whether these results scale up to predict ecosystem-level impacts of LMH declines, which often alter fire regimes, trigger compensatory responses of other herbivores and accompany anthropogenic land-use changes. Moreover, theory predicts that grazers and browsers should have opposing effects on tree cover, further complicating efforts to forecast the outcomes of community-wide declines.

3. We used the near-extirpation of grazing and browsing LMH from Gorongosa National Park during the Mozambican Civil War (1977–1992) as a natural experiment to test whether megafaunal collapse increased tree cover. We classified herbaceous and tree cover in satellite images taken (a) at the onset of war in 1977 and (b) in 2012, two decades after hostilities ceased.

4. Throughout the 3620-km<sup>2</sup> park, proportional tree cover increased by 34% (from 0.29 to 0.39) – an addition of 362 km<sup>2</sup>. Four of the park's five major habitat zones (including miombo woodland, *Acacia–Combretum*–palm savanna, and floodplain grassland) showed even greater increases in tree cover (51–134%), with an average increase of 94% in ecologically critical Rift Valley habitats. Only in the eastern Cheringoma Plateau, which had historically low wildlife densities, did tree cover decrease (by 5%).

5. The most parsimonious explanation for these results is that reduced browsing pressure enhanced tree growth, survival and/or recruitment; we found no directional trends in rainfall or fire that could explain increased tree cover.

6. *Synthesis.* Catastrophic large-herbivore die-offs in Mozambique's flagship national park were followed by 35 years of woodland expansion, most severely in areas where pre-war wildlife biomass was greatest. These findings suggest that browsing release supersedes grazer–grass–fire feedbacks in governing ecosystem-level tree cover, consistent with smaller-scale experimental results, although the potentially complementary effect of CO<sub>2</sub> fertilization cannot be definitively ruled out. Future work in Gorongosa will reveal whether recovering LMH populations reverse this trend, or alternatively whether woody encroachment hinders ongoing restoration efforts.

**Key-words:** biodiversity loss, bush encroachment, elephants *Loxodonta africana*, extinction, Hexagon satellite, plant–herbivore interactions, remote sensing, top-down effects, tree–grass coexistence, trophic cascade

## Introduction

Understanding the frequency, severity and drivers of extreme population declines in animal populations is integral to ecology, with much effort focused on the population ecology and

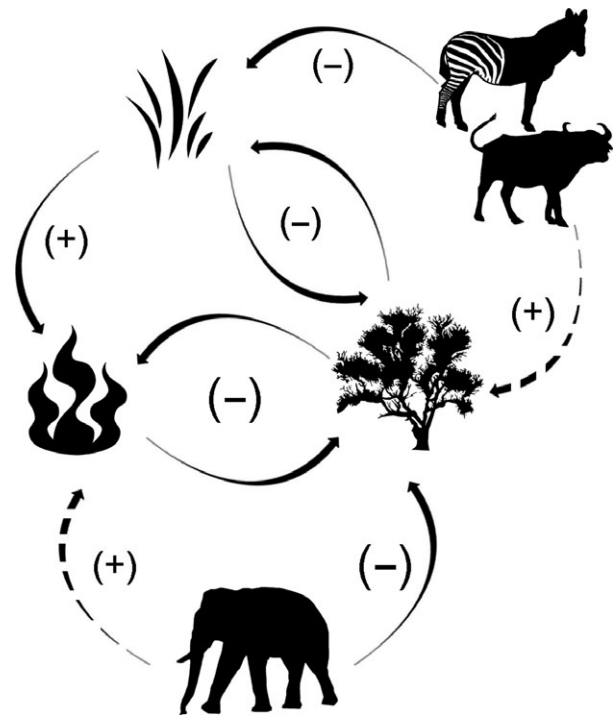
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management of declining species themselves (Young 1994; Erb & Boyce 1999; Reed *et al.* 2003; Fey *et al.* 2015). However, catastrophic die-offs have community- and ecosystem-level implications that are less well understood (e.g. Colon-Gaud *et al.* 2010; Gill 2013), in part because die-offs cannot be anticipated and are difficult to study or simulate at relevant scales. Thus, whereas small-scale experiments manipulating species presence/absence and richness remain a staple of ecological research (Hooper *et al.* 2005; Pringle 2012), comparatively few studies have documented the downstream consequences of severe population declines or the removal of entire guilds and functional groups from real ecosystems (but see Prins & van der Jeugd 1993; Connelly *et al.* 2008; Holdo *et al.* 2009; Ripple *et al.* 2014).

In African savannas, many populations of large mammalian herbivores (LMH) have undergone severe declines of > 50% over the last several decades (Craigie *et al.* 2010), which may have profound impacts on the savanna habitats that cover most of the continent. Savannas are defined by the presence of a grass layer with an overstorey tree layer of variable density, and a key question is to what extent LMH declines are likely to shift this balance of herbaceous and woody vegetation. In the extreme, changes in relative tree cover may even precipitate transitions from savanna to the alternative states of forest (high tree cover with little grass), on the one hand, or grasslands (with few-to-no trees), on the other (Hirota *et al.* 2011). The relative dominance of woody and herbaceous plants is in turn of great importance for savanna biodiversity and management (Ward 2005; O'Connor, Puttick & Hoffman 2014). The amount of tree cover in savannas strongly affects ecosystem function. For example, nutrients collect at the base of woody plants, altering spatial patterns of soil fertility (Scholes & Archer 1997), and trees can both decrease soil moisture by evapotranspiration (Joffre & Rambal 1993) and increase it through shading and hydraulic lift (Ludwig *et al.* 2002). The distribution of tree cover likewise governs the relative abundances of animal populations (Parr, Gray & Bond 2012; Sirami & Monadjem 2012) and can alter trophic interactions by modulating the degree of concealment vs. visibility for predators and prey (Tambling *et al.* 2013; Ford *et al.* 2014).

Some drivers of savanna tree cover are well known. In Africa, below a threshold of ~650 mm mean annual precipitation, rainfall puts an upper bound on savanna tree cover; above this threshold, the amount of tree cover depends on disturbance (Sankaran *et al.* 2005). The best-studied source of disturbance is fire, which reduces tree cover by consuming seedlings and saplings (Trollope & Tainton 1986; Bond 2008). Feedback loops between fire and vegetation structure are important in this process: frequent fires reduce tree cover and promote herbaceous species, which fuel additional fires; conversely, infrequent fires promote tree cover that shades out herbaceous fuels, further reducing fire (Van Langevelde *et al.* 2003; Staver, Archibald & Levin 2011a).

LMH are another source of disturbance that affects savanna tree cover (Fig. 1; Sankaran, Ratnam & Hanan 2008; Asner & Levick 2012), although their effects are less well under-



**Fig. 1.** Schematic illustrating direct and indirect (dashed arrows) interactions among large mammalian herbivores, herbaceous vegetation, trees and fire in African savannas. Browsers reduce tree biomass by feeding on adult trees and saplings. Because trees compete with the herbaceous plants that fuel fires, browsers have an indirect positive effect on fire. Grazers have indirect positive effects on trees by reducing grass biomass that would otherwise fuel fires. Figure patterned after Van Langevelde *et al.* (2003).

stood and their collective significance in determining vegetation structure over large spatio-temporal scales remains uncertain. In contrast to fire – an extremely generalist ‘herbivore’ (Bond & Keeley 2005) – LMH assemblages comprise multiple species with distinct diets (Kartzinel *et al.* 2015) and non-redundant impacts on shared forage plants (Goheen *et al.* 2013; Pringle *et al.* 2014). In particular, the two main LMH trophic guilds, grazers and browsers, are expected to have contrasting direct and indirect effects on tree cover and fire regimes (Van Langevelde *et al.* 2003; Holdo, Holt & Fryxell 2009). Grazers such as buffalo, zebra and wildebeest consume mainly herbaceous fuels, which should promote tree cover by reducing fire frequency, extent and intensity, and releasing trees from competition with grasses (Scholes & Archer 1997; Holdo *et al.* 2009). Conversely, browsers such as elephant, kudu and impala reduce tree cover by consuming woody plants (Dublin, Sinclair & McGlade 1990; Prins & van der Jeugd 1993; Staver & Bond 2014) and, in the case of elephants, toppling adult trees (Laws 1970; Asner & Levick 2012); this produces more grassy, fire-prone states, which further suppresses tree cover (Van Langevelde *et al.* 2003). Thus, whereas increases or decreases in the density of just one of these guilds may have predictable effects on tree cover, the impacts of changes in whole LMH assemblages are difficult to forecast. Moreover, the lack of continental-scale data sets on LMH (Staver, Archibald & Levin 2011b) compa-

rable to those for fire (e.g. Boschetti, Roy & Hoffmann 2009) and rainfall (Huffman *et al.* 2007) precludes macro-ecological assessment of covariation between herbivory and tree cover.

Experimental enclosure studies have yielded considerable mechanistic insight into the effects of LMH on vegetation structure in African savannas (e.g. Pringle *et al.* 2011; Sankaran, Augustine & Ratnam 2013; Ford *et al.* 2015). These studies have repeatedly shown increased tree cover following wholesale LMH removal due to increased growth (Staver *et al.* 2009), recruitment (Augustine & McNaughton 2004) and survival (Asner & Levick 2012). However, these studies are unavoidably constrained in spatial and temporal scale: plot sizes are small (almost all < 0.05 km<sup>2</sup>, maximum 3 km<sup>2</sup>), and study durations are short (typically < 10 years). Consequently, such manipulations may not reliably simulate the full range of processes associated with real-world LMH die-offs, including scale-dependent feedbacks among herbivory, fire and vegetation structure (House *et al.* 2003), and compensatory responses by small herbivores or livestock (Young *et al.* 2013, 2015).

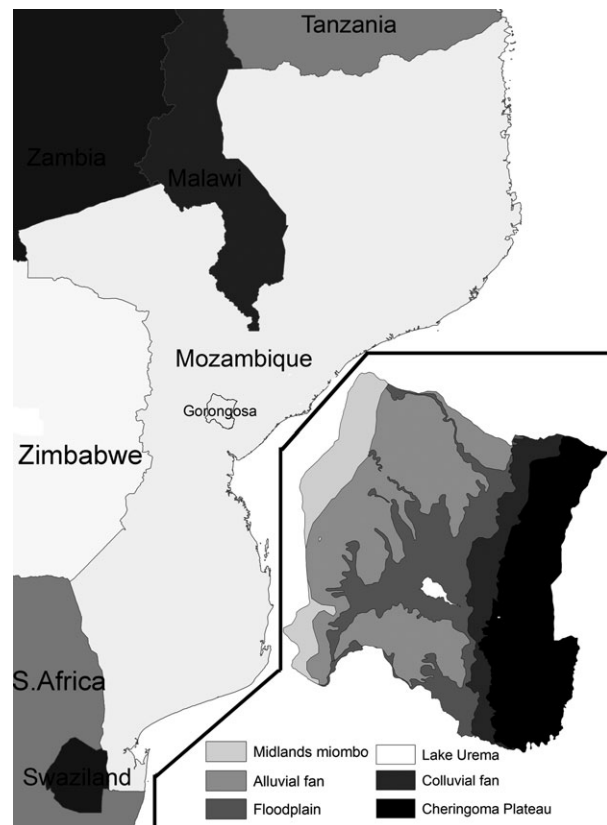
In cases where adequate survey and/or remotely sensed data are available, severe LMH declines (e.g. Prins & van der Jeugd 1993; Holdo *et al.* 2009) can be used as natural experiments to test for shifts in vegetation structure and assess the scalability of smaller controlled manipulations. In Gorongosa National Park, Mozambique, populations of all LMH species declined precipitously due to intensive hunting during the Mozambican Civil War (1977–1992) (Tinley 1977; Pringle 2012; Stalmans 2012). We compared estimates of tree cover across the entire 3620-km<sup>2</sup> park derived from satellite imagery collected in 1977 and 2012 to determine how the near-extirpation of LMH in Gorongosa affected vegetation structure, and we resurveyed a 1-ha vegetation plot established in 1972 to test for concordance between ground-based tree-cover trends and remote-sensing results. In addition, we reconstructed rainfall (1951–2012) and fire (2000–2012) regimes, to assess whether directional changes in these abiotic factors were likely to have contributed to vegetation trends.

We hypothesized that the release of woody plants from browsing pressure has led to increased tree cover and that impacts would be stronger in regions of the park with historically higher LMH densities. Although theory predicts opposing impacts of browser vs. grazer declines, we favoured the browsing-release hypothesis in light of the (i) mounting experimental evidence that ‘release from browsing trumps grazer–grass–fire interactions’ (Staver & Bond 2014), (ii) profound and well-known impacts of elephants in particular (Guldmond & van Aarde 2008) and (iii) relative scarcity of empirical evidence linking grazer declines to decreased tree cover (but see Holdo *et al.* 2009). Our hypothesis would be rejected under either of two plausible alternative outcomes: (i) decreased tree cover, if release of grasses from grazing pressure intensified grass competition with trees and/or increased fire frequency/extent, or (ii) negligible net change, if LMH do not control tree cover or if impacts of grazer and browser loss offset.

## Materials and methods

### SITE DESCRIPTION

Gorongosa National Park (Fig. 2) lies at the southern end of the Great Rift Valley and was created in 1960 (previously having been a hunting reserve). Primarily between November and April, the Rift Valley in the centre of the park receives an average of 840 mm rain annually (Tinley 1977), with higher rainfall as elevation increases to the west and east (up to ~1200 mm annually). Several rivers flow into Lake Urema at the centre of the park, and up to 40% of Gorongosa floods each year. Fires are common in savanna and grassland habitats during the dry season. The park encompasses a wide range of vegetation types, including closed-canopy forest, various savanna physiognomies and floodplain grassland. Stalmans & Beilfuss (2008) identified and mapped 15 broad landscapes within Gorongosa based on dominant vegetation type and hydrology, which we lumped into five major habitat types (Fig. 2 and photographs in Appendix S1, in Supporting Information). In order from west to east, these are the following: (i) Midlands miombo woodland (*Brachystegia* and *Julbernardia* spp.) on the western rim of the Rift Valley (331 km<sup>2</sup>); (ii) Alluvial Fan *Acacia*, *Combretum* and palm savannas (1265 km<sup>2</sup>); (iii) Floodplain grasslands (759 km<sup>2</sup>) around Lake Urema; (iv) Colluvial Fan savannas (326 km<sup>2</sup>) within the Rift Valley; and (v) Cheringoma Plateau miombo woodlands and forested limestone gorges on the eastern rim of the Rift Valley (938 km<sup>2</sup>).



**Fig. 2.** Gorongosa National Park in central Mozambique. Inset: park habitat types derived from Stalmans & Beilfuss (2008). The Alluvial Fan, Floodplain, Lake Urema and Colluvial Fan habitat types all fall within the Rift Valley, whereas the Midlands miombo and Cheringoma Plateau comprise the eastern and western escarpments, respectively.

As of 1972, Gorongosa supported large populations of LMH (Tinley 1977). Common grazers, in decreasing order of total biomass, included buffalo (*Syncerus caffer*), hippo (*Hippopotamus amphibius*), wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), zebra (*Equus quagga*), sable (*Hippotragus niger*) and hartebeest (*Alcelaphus buselaphus*). Browsers and mixed feeders were dominated by elephants (*Loxodonta africana*); also common were impala (*Aepyceros melampus*), eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), nyala (*T. angasii*) and bushbuck (*T. sylvaticus*) (Tinley 1977).

#### LMH POPULATIONS

Aerial wildlife counts were conducted in the dry and wet seasons in Gorongosa between 1968 and 1972 (pre-war), once in 1994 (2 years post-war) and seven times between 2000 and 2012 (Tinley 1977; Cumming *et al.* 1994; Dutton & Carvalho 2002; Dunham 2004; Stalmans 2012). Pre-war surveys were total counts covering 100% of the park, but only total population estimates calculated from aerial transect samples using Jolly's 'Method Two' for unequal-sized units are available for the 1994 survey (Jolly 1969; Cumming *et al.* 1994). Between 2000 and 2012, the arrangement and coverage of transects flown varied, with anywhere from 9 to 23% of the park area surveyed. In addition, many of the transects flown contained zero individuals of most mammal species. Frequent zero values make calculation of meaningful population estimates and confidence intervals difficult, at best (Jachmann 2001). Therefore, we present (i) raw counts from the dry season whole-park pre-war surveys (1968, 1969 and 1972), (ii) the available population estimates from 1994 (Cumming *et al.* 1994) and (iii) the average total number of individuals counted in a survey scaled to the area of the whole park for two additional post-war periods (2000–2004 and 2007–2012). Scaling aerial sample data to the full park size unavoidably overestimates some populations and underestimates others, especially for rare species clumped into a small number of herds that may by chance be either overrepresented or missing from aerial transects. However, the uncertainty introduced by these caveats is dwarfed by the near-complete extermination of Gorongosa's wildlife; the data clearly show the magnitude of this shift, even though the precise numerical estimates should be interpreted cautiously. Tinley (1977) also mapped the location of LMH herds that were counted in the 1969–1972 aerial surveys. We superimposed the LMH distribution map from the 1969 dry season and 1970 wet season counts onto a map of the five park habitat types for comparison of the spatial distributions of pre-war LMH herds and post-LMH-decline tree-cover changes.

#### TREE COVER

We assessed pre-war tree cover from a cloudless 5.5-m-resolution black-and-white satellite photograph that was originally captured on 6 July 1977 (early-mid-dry season) by the US intelligence services Hexagon satellite program (KH9) and declassified in 2011. We georeferenced this image to the Microsoft Bing Maps base map in ArcMap 10.0 (© 2010 ESRI, Inc., Redlands, CA, USA). Post-war tree cover in 2012 was measured from two contiguous mosaics of cloudless 5-m-resolution multispectral RapidEye satellite images (© 2012 RapidEye US, LLC.). These were supplied orthorectified and radiometrically corrected. The individual images contributing to the mosaics were taken on 31 August and 28 September 2012 (late-mid-dry season). For the 2012 imagery, we used a false-colour composite of bands 4 (blue), 5 (red edge) and 1 (near infrared) displayed in the

red, green and blue channels, respectively, because this provided the best contrast between open grassland and woody vegetation types. The red edge band is particularly useful for classifications of open, savanna-like vegetation (Schuster, Förster & Kleinschmit 2012). Prior to classification, areas burned in the 1977 image and totalling 56.4 km<sup>2</sup> were removed manually for both dates because they are spectrally similar to dark trees on the black-and-white 1977 image and therefore likely to be misclassified.

We performed both object- and pixel-based supervised classifications of vegetation using both sets of imagery (cf. Pringle *et al.* 2009). Object-based classifications were completed in ERDAS Imagine Objective 14.0 (Intergraph, 2014) with two classes: 'tree cover' and 'other'. Pixels were classified by the single-feature probability algorithm (Karagiannis & Argialas 2012) and segmented into objects based on proximity and spectral similarity; these objects were then filtered based on the probability that each belonged to the tree cover class, and smoothed moderately to better represent the shape of actual vegetation patch edges. Pixel-based classifications were performed in ArcMap; pixels were assigned to 'tree cover', 'herbaceous cover' or 'bare ground' for the 1977 image, and to these classes plus 'burned area' for the 2012 image. The raw classification of pixels was corrected using the majority filter and boundary clean tools in ArcMap to eliminate isolated pixels and irregular edges that were possibly misclassified and unlikely to represent actual vegetation patches. We report the per cent of the landscape classified as tree cover at each time point for the whole park, and for each of the five park habitat types described above.

The accuracy of each tree-cover classification was assessed by comparing automated and visual (i.e. user-defined assignment) classifications for 150 randomly selected pixels in each classification type and image (Foody 2009). Although results from the pixel- and object-based classifications yielded qualitatively similar results, accuracy was slightly higher for the object-based analyses, consistent with prior studies of historical vegetation change (Pringle *et al.* 2009; Gibbes *et al.* 2010). We therefore report the object-based results below and report the pixel-based results along with full accuracy, sensitivity and specificity assessments in the online supporting information (Appendices S2 and S3).

As an independent complement to these remote-sensing analyses, we conducted a ground-based resurvey of tree abundance in a one-hectare plot within the Floodplain, comprising *Acacia*-palm woodland at the floodplain margin. This plot was initially established and surveyed by K.L. Tinley (1977 and personal communication) in March 1972. Tinley counted and identified all mature trees (> 3 m tall). In March–April 2014, we located the plot (according to Tinley's description at the intersection of park roads 3 and 4, with ours centred at 18°54'19.7"S, 34°26'05.1"E), and resurveyed it using the same methods. We compared the number of mature trees in 1972 and 2014 to determine whether the direction and magnitude of change was consistent with remotely sensed estimates.

#### RAINFALL AND FIRE REGIMES

To evaluate trends in rainfall, we obtained mean daily precipitation data for each year 1951–2012 from the climate model embedded in the African Flood and Drought Monitor (Sheffield, Goteti & Wood 2006; Sheffield *et al.* 2014). These estimates are derived from a set of remotely sensed and ground-based observations combined with climate model outputs. We used ordinary least squares linear regression in R (v3.0.2; R Core Team 2013) to test for a temporal trend in the annual rainfall by year. The estimates produced by the African Flood

and Drought Monitor have been validated for southern Africa (Sheffield *et al.* 2014). To cross-validate the model estimates for our specific study location, we also regressed measured annual rainfall values from Chitengo Camp in the Alluvial Fan of the Rift Valley in Gorongosa for 1967–1976 (Tinley 1977) against the values from the African Flood and Drought Monitor.

Because comprehensive fire records for Gorongosa do not exist, we used multiple lines of evidence to evaluate whether Gorongosa's fire regime is likely to have changed since 1960. First, we used the 500-m-resolution burned-area product from NASA's MODIS satellites (MCD45A1, 2000–2012; Boschetti, Roy & Hoffmann 2009) to describe the fire regime of the park over the last thirteen years (2000–2012). Preliminary analysis of the MODIS active fire product for 2003–2012 (MCD14ML; Giglio 2013) revealed that fewer than 0.005% of all pixels were classified as burned area for the months January–April in each year. We therefore restricted our analyses to the annual fire season (May–December). We removed fires detected with the MODIS agricultural fire algorithm because these are considered low-confidence detections (Boschetti, Roy & Hoffmann 2009). We then calculated the extent of burned area for each of the park's five habitat types in each month using ArcMap, as well as the average fire-return interval (fire frequency) for all areas of the park that burned (i) at least once and (ii) at least twice in the 13-year time series. We used linear regression to test for temporal trends in the annual proportion of the park burned.

The incidence of fire in African savannas rises with human population densities up to ~10 people per km<sup>2</sup> and then falls at higher population densities, while burned area is steady up to 10 people per km<sup>2</sup> and then falls (Archibald *et al.* 2009, 2010). We therefore calculated human population densities for Gorongosa NP and a 10-km buffer around the park from 1960 to 2000 as a proxy for the historical fire regime. We included the buffer along with the park proper because fires are set within the park by hunters who live outside the park boundary, and for scattered agricultural clearing; we chose 10 km for consistency with prior work on human impacts in African savanna parks (Wittemyer *et al.* 2008). We obtained human density estimates from the United Nations Environment Programme's (UNEP) African Population Distribution Database, a set of gridded rasters of 2.5 min resolution (approximately 16 km<sup>2</sup> at Gorongosa's latitude; UNEP & CIESIN 2004; Balk *et al.* 2006). These estimates were derived by spatially distributing national population estimates based on 'accessibility', as determined by transportation networks, urban centres and administrative boundaries, and where validated, have matched well with local census records (Wittemyer *et al.* 2008). We used the World

Database on Protected Areas polygon for Gorongosa (IUCN & UNEP-WCMC 2013) to calculate the mean and standard deviation of estimated human population density for the park and its buffer in ArcMap. We compared the calculated population densities with the published relationships between human density and fire regimes for southern Africa (Archibald *et al.* 2009, 2010) to infer the most likely historical pattern of burning in Gorongosa.

## Results

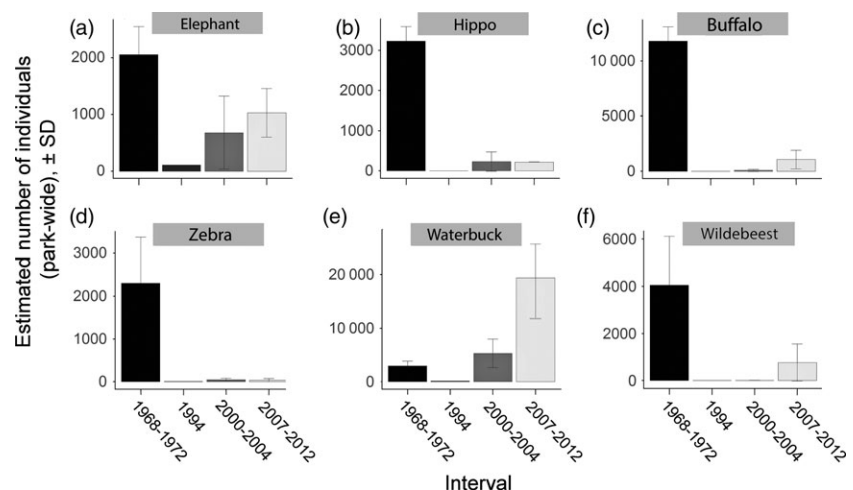
### LMH POPULATIONS

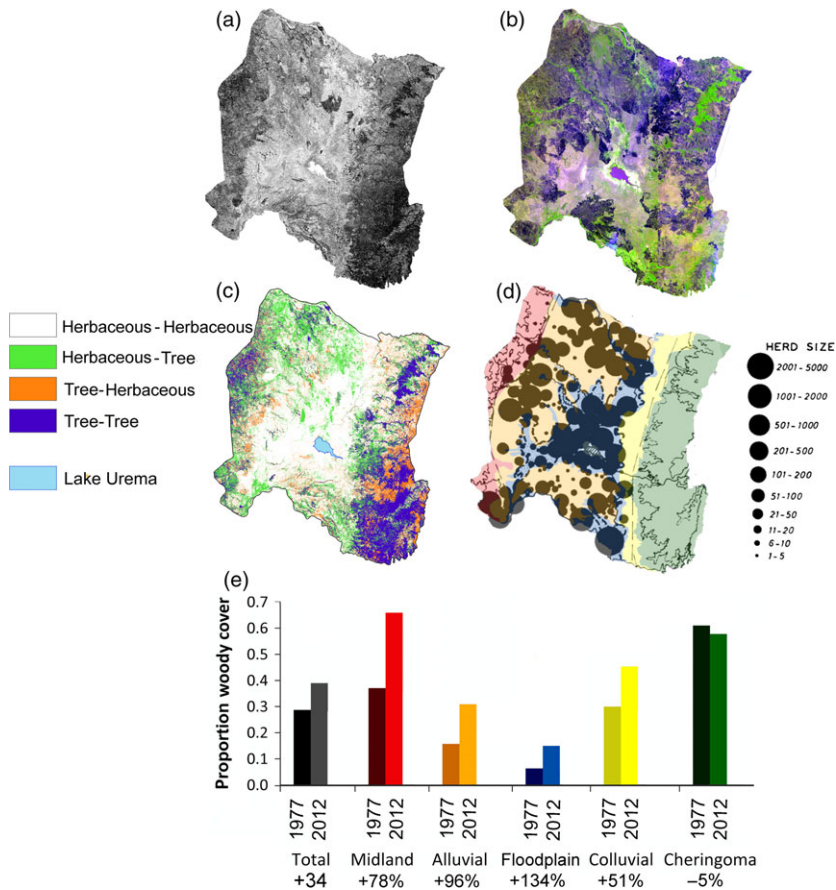
Aerial survey data revealed dramatic declines (> 95%) between 1972 and 1994 in the populations of the six formerly dominant LMH species (Fig. 3). These population crashes were not guild-specific: dominant browsers (elephant, Fig. 3a) and grazers (Fig. 3b–f) exhibited similarly severe declines, and available evidence suggests the same was true for all other species (Cumming *et al.* 1994). In 1968–72, LMH densities were greatest in the Alluvial and Colluvial Fan and Floodplain within the Rift Valley (Fig. 4; Appendix S4; Tinley 1977). Lower LMH densities were present in the western Midlands miombo, and the eastern Cheringoma Plateau had the lowest densities. Elephants in particular were rare in Cheringoma relative to the three Rift Valley habitat types (Tinley 1977). Many LMH populations have grown since 2007, but at different rates: for example, although waterbuck now exceed historical numbers, most other LMH species remain at small fractions of their prior abundances (Stalmans, Peel & Massad 2014).

### TREE COVER

All object-based classifications had > 80% overall accuracy and > 70% sensitivity and specificity (full accuracy assessment in Appendix S3). Parkwide, proportional tree cover increased 34% from 0.29 in 1977 to 0.39 in 2012, adding ~362 km<sup>2</sup> of tree cover (Fig. 4). Within four of the five habitat types, the increases in tree cover were even greater, and their relative magnitudes corresponded with the pre-war distribution of LMH density (Fig. 4, Appendix S5). The greatest

**Fig. 3.** Population data for four time periods for the six large mammalian herbivore species with the greatest total biomass in 1968–1972. (a) Elephants are browsers, and (b–f) grazers are in decreasing order of adult body mass. Counts for the pre-war 1968–1972 period were total counts (Tinley 1977). The 1994 data are parkwide modelled population estimates (Cumming *et al.* 1994). Data from the four 2000–2004 (Dutton & Carvalho 2002; Dunham 2004) and three 2007–2012 (Stalmans 2012) surveys were extrapolated from the aerial sampling coverage to the total park area and then averaged across years. Error bars show  $\pm 1$  SD for interannual averages.





**Fig. 4.** (a) 1977 Hexagon and (b) 2012 RapidEye© false-colour satellite imagery of Gorongosa National Park. (c) Difference image for the object-based vegetation classifications performed on the images in (a) and (b); ‘Tree-Herbaceous’ denotes areas that changed from woody vegetation to herbaceous, and ‘Herbaceous-Tree’ from herbaceous to woody vegetation between 1977 and 2012. (d) The size and location of large mammalian herbivore herds recorded in the October 1969 total aerial survey (inset adapted from Tinley 1977 Fig. 9.12; Stalmans & Beilfuss 2008). A similar wet season (January 1970) map is in the online Appendix S4. (e) Proportional tree cover for Gorongosa and its five habitat types in 1977 and 2012. Results here from the object-based classification. The bar colours correspond to the habitat types in part d. Note the absence of any tree-cover increase on the eastern Cheringoma Plateau, where herbivores were historically rare.

LMH densities and percentage increase in tree cover were on the Floodplain (+134% tree cover), and both decreased sequentially from the Alluvial Fan (+96%) to Midlands miombo (+78%) and Colluvial Fan (+51%). Only on the Cheringoma Plateau, which historically had the lowest LMH densities (Tinley 1977), did tree cover decrease slightly (−5%; Fig. 4e). Due to Cheringoma’s large size (~29% of total park area), the parkwide tree-cover increase of 34% was considerably lower than the habitat-specific values for Rift Valley and Midlands habitat types.

Tinley (personal communication) recorded 24 mature trees in his 1972 survey of the 1-ha floodplain-margin plot: 14 fever trees (*Acacia xanthophloea*), eight palms (*Hyphaene petersiana*) and two buffalo thorns (*Ziziphus mucronata*). In our 2014 resurvey, we recorded 62 mature trees (47 *A. xanthophloea*, 15 *H. petersiana*), an increase of 158%, which is consistent with the 134% tree-cover increase estimated from the satellite imagery for the Floodplain habitat type.

#### RAINFALL AND FIRE TRENDS

We found no detectable trend in annual rainfall between 1951 and 2012 (Fig. 5a;  $r = 0.084$ ,  $F_{1,60} = 0.44$ ,  $P > 0.5$ ). The African Flood and Drought Monitor estimates accurately predicted measured annual rainfall for 1967–1976 (Appendix S6;  $R^2 = 0.68$ ,  $F_{1,8} = 17.11$ ,  $P = 0.003$ ).

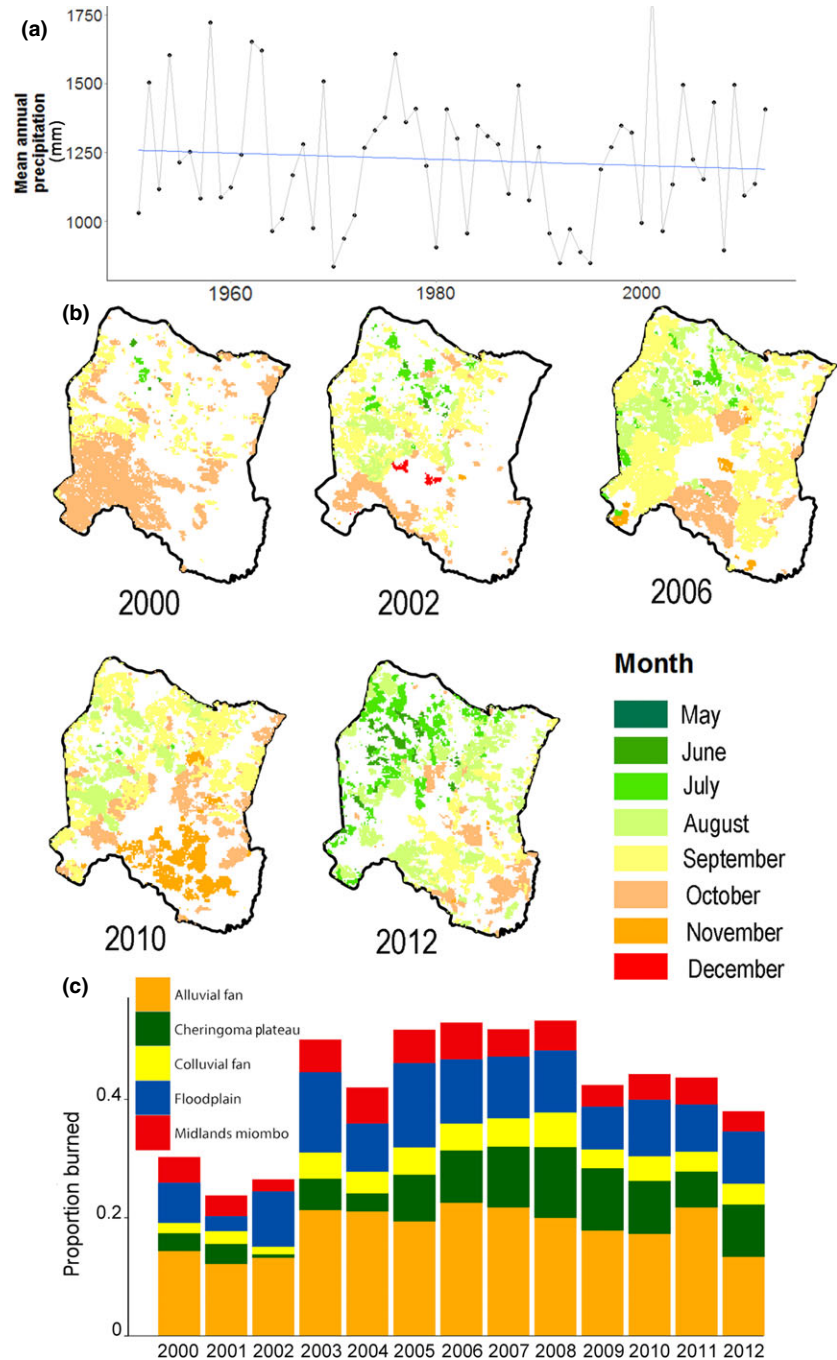
Between 25 and 55% (mean 43%; median 45%) of Gorongosa NP burned annually between 2000 and 2012, with the

greatest number of fires and the largest burned area occurring between August and October (Fig. 5b and Appendix S7). We found no detectable trend in the proportion of the park burned over time (Fig. 5c;  $r = 0.27$ ,  $F_{1,12} = 0.98$ ,  $P > 0.3$ ). The mean fire-return interval was 3.3 years when excluding areas that never burned and was 2.6 years when also excluding areas that only burned once.

Estimated human population density within the park remained low between 1960 and 2000, rising from an average of 1.3 ( $\pm 2.2$  SD) to 3.3 ( $\pm 5.8$ ) people per km<sup>2</sup> (Appendix S8). In the 10-km buffer around Gorongosa NP, estimated population density rose from 8.1 ( $\pm 7.1$ ) to 20.4 ( $\pm 18.1$ ) people per km<sup>2</sup>. Thus, only in the buffer zone has human population density exceeded the level at which annual burned area is expected to decline (Archibald *et al.* 2010).

#### Discussion

Our results show that the near-extirpation of the entire LMH assemblage from a 3620-km<sup>2</sup> national park in south-eastern Africa was followed by a 34% increase in tree cover across the entire park after 35 years, an increase in total woody area of 362 km<sup>2</sup>. The magnitude of woody expansion was spatially heterogeneous, being greater in the areas with higher pre-war LMH biomass. The eastern Cheringoma Plateau was the only region that did not experience tree-cover expansion; this is consistent with our browsing-release hypothesis (Fig. 1), given the region’s low pre-war densities of elephants and



**Fig. 5.** Temporal trends in abiotic drivers. (a) Annual rainfall from the African Flood and Drought Monitor (Sheffield, Goteti & Wood 2006; Sheffield *et al.* 2014) vs. year. Blue line is the non-significant OLS regression. (b) Gorongosa fire regime for 2000–2012 as reconstructed from the MODIS MCD45A burned-area product. Monthly burned areas for selected years (full time series in Appendix S7). (c) The proportion of Gorongosa burned annually, 2000–2012. Colours represent park habitat types.

LMH generally, relative to the Rift Valley savanna and floodplain habitats (Fig. 4d, Appendix S5; Tinley 1977). Although we were unable to replicate our ground-based resurvey beyond a single 1-ha plot, the 158% increase in mature tree density observed there was consistent in direction and magnitude with the remotely sensed data. We found no evidence that rainfall increased, or that fire frequency/extent decreased (discussed further below). We therefore conclude that enhanced tree growth, survival, reproduction and recruitment following the rapid anthropogenic collapse of LMH populations are the most parsimonious explanation for tree-cover expansion in Gorongosa. Because elephants were by far the

historically dominant browsing species (Fig. 3; Tinley 1977), we further propose that elephant declines were the primary driver of increased tree cover and that the similarly severe declines (Stalmans 2012) of eland, kudu, impala and other smaller browsers reinforced this outcome via complementary mechanisms.

This interpretation is consistent with abundant evidence that browsers govern local tree cover. Elephants create and maintain open savanna landscapes (Laws 1970; Caughley 1976) by increasing mortality of large trees (Dublin, Sinclair & McGlade 1990; Asner & Levick 2012). Smaller-bodied browsers collectively suppress growth, survival, reproduction and

recruitment (Augustine & McNaughton 2004; Goheen *et al.* 2007), generating effects on tree cover that are non-redundant with those of elephants (Pringle *et al.* 2014). Our results from Gorongosa align well with recent results from decadal manipulative experiments pointing to a 'browse trap' inhibiting tree recruitment (Sankaran, Augustine & Ratnam 2013) and suggesting that 'release from browsing trumps grazer–grass–fire interactions' to increase tree cover following partial or total experimental exclusion of savanna LMH assemblages (Augustine & McNaughton 2004; Sankaran, Augustine & Ratnam 2013; Staver & Bond 2014). In contrast, we found no support for the theoretical prediction that grazer declines decreased tree cover by increasing herbaceous biomass, fire frequency or extent, or grass–tree competition (Fig. 1; Van Langevelde *et al.* 2003; Holdo, Holt & Fryxell 2009). This is despite the fact that grazers accounted for > 60% of pre-war LMH biomass in Gorongosa (Tinley 1977) and that > 90% of grazer biomass consisted of four bulk roughage feeders (hippo, buffalo, zebra and wildebeest) expected to strongly reduce grass biomass; yet in the Floodplain, where bulk grazers previously exerted particularly strong grazing pressure, tree cover increased by 134%. It is possible that grazer declines did have negative effects on tree cover via the theorized grass–fire pathway, but that this effect was simply dwarfed by those browser declines. Alternatively, grazer declines might actually have contributed to woody expansion, as high densities of bulk grazers may prevent seedling establishment via both trampling and consumption. In Kenya, 59% of buffalo faecal samples contained DNA from the dominant tree *Acacia brevispica*, and > 20% of samples contained woody *Croton* and *Grewia* species (Kartzinel *et al.* 2015). The propensity of even relatively strict 'grazers' to consume (often protein-rich) woody seedlings may be one reason why so few experimental studies have documented reduced tree cover following LMH exclusion.

In contrast to the growing number of experimental studies, there remain few quantitative evaluations of the impacts of large-scale LMH die-offs on savanna tree cover. The 19th-century rinderpest pandemic has been implicated in woodland expansion in national parks throughout northern Tanzania (Dublin, Sinclair & McGlade 1990; Prins & van der Jeugd 1993), although baseline pre-rinderpest data are virtually non-existent. In Serengeti, release of wildebeest from rinderpest after 1960 coincided with reductions in fire extent and increased tree cover (McNaughton 1992; Holdo *et al.* 2009), providing some of the best empirical support for the importance of the grazer–grass–fire pathway (see also Waldram, Bond & Stock 2008). In nearby Lake Manyara National Park, shrub establishment was linked to anthrax outbreaks that intermittently decimated the impala population (Prins & van der Jeugd 1993). In all prior cases, however, inferences about the downstream ecological consequences of LMH mass-mortality have been largely species- or guild-specific (even when the mortality event itself was not; McNaughton 1992) and are constrained by the absence of baseline data. Gorongosa is unique in that rigorous quantitative estimates of both herbivore populations and vegetation structure are possible for an

entire 3,620-km<sup>2</sup> national park both immediately before and after an extraordinarily severe community-wide LMH die-off, and our results show that this wholesale decline was followed by rapid and pronounced gains in tree cover.

Alternative explanations for the observed increase in tree cover include increased rainfall, decreased fire, or systemwide effects of enhanced atmospheric CO<sub>2</sub> concentrations (Bond 2008). The absence of any directional trend in precipitation or fire strongly suggests that these drivers were not major factors. For rainfall, this supposition is strengthened by the observation that Gorongosa's precipitation throughout the study period was likely higher than that at which rainfall is thought to constrain savanna tree cover, which different studies have placed between 650 and 1000 mm year<sup>-1</sup> (Sankaran *et al.* 2005; Staver, Archibald & Levin 2011a). In Gorongosa, mean annual rainfall from 1951 to 2012 was between ~840 (as measured in the Rift Valley, where rainfall is lowest) and ~1200 (as estimated by the African Flood and Drought Monitor over the whole park and adjacent areas; Appendix S6). Additionally, although there is potential for interannual rainfall variability to alter savanna tree cover (Holmgren *et al.* 2013), with wet periods providing windows of opportunity for tree recruitment, we found no directional trend in the variability of rainfall in Gorongosa over the period studied.

Our interpretation of the lack of a trend in the fire data is subject to the obvious caveat that we were only able to reconstruct historical data back to the year 2000; this is especially relevant for our estimates of the mean fire-return interval. However, if altered fire regimes explain the increase in tree cover, we would expect to see a limited extent of fire. If anything, the near-extirpation of grazing buffalo, hippo, waterbuck, wildebeest and zebra should have *increased* fire frequency and/or extent in the park's formerly wildlife-rich and grass-dominated Rift Valley habitats from the 1980s onwards. Indeed, the MODIS burned-area data showed that an unusually large portion of the park burns annually: the median per cent of Gorongosa burned annually (45%) is much higher than that of other savanna protected areas in Mozambique (median = 17%), and of both savanna and grassland parks in nearly every country in sub-Saharan Africa (Archibald *et al.* 2010). Thus, it is possible that LMH declines did increase fire regimes, but that even this was insufficient to offset effects of browsing release. We further note that the Cheringoma Plateau burned the least from 2000 to 2012 (Appendix S7), yet was the only habitat type in the park where tree cover decreased. In short, it is difficult to identify a plausible mechanism by which fire-mediated feedbacks could explain our results.

Further, in light of known relationships between fire regimes and human population densities in southern Africa (Archibald *et al.* 2009, 2010), the UNEP human population estimates suggest that decreased fire extent or frequency during the period studied is unlikely. Although the buffer population now exceeds the 10 people per km<sup>2</sup> level at which burned area tends to decrease (Archibald *et al.* 2009), human density within the park remains well below this threshold. While the growth of human settlements around the park may



have reduced fire frequency/extent in the buffer zone since 1960, fires continue to be routinely set within the buffer zone (*personal observations*) as well as by hunters within the park boundaries.

Elsewhere in southern Africa, woody encroachment in savannas has been attributed to overgrazing by domestic livestock and subsequent release of woody vegetation from competition with grass (Ward 2005). However, this is not a potential cause of the increased tree cover in Gorongosa. Tinley (1977) reported that no cattle and few goats were kept in the region, due to the prevalence of trypanosomiasis (nagana). Furthermore, any livestock formerly present appear to have disappeared during the civil war. Not a single domestic animal larger than a goat was observed within the park during any of the eight aerial wildlife counts undertaken between 2000 and 2014 (Stalmans, Peel & Massad 2014).

The available data do not enable us to definitively rule out one potential driver of woody expansion, namely rising atmospheric CO<sub>2</sub> concentrations. Carbon dioxide enrichment may tend to increase woody biomass in tropical savannas by enhancing the physiological advantage of C<sub>3</sub> trees relative to C<sub>4</sub> grasses and accelerating the escape of woody saplings from fire (Polley 1997; Bond & Midgley 2000). However, the absence of field-based tests of this proposition within tropical Africa makes it difficult to define the expected effect size. Ideally, we might have controlled for potential effects of CO<sub>2</sub> in the present study by quantifying tree-cover changes outside the park in an area where LMH biomass was low even before the war. However, we were unable to identify any such areas: LMH populations historically extended well north of the park (Tinley 1977), and human populations have grown on all sides of the park, with substantial impacts on tree cover.

Importantly, however, CO<sub>2</sub> enrichment is not mutually exclusive with our 'browsing release' hypothesis, and the latter remains the more parsimonious explanation for the observed increases in tree cover. In particular, we note that the magnitude of tree-cover increase was highly heterogeneous across Gorongosa: tree cover actually decreased slightly on the Cheringoma Plateau, where pre-war LMH densities were lowest, and increased most in the Rift Valley habitat types with the greatest historical herbivore densities (Appendix S5). Although the magnitude of woody encroachment in Cheringoma might have been lower simply because this area had ~60% tree cover to begin with, the net change in tree cover should still have been positive under the CO<sub>2</sub> enrichment hypothesis. On the contrary, the net change in Cheringoma was slightly negative, and large areas transitioned from tree to herbaceous cover (Fig. 4c). Cheringoma also comprises a substantial fraction of Gorongosa, indicating that CO<sub>2</sub> enrichment failed to manifest over nearly a third of the total area studied.

Fortunately, the rapidly recovering LMH fauna in Gorongosa (Fig. 3) may soon allow a direct test of the browsing-release hypothesis: if LMH declines were responsible for woody expansion, then LMH recovery should reverse this

trend. Anecdotal observations suggest that elephant-induced mortality is already starting to open up dense fever tree (*Acacia xanthophloea*) woodlands that emerged following the civil war. Continued monitoring of LMH populations and tree cover will be essential in conclusively establishing the mechanisms underlying both historical and future vegetation dynamics.

Woody encroachment is a significant conservation and management concern in savannas, grasslands and rangelands where it threatens native herbaceous plant species and the animals and ecosystem processes that depend on them (Parr, Gray & Bond 2012). Further tree-cover expansion in Gorongosa could inhibit recolonization of some areas by species that prefer open habitats (including buffalo, wildebeest and zebra). The recovery of these species is a primary goal of the ongoing Gorongosa Restoration Project, which seeks to restore LMH populations and ecosystem functioning to pre-war levels. Although population growth rates of these LMH species do not currently appear to be limited by woody encroachment, areas with pronounced tree-cover gains may inhibit the expansion of grazers in the future and could exacerbate or prolong the asymmetric recovery of grazer species (currently disproportionately dominated by waterbuck, which are tolerant of woodland: Fig. 3). Of particular concern in this respect is the thicket-forming species *Mimosa pigra*, the occurrence of which has increased in the Urema floodplain since 1972 (Tinley 1977; J.H.D. & R.M.P. *unpublished data*). It remains to be seen whether the ongoing recovery of elephants and other browsers (Stalmans, Peel & Massad 2014) can arrest tree-cover expansion and reopen areas that have become more dominated by trees.

Meanwhile, despite its tragic conservation history, Gorongosa presents an unparalleled opportunity to study the impacts of severe LMH declines over large spatio-temporal scales. Current and former conflict zones are almost certainly under-represented in the literature, possibly contributing to a bias towards sites with stable and abundant populations (e.g. Guldmond & van Aarde 2008). Future work in Gorongosa should include careful monitoring of tree cover; if management intervention is ultimately deemed necessary to strategically reduce tree cover, this study will be useful in delineating the pre-war distribution of open habitats.

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## Data accessibility

Data deposited in the Dryad repository: <http://datadryad.org/resource/10.5061/dryad.2jj16> (Daskin *et al.* 2015).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Representative photographs of Gorongosa habitat types.

**Appendix S2.** Results of object and pixel-based classifications of tree cover.

**Appendix S3.** Accuracy assessment of vegetation classifications.

**Appendix S4.** Pre-war LMH distribution maps.

**Appendix S5.** Pre-war LMH densities and post-war tree-cover increases.

**Appendix S6.** Correspondence of modelled and measured rainfall, 1967–1976.

**Appendix S7.** Gorongosa National Park fire regime, 2000–2012.

**Appendix S8.** Human population density.