ARTICLES
https://doi.org/10.1038/s41559-019-1068-y

nature ecology & evolution

Trophic rewilding revives biotic resistance to shrub invasion

Jennifer A. Guyton[1], Johan Pansu[1,2,3], Matthew C. Hutchinson[1], Tyler R. Kartzinel[1,4], Arjun B. Potter[1], Tyler C. Coverdale[1,5], Joshua H. Daskin[1,6], Ana Gledis da Conceição[7], Mike J. S. Peel[8], Marc E. Stalmans[7] and Robert M. Pringle[1,7]*

Trophic rewilding seeks to rehabilitate degraded ecosystems by repopulating them with large animals, thereby re-establishing strong top-down interactions. Yet there are very few tests of whether such initiatives can restore ecosystem structure and functions, and on what timescales. Here we show that war-induced collapse of large-mammal populations in Mozambique's Gorongosa National Park exacerbated woody encroachment by the invasive shrub *Mimosa pigra*—considered one of the world's 100 worst invasive species—and that one decade of concerted trophic rewilding restored this invasion to pre-war baseline levels. Mimosa occurrence increased between 1972 and 2015, a period encompassing the near extirpation of large herbivores during the Mozambican Civil War. From 2015 to 2019, mimosa abundance declined as ungulate biomass recovered. DNA metabarcoding revealed that ruminant herbivores fed heavily on mimosa, and experimental exclosures confirmed the causal role of mammalian herbivory in containing shrub encroachment. Our results provide mechanistic evidence that trophic rewilding has rapidly revived a key ecosystem function (biotic resistance to a notorious woody invader), underscoring the potential for restoring ecological health in degraded protected areas.

Large animals, known as megafauna, shape the structure and functioning of ecosystems by exerting strong top-down pressure in food webs, by altering habitat architecture, and by transporting large quantities of organic matter[1–3]. Megafauna are also generally among the first species to go extinct when human activity intensifies[4,5]. The human-induced decline of wild megafaunal populations (defaunation) has been in progress for millennia. One major extinction spasm coincided with the globalization of humankind in the late Pleistocene[5,6], and another is looming as landscape conversion, hunting, and armed conflict threaten the world's largest surviving animal species with annihilation[2,4,7,8]. Given the well-documented ecological importance of megafauna, these population declines and extinctions should have profound effects on ecosystems[1,2,9]. Yet such effects are hard to pinpoint—in part because baseline data are frequently unavailable, and in part because it is difficult to establish that defaunation is the causal agent of large-scale environmental changes.

Alongside efforts to conserve megafaunal populations where they still occur, a growing number of initiatives seek to re-establish populations in places where they have disappeared or severely declined[10–13]. Trophic rewilding is a management strategy in which the restoration of large-animal populations is used to revive top-down interactions and reverse anthropogenic environmental degradation[14–17]. A key premise of this approach is that such degradation is indeed reversible—in other words, that defaunation does not lead to alternative stable states that resist restoration[18,19]. However, as noted by Bakker and Svenning[15], "data on the effects of explicit rewilding efforts are scarce and the scientific literature on rewilding is strongly dominated by essays, perspectives and opinion papers." Authors have stressed the need for rewilding research to "move beyond anecdote, personal experience, expert criteria and conventional wisdom, towards a more systematic appraisal of evidence"[20], and to identify "monitoring approaches that can verify progress"[21]. Identifying the timescales of progress is also crucial, because it is easier to mobilize support and resources for projects that can rapidly yield transformative results[17].

One pervasive form of ecological degradation is woody-shrub encroachment, which is increasing in open biomes worldwide[22] and can have profound effects on biodiversity and ecosystem functions[23,24]. Both global (elevated CO_2) and local (fire suppression, displacement of native ungulates by livestock) drivers have been implicated in woody encroachment[25–27]. The effects of woody encroachment are often particularly severe when the encroacher is an alien invasive species[28]. For example, the shrub *Mimosa pigra* (Fabaceae), a pan-tropical invasive species in seasonally inundated habitats, has been listed among the world's 100-worst invasive alien species[29] because of the threats it poses to biodiversity, ecosystem services, and human livelihoods. In the extreme, woody encroachment can lead to persistent alternative states that are reinforced by positive feedbacks[30]. Trophic rewilding with large herbivores has been suggested as a strategy for mitigating woody encroachment[31] and exotic-plant invasions[32]. Yet there is also concern about unintended consequences: reintroduced herbivores might exacerbate, rather than mitigate, plant invasions[32,33]. The net effect of generalist large mammalian herbivores (LMH) on long-lived woody plants is particularly uncertain, owing to the diversity of potential direct and indirect interaction pathways. Ungulates can suppress shrubs via direct consumption, but can

---

[1]Department of Ecology & Evolutionary Biology, Princeton University, Princeton, NJ, USA. [2]Station Biologique de Roscoff, UMR 7144 CNRS-Sorbonne Université, Roscoff, France. [3]CSIRO Ocean & Atmosphere, Lucas Heights, New South Wales, Australia. [4]Department of Ecology & Evolutionary Biology, Brown University, Providence, RI, USA. [5]Department of Ecology & Evolutionary Biology, Cornell University, Ithaca, NY, USA. [6]Department of Ecology & Evolutionary Biology, Yale University, New Haven, CT, USA. [7]Department of Scientific Services, Parque Nacional da Gorongosa, Sofala, Mozambique. [8]ARC-Animal Production Institute, Rangeland Ecology Group, Nelspruit, South Africa. *e-mail: rpringle@princeton.edu

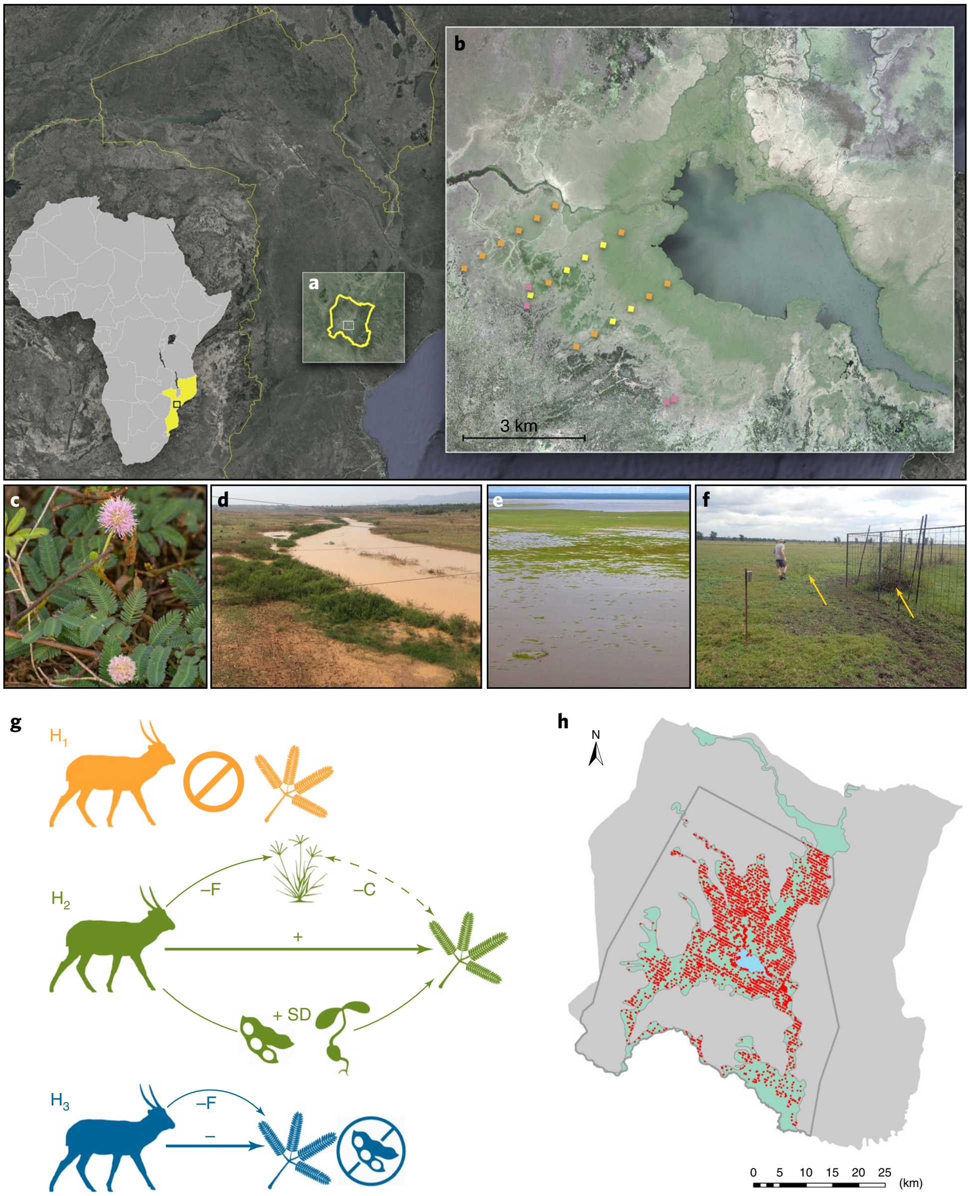


Fig. 1 | Study system, experimental design, and hypotheses. **a**, Study area, the Urema floodplain of Gorongosa National Park. **b**, Locations of 18 1-ha monitoring plots established in 1972 (plots where experimental exclosures were added in 2015 are shown in yellow, plots without exclosures are shown in orange) and four 200-m^2 plots monitored between 2011 and 2019 (pink). **c**, Prostrate *M. pigra*. **d**, Dense riparian mimosa thicket outside the park. **e**, Flooded exclosure (lower left) with Lake Urema in the background. **f**, Defoliated mimosa outside an exclosure and shrubby growth inside (arrows) in July 2017 (see also Extended Data Fig. 5). **g**, Hypotheses evaluated in this study. H_1, no interaction. H_2, net-positive effect. H_3, net-negative effect. Thick, straight arrows indicate the net effect. Thin, curved arrows illustrate direct (solid) and indirect (dashed) interactions that might generate the net effect (F, feeding; C, competition; SD, seed dispersal). In H_3, herbivores reduce mimosa performance and abundance via consumption of foliage, stems, and reproductive parts. **h**, Wildlife were counted in a 1,832-km^2 block (solid line) that contains >90% of Gorongosa's floodplain landscape (turquoise); red dots are the locations of waterbuck counted in the floodplain in 2018, illustrating the process used to generate Fig. 2a. Map data in **a**,**b**: Google, US Dept of State Geographer, Landsat/Copernicus, SIO, NOAA, US Navy, NGA, GEBCO, Maxar Technologies, CNES/Airbus.

also facilitate them by dispersing seeds, disturbing soil, and suppressing competitors[33,34].

We tested the effects of defaunation and trophic rewilding on *M. pigra* encroachment in Mozambique's Gorongosa National Park (Fig. 1). In Gorongosa, large mammals were nearly extirpated during the Mozambican Civil War (1977–1992) and its aftermath[35]. Since 2007, the Gorongosa Project has sought to restore a diverse and self-regulating ecosystem by facilitating the recovery of remnant megafaunal populations and by reintroducing translocated individuals of multiple species[35–37]. Mimosa has been present for decades in Gorongosa's 780-km^2 Urema floodplain, but was not considered a management concern in the 1970s[38]. By 2007, however, park officials argued that mimosa had encroached drastically during the preceding 30 years and recommended "urgent action" to control the plant[39].

Our research was guided by three alternative hypotheses (Fig. 1g). The first hypothesis (H_1) was that LMH infrequently eat mimosa[40,41] and thus have a negligible effect on its population, an outcome consistent with the enemy-release hypothesis[42]. The second (H_2) was that LMH benefit mimosa (for example, by dispersing

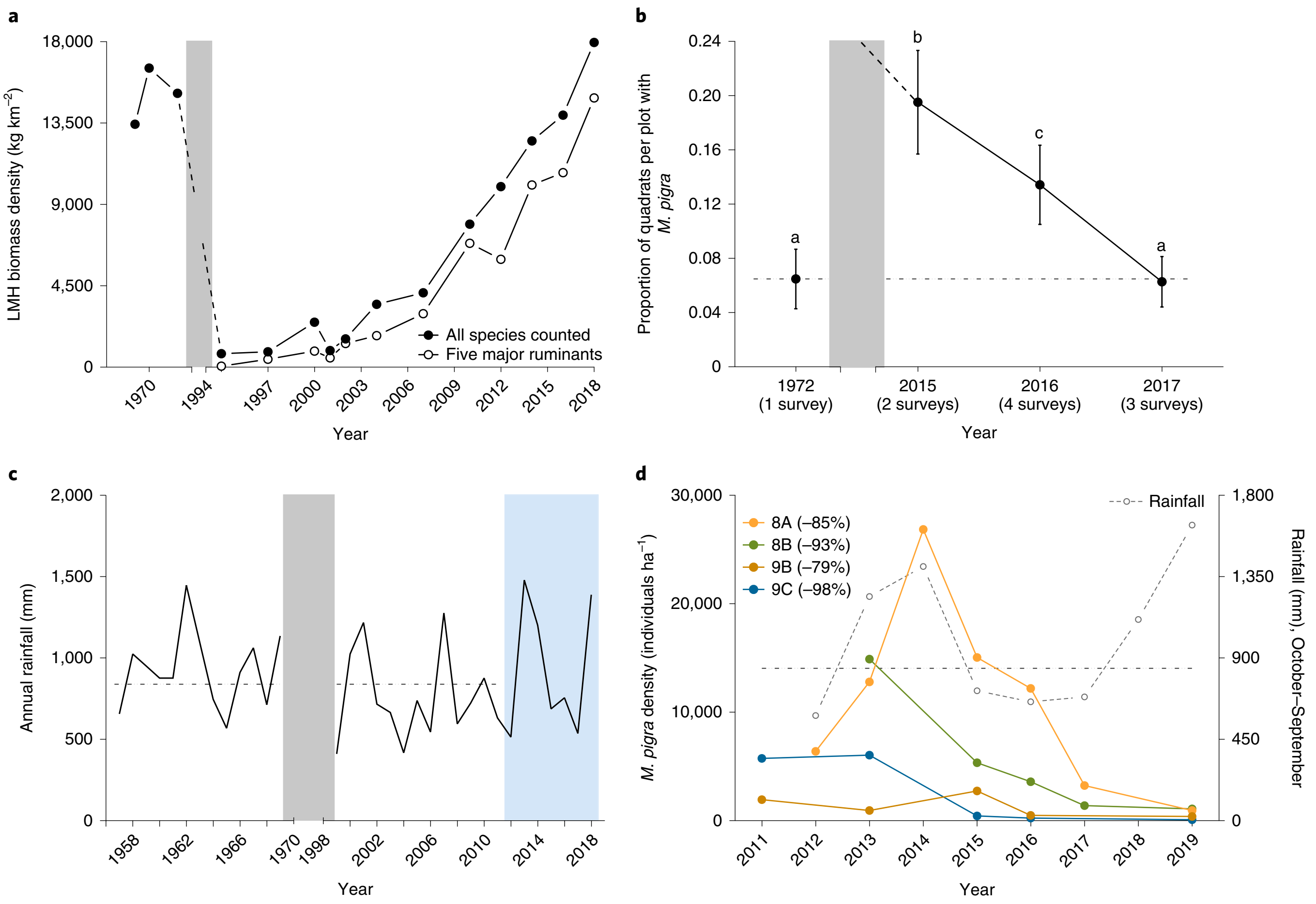


Fig. 2 | Trends in ungulate biomass, *M. pigra* abundance, and rainfall. **a**, LMH biomass density in the Urema floodplain, showing war-induced collapse from the 1970s to the 1990s and rapid recovery since 2007. The five major ruminant species are those identified as mimosa consumers in Fig. 3, and they accounted for 83% of total LMH biomass in 2018. The grey bar indicates the period for which no data are available (note the break in the *x* axis). The pre-war values of total LMH biomass are underestimates, as they included only nine of the largest-bodied species (see Methods). **b**, Occurrence of mimosa in 18 plots established in 1972. The points show the mean (±1 s.e.m.) proportion of 1-m^2 quadrats per 1-ha plot that contained mimosa ($n = 18$ plots for 1972, 2015, and 2016; $n = 17$ for 2017). For each year, the proportional occurrence of mimosa in each plot was averaged across all surveys to obtain a single plot-level value. The grey bar indicates the period for which no data are available. The horizontal dotted line indicates the pre-war baseline. Mimosa occurrence was strongly predicted by survey year ($\chi^2 = 38.07$, d.f. = 3, $P < 0.00001$) and plot identity ($\chi^2 = 70.29$, d.f. = 17, $P < 0.00001$) (binomial generalized linear model (GLM), whole-model $\chi^2 = 106.33$, d.f. = 20, $n = 71$ plot-year observations, $P < 0.00001$). Superscript letters indicate statistically significant differences in pairwise contrasts between years (1972 versus 2015 $\chi^2 = 30.02$, $P < 0.00001$; 1972 versus 2016 $\chi^2 = 10.73$, $P = 0.001$; 1972 versus 2017 $\chi^2 = 0.01$, $P = 0.92$; 2015 versus 2016 $\chi^2 = 3.75$, $P = 0.05$; 2015 versus 2017 $\chi^2 = 21.45$, $P < 0.00001$; 2016 versus 2017 $\chi^2 = 7.91$, $P = 0.005$; all d.f. = 1). The dashed line reflects evidence from a 2013 survey suggesting that mimosa occurred in as many as 50% of quadrats (see Methods). **c**, The mean annual rainfall in the period bracketing most of our data, 2012–2018 (blue shading), was 937.4 mm yr^{-1} and typical of long-term trends (average of 842.6 mm yr^{-1} from 1957 to 2011, indicated by the horizontal dotted line; the grey bar indicates the period for which no data are available). However, our 2015–2017 surveys (**b**) coincided with 3 years of below-average rainfall. **d**, Mimosa densities in four floodplain plots (8A, 8B, 9B, and 9C) surveyed between 2011 and 2019 corroborate the occurrence data in **b** and indicate that rainfall is insufficient to explain mimosa decline: in all plots, densities declined monotonically from 2015 to 2019, despite above-average rainfall in 2018 and 2019. The net percentage decrease from the first to last survey is shown next to each plot name in the legend. The dashed trend line indicates the rainfall during the seasonal year encompassing each survey (October in the year before the survey to September in the year of the survey; right *y* axis). The horizontal dotted line indicates the long-term average rainfall.

seeds or by suppressing competing plant species)[34]. The third (H_3) was that LMH consumptively suppress mimosa, thereby conferring biotic resistance[43,44] to shrub encroachment. We evaluated these possibilities by testing three specific predictions of H_3. The first prediction (p_1) was that the occurrence of mimosa in the Urema floodplain increased in concert with LMH population declines and has subsequently decreased as LMH populations have recovered. We tested this prediction using the 'unnatural experiment' created by war-induced defaunation and subsequent trophic rewilding, drawing on data from a pre-war survey[38] of 18 1-ha plots (Fig. 1b) along with repeated post-war surveys of these same plots and others. The second prediction (p_2) was that the current LMH assemblage feeds heavily on mimosa. To test this prediction, we used DNA metabarcoding to quantify mimosa consumption by six dominant floodplain ungulate species between 2013 and 2018. The third prediction (p_3) was that experimental exclusion of LMH releases mimosa from top-down control, thus increasing plant growth, reproduction, recruitment, survivorship, density, and biomass. Support for this last prediction would constitute mechanistic evidence linking the consumption of mimosa (p_2) with the long-term dynamics of mimosa abundance (p_1). Support for all three predictions would refute H_1 and H_2 and would confirm H_3.

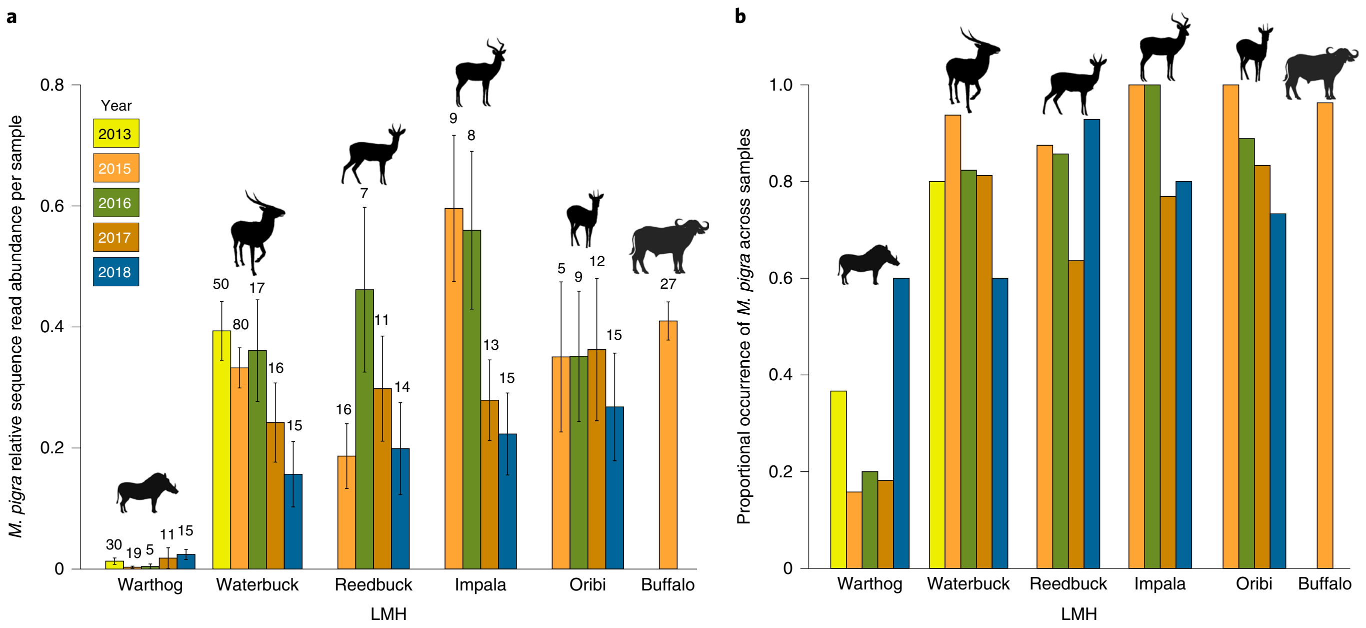


Fig. 3 | Consumption of *M. pigra* by LMH in the Urema floodplain. a, Estimated proportional contribution of mimosa to the diets of six dominant floodplain ungulate species in Gorongosa between 2013 and 2018, indexed by the RRA of mimosa DNA sequences in faecal samples. The bars show the mean (±1 s.e.m.) RRA across all faecal samples from each species in each year (sample sizes are shown above the bars). **b**, Frequency of occurrence of mimosa in the same set of faecal samples. This metric reflects the proportion of samples that contained mimosa DNA (presence–absence); a 1% threshold of RRA was used to infer that mimosa DNA was present in a sample[59]. Sample sizes match those in **a**. Quantitative comparisons between years should be interpreted cautiously, as samples from different years were processed and sequenced separately (see Methods); nonetheless, the data show that mimosa was an abundant and frequent forage of all five ruminant species in each year sampled. The top three food-plant taxa for each LMH species in each year are shown in Extended Data Fig. 1. Comparisons of mimosa consumption in the early versus late dry season are shown in Extended Data Fig. 2. Illustrative video footage of waterbuck and oribi eating mimosa is presented in Supplementary Videos 1 and 2.

Results

The biomass density of LMH in the Urema floodplain declined by 95% from the 1970s to the 1990s (Fig. 2a). Recovery was initially slow but accelerated with the onset of trophic rewilding under the Gorongosa Project[35,36], with a greater-than-fourfold increase in floodplain LMH biomass from 2007 to 2018 (Fig. 2a). Floodplain LMH biomass also rose sharply during the shorter interval encompassing our fieldwork, increasing by 80% from 2012 (9,989 kg km^{-2}) to 2018 (17,958 kg km^{-2}). Four mid-sized antelope species (waterbuck, reedbuck, impala, and oribi) accounted for 80.4% of total LMH biomass in the floodplain in 2018, and buffalo (the numerically dominant pre-war species[38]) contributed an additional 2.5%; the biomass of these five species increased by 150% from 2012 (5,964 kg km^{-2}) to 2018 (14,889 kg km^{-2}) (Fig. 2a). Among just the nine large-bodied species that were counted in both pre-war and post-war surveys (see Methods), the three largest (elephant, hippo, and buffalo) accounted for 85% of floodplain LMH biomass in 1972 but only 14% in 2018, whereas waterbuck alone accounted for 6% in 1972 but 84% in 2018.

In 1972, mimosa occurred in 6.5 ± 2.2% (1 s.e.m.) of 1-m^2 quadrats, on average, in the 18 1-ha monitoring plots. In 2015, the mean frequency of occurrence was threefold greater than this pre-war baseline (19.5 ± 3.8% of quadrats per plot; Fig. 2b). From 2015 to 2017, mimosa occurrence progressively declined to match the pre-war baseline (6.3 ± 1.9% of quadrats per plot; Fig. 2b). All years differed significantly ($P \leq 0.05$) in pairwise contrasts, except for 1972 and 2017 (Fig. 2b). Rainfall from 2012 to 2018 was broadly typical of long-term trends (Fig. 2c); however, rainfall in each year from 2015 to 2017 was lower than the long-term average (by 18%, 10%, and 36%, respectively). To evaluate whether the decline in mimosa occurrence over these years was driven by below-average rainfall, we used data from four floodplain plots that were monitored between 2011 and 2019. From 2015 to 2019, mimosa density declined monotonically to very low levels in all four plots, despite above-average rainfall in 2018 and 2019 (Fig. 2d). Thus, all data are consistent with our first prediction that shrub encroachment in the floodplain increased during several decades of defaunation, decreased with the rapid increase in floodplain LMH biomass, and has been restored to pre-war baseline levels.

Mimosa was the most abundant plant overall in the diets of five dominant ruminant herbivore species in the floodplain between 2013 and 2018. Using the relative abundance of mimosa DNA sequence reads in faecal samples as a proxy for proportional consumption (see Methods), mimosa accounted for at least 16% and up to 59% of each ruminant species' total diet in every year, with averages ranging from 29 ± 6% (reedbuck) to 41 ± 9% (impala) of the diet across years (Fig. 3a). The only abundant floodplain LMH species that abstained from mimosa (1.2 ± 0.3% of the diet on average) was warthog—the lone non-ruminant in our sample set. A complementary analysis based on the frequency of occurrence of plant taxa (that is, presence–absence; see Methods) was congruent with the results based on relative read abundance (RRA): on average, mimosa was detected in 79–96% of the samples from each ruminant species across years (Fig. 3b). The top three forages for warthog in each year were graminoids, making it the only strict grazer in our sample set, whereas ruminants consumed a mix of grasses and forbs in addition to mimosa (Extended Data Fig. 1). Our sampling spanned wetter-than-average (2013 and 2018) and drier-than-average (2015–2017) years, indicating that the consumption of mimosa by putative grazers (waterbuck, reedbuck, and oribi)[45] was not an artefact of rainfall deficit. Similarly, evaluation of early (June–August) and late (October–November) dry season

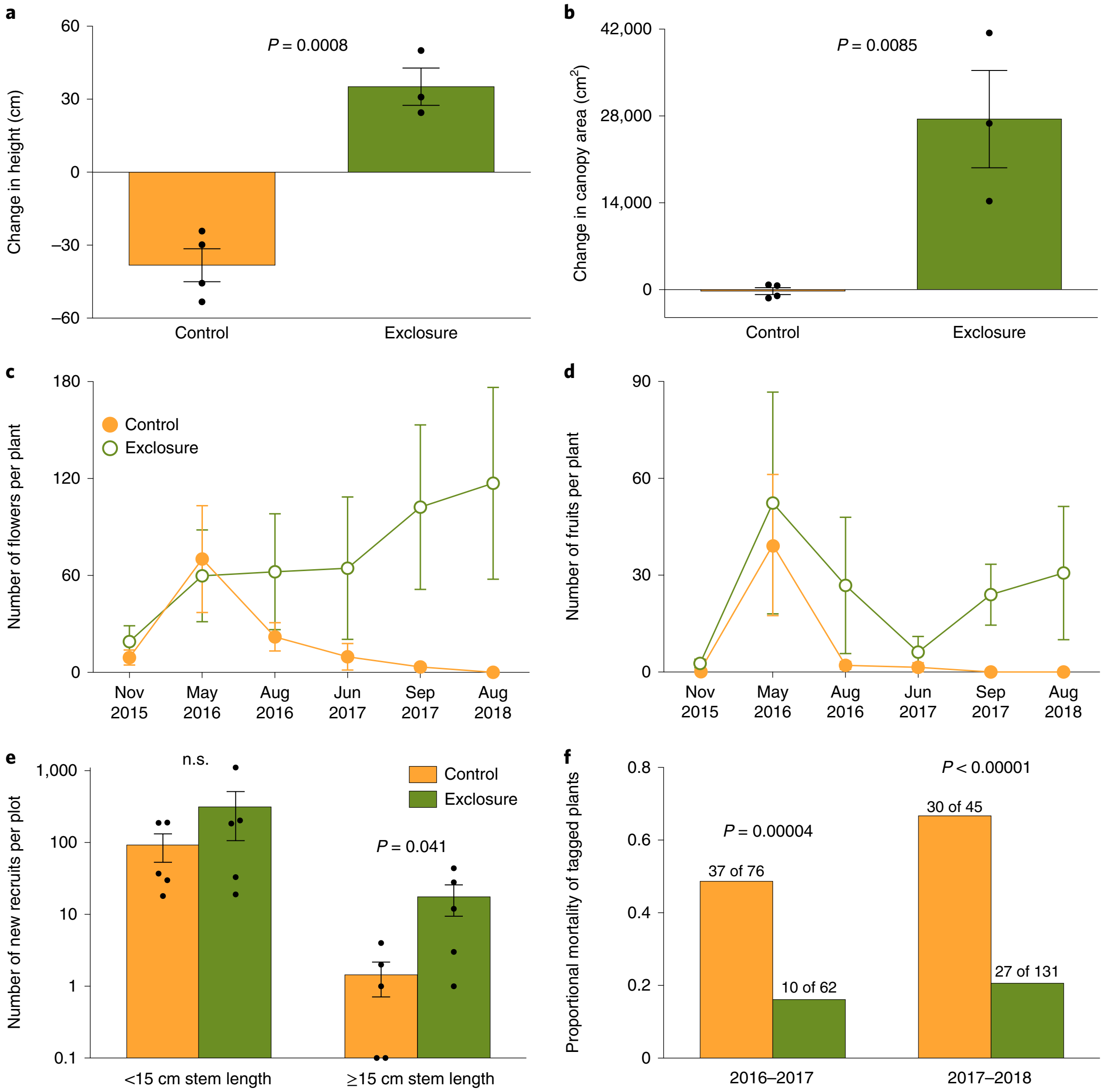


Fig. 4 | Large herbivores suppressed vital rates of *M. pigra*. a,**b**, The mean change in height (**a**) and canopy area (**b**) of tagged plants per plot that survived from November 2015 to September 2017. Error bars show ±1 s.e.m. and dots show the mean value for each of $n=7$ plots (containing a total of 55 tagged plants). Analysis of variance (ANOVA) of plot-level means by treatment: height $F_{1,5}=51.23$, $P=0.0008$; area $F_{1,5}=17.68$, $P=0.008$. **c**,**d**, Mean (±1 s.e.m.) numbers of mature and immature flowers (**c**) and fruits (**d**) per live plant per plot over 3 years (from left to right in each panel, $n=12$, 6, 12, 9, 10, and 9 plots per survey). Statistical analysis was superfluous owing to negligible reproduction in the control plots after 2016. Mature and immature flowers and fruits are shown separately in Extended Data Fig. 3. **e**, Recruitment of new individuals per plot in September 2017, showing a non-significant (n.s.) treatment effect for seedlings (left; ANOVA on square-root-transformed data, $F_{1,8}=1.00$, $P=0.35$), but an order-of-magnitude greater number of post-seedling recruits in the exclosures than in the controls (right; 17.6 versus 1.4 per plot; ANOVA on square-root-transformed data, $F_{1,8}=5.91$, $P=0.041$). The bars show the mean (±1 s.e.m.), and dots show the value for each of $n=10$ plots (owing to the logarithmic y axis scale, values of 0 are represented by dots at 0.1). **f**, Proportional mortality from August 2016 to September 2017 (left) and from September 2017 to August 2018 (right) (binomial GLM of mortality events per plot by treatment: 2016–2017, $\chi^2=16.94$, $P=0.00004$; 2017–2018, $\chi^2=31.09$, $P<0.00001$; d.f. = 1 and $n=9$ plots for each contrast). Unlike **a**–**e**, which show plot-level values, **f** gives treatment-wide proportions of plants that died, pooled across plots for graphical convenience (but the statistical analyses still used plot-level values).

diets in 2017 and 2018 showed that the four antelope species consumed mimosa in appreciable quantities throughout the dry season (Extended Data Fig. 2).

Thus, both abundance- and frequency-based diet analyses support our second prediction that Gorongosa's LMH assemblage feeds heavily on mimosa. Analysis of the foliar-nutrient contents of the most abundant floodplain plant species of each life-form (grasses, forbs, and woody plants) suggested one possible explanation for this pattern. The crude-protein content of mimosa (26.0%) was considerably higher than that of the dominant grasses *Cynodon dactylon* (15.5%) and *Digitaria swazilandensis* (18.7%), the dominant forb *Heliotropium ovalifolium* (19.6%), and the confamilial leguminous tree species *Acacia xanthophloea* (15.6%).

A 3-year LMH-exclusion experiment, comprising six fenced 260-m^2 exclosures and paired unfenced control plots (Fig. 1b,e,f), revealed that ungulates strongly suppressed mimosa growth and reproduction. The mean heights of individually tagged plants in the exclosure and control plots were indistinguishable at the outset

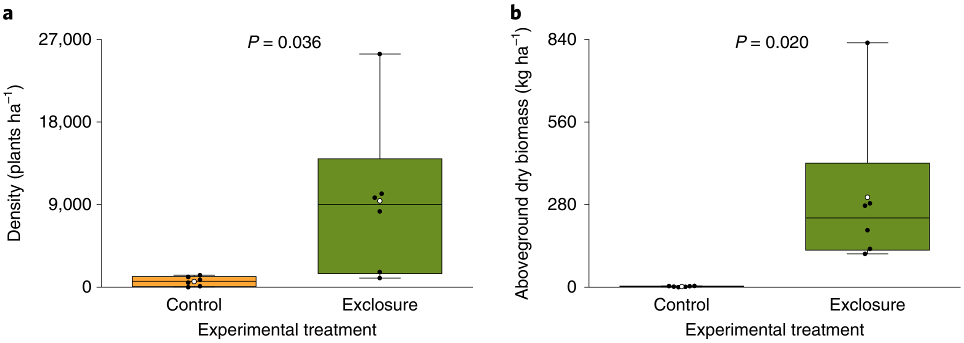


Fig. 5 | Large herbivores regulate the density and biomass of *M. pigra*. a,b, Density (**a**) and aboveground dry biomass (**b**) of mimosa per hectare in the control and herbivore-exclusion plots in August 2018. The box limits represent the interquartile range, whiskers the minimum and maximum, centre lines the median, white dots the mean, and black dots the value for each of $n = 6$ plots in each treatment. Within 3 years of the experiment, mean mimosa density was nearly 15-fold greater in the absence of LMH (641 individuals ha^{-1} in the control plots versus 9,385 individuals ha^{-1}, roughly one plant m^{-2}, in the exclosures), and mean mimosa biomass was more than two orders-of-magnitude greater (2.6 kg ha^{-1} in the control plots versus 304.6 kg ha^{-1} in the exclosures). One-way ANOVA of plot-level values by treatment: density $F_{1,10} = 5.87$, $P = 0.036$; biomass $F_{1,10} = 7.69$, $P = 0.020$; $n = 12$ plots.

of the experiment in 2015 (45.6 ± 4.1 cm and 46.6 ± 6.7 cm, respectively). Within 2 years, the surviving tagged plants in the exclosures had increased in height by an average of 35.1 ± 7.7 cm, whereas those in the control plots had decreased in height by 38.3 ± 6.8 cm (Fig. 4a). Over the same interval, these plants grew in canopy area by 27,475 ± 7,836 cm^2 in the exclosures, but exhibited no net growth in the controls (−230 ± 559 cm^2; Fig. 4b). Reproductive output, although variable across surveys, was consistently greater in the exclosures than in the controls after 1 year (Fig. 4c,d). Within 2 years (September 2017), herbivores had essentially eliminated mimosa reproduction, with no fruits, no mature flowers, and just 3.5 ± 2.0 floral buds per live plant in the control plots (Extended Data Fig. 3). After 3 years, no reproductive parts of any stage were found in the control plots (Extended Data Fig. 3), versus an average of 30.7 ± 20.6 fruits and 116.9 ± 59.5 flowers and floral buds per tagged plant per plot inside the exclosures (Fig. 4c,d).

Ungulates also suppressed demographic rates of mimosa. In September 2017, the mean number of new seedlings (<15 cm stem length) per plot was non-significantly higher in the exclosures (309 ± 203) than in the controls (93 ± 39; Fig. 4e). However, the mean number of new post-seedling recruits (≥15 cm stem length) per plot was negligible in the controls (1.4 ± 0.7) and more than tenfold greater in the exclosures (17.6 ± 8.1; Fig. 4e). Hence, LMH acted as a filter preventing seedlings from reaching mature stages. Mortality of tagged adult plants from 2016 to 2017 and 2017 to 2018 was also greater in the presence of LMH (Fig. 4f). Overall, 37 of 76 (49%) tagged individuals in the control plots died between August 2016 and September 2017, compared with just 10 of 62 (16%) individuals in the exclosures; likewise, from September 2017 to August 2018, 30 of 45 (67%) tagged plants died in the control plots, compared with 27 of 131 (21%) in the exclosures.

Within 3 years of the experiment, mimosa density in the exclosures was nearly one plant per square metre, 15-fold greater than in the control plots (Fig. 5a). The effect on estimated mimosa biomass was even more pronounced (Fig. 5b)—more than two orders-of-magnitude greater in the exclosures (304.6 ± 108.9 kg ha^{-1}) than in the controls (2.6 ± 0.7 kg ha^{-1}; see also Extended Data Figs. 4 and 5).

Discussion

Our results show that native African ungulates confer biotic resistance against encroachment by one of the world's most notorious invasive shrubs, *M. pigra*. This ecosystem function was lost during three decades of severe defaunation, but was restored within one decade of concerted trophic rewilding. In 2015, mimosa was threefold more common than the pre-war baseline. Although this baseline was inferred from a single survey in 1972[38], that survey was spatially extensive and well replicated (Fig. 1b). Moreover, our conclusion that mimosa abundance increased following defaunation is reinforced by a previous study of satellite imagery[46], which found that floodplain woody cover increased by 134% between 1977 and 2012 (mimosa is the only woody plant species throughout much of the floodplain). Tinley's observation[38] that LMH suppressed mimosa in the pre-war era, coupled with Beilfuss's observation[39] that mimosa was expanding in 2007, is also consistent with our interpretation. From 2015 to 2017, we documented the decline of mimosa to pre-war baseline levels, in concert with the continuing rapid increase of LMH biomass in the floodplain (Fig. 2a,b). These data, too, are temporally limited, comprising nine surveys over 3 years with below-average rainfall. However, data from an independent set of plots monitored over timespans of up to 9 years corroborate the progressive decline in mimosa abundance from 2015 onwards (Fig. 2d).

We established the mechanistic role of LMH in regulating mimosa encroachment via diet analysis and a 3-year manipulative experiment. DNA metabarcoding revealed that mimosa, a high-protein resource, accounted for a large proportion of the diets of the dominant floodplain ruminant species (Fig. 3). One of these species, buffalo, was historically the most abundant ungulate in Gorongosa (>14,000 individuals)[38] and probably contributed to controlling mimosa in the pre-war era. The other four species accounted for >80% of current floodplain LMH biomass, which increased by 80% from 2012 to 2018, helping to explain the recent decline of mimosa. Our experiment showed that LMH suppressed all measured components of mimosa performance and fitness (Fig. 4 and Extended Data Fig. 3), and that release from herbivory caused a 15-fold difference in density and a 117-fold difference in biomass relative to control plots within 3 years (Fig. 5 and Extended Data Fig. 5). These experimental results are the crux of our conclusions (monitoring data are invariably subject to potentially confounding influences such as rainfall variability, but the experimental results can be explained only by the manipulation), and they further reinforce our inference that mimosa abundance increased during several decades of defaunation (effectively an ecosystem-scale LMH-exclusion event). The dietary data show that consumption is one mechanism by which LMH suppress mimosa encroachment (but do not rule out additional effects of trampling), and the observational survey data show that the experimental results are reflected in landscape-scale trends.

Collectively, these results are wholly consistent with H_3 and refute the alternatives H_1 and H_2 (Fig. 1g). H_1 proposed that LMH ignore mimosa, which was not the case: mimosa was the predominant food plant of floodplain ruminant species. H_2 proposed that LMH facilitate mimosa, perhaps by dispersing seeds or suppressing competing plants, as has been hypothesized for feral ungulates in tropical Australia[47–50]. Our experiment (Figs. 4 and 5), reinforced by landscape-scale monitoring (Fig. 2), rules out H_2. If LMH exerted a facilitative net effect on mimosa, then mimosa performance and abundance should have decreased (instead of increased) when LMH were experimentally excluded, and mimosa occurrence and density should have increased (instead of decreased) as LMH biomass increased in the floodplain.

Trophic rewilding aims to use megafaunal restoration to create self-regulating ecosystems that require little additional management intervention[17,51]. One uncertainty about the feasibility and practicality of such initiatives is that defaunation may lead to alternative states that cannot be reversed by wildlife recovery alone (and that might even impede wildlife recovery)[19]. This is a salient concern in the context of shrub encroachment in grassy biomes, where woody- and grass-dominated states are thought to represent stable alternatives[30,52–54]. Mimosa can form impenetrably dense thickets[40] (Fig. 1d), which could in principle obstruct browsing mammals and prevent them from exerting strong top-down control. Yet our results show that 35 years of defaunation-induced shrub encroachment[46] was reversible within 10 years, indicating that no persistent alternative state was reached.

Although hydrological regimes influence woody-plant encroachment in seasonally flooded ecosystems, hydrology alone cannot explain the dynamics of mimosa in Gorongosa. Surface-water maps[55] suggest that inundation of our study area may have been less frequent from 2000 to 2015 than from 1984 to 1999 (although there is no discernible trend in rainfall over this interval: Fig. 2c and ref. [46]). Moreover, a directional long-term drying trend would not in itself explain the initial expansion and subsequent decline of mimosa in Gorongosa (Fig. 2b). Mimosa thrives in flooded areas and riparian ecotones[40], which suggests that a reduction in flood frequency would, if anything, have reduced the extent of mimosa between 1972 and 2015; indeed, mimosa invasions elsewhere have increased with the creation of permanently flooded areas through damming[56]. Our survey data (Fig. 2d) suggest that short-term rainfall fluctuations may have limited mimosa before 2015, but an overriding effect of rainfall is not consistent with the decline in mimosa density from 2015 to 2019 (although it is possible that below-average rainfall from 2015 to 2017 interacted with the increase in LMH biomass to accelerate mimosa decline). Ultimately, our experimental results (Fig. 5) confirm the role of herbivory in suppressing mimosa, irrespective of moisture availability, but the interactive effects of shifting herbivory and hydrology regimes on shrub encroachment warrant further study.

The heavy consumption of mimosa by floodplain ruminants is arguably surprising given that four of these species (buffalo, waterbuck, reedbuck, and oribi) are typically classified as grazers with overwhelmingly grass-based diets[45,57]. These consumption patterns are not an artefact of rainfall (Fig. 3 and Extended Data Figs. 1 and 2), nor can they be explained purely by relative plant availability—a previous study[58] showed that Gorongosa herbivores specifically selected for mimosa, presumably for its nutritive value. We note that the RRA of plant DNA in faecal samples may not perfectly reflect the quantitative consumption of biomass[59], owing to differences in digestibility, chloroplast density, or taxon-specific recovery biases among plant species[60]. The estimates of mimosa consumption in Fig. 3a should therefore be interpreted as approximations. That said, studies using both controlled-feeding trials[61] and correlations between molecular and isotopic dietary reconstructions[60,62] have found that grass RRA is strongly positively correlated with the proportion of grass in the diet; accordingly, our finding that even putative grazers browsed heavily on mimosa is very unlikely to be a methodological artefact. Indeed, our results did reveal the existence of one strict grazer, warthog, indicating that our methods were capable of resolving grass-dominated diets.

It remains unclear whether wild and/or domesticated LMH are capable of containing mimosa invasions elsewhere in the tropics, or whether our results reflect a unique capacity of diverse African ungulate assemblages. In Costa Rica, where mimosa is native, mimosa was reportedly rejected as food by deer, peccary, and tapir[41]. Most previous work on invasive mimosa populations is from Australia, where LMH assemblages comprise non-native feral buffalo and pigs as well as native macropods[47]. The impact of these species on mimosa is generally assumed to be either facilitative[47–50] or neutral[63]. Mammalian herbivory has been discounted on the grounds that "in general, the plant seems low in palatability to higher animals"[40]. Our results counter that view. Yet herbivore traits, and the functional diversity of LMH assemblages, might be important in determining the extent to which LMH can contain shrub encroachment. Mimosa produces the uncommon amino acid mimosine[40], which ruminant gut bacteria can detoxify[64,65]. It is notable that warthog, the only non-ruminant species tested in our study, was also the only species that avoided mimosa. If the ruminant microbiome is important in processing secondary metabolites of mimosa, then this might explain why mimosa is unpalatable to suids and other hindgut fermenters (such as tapir). We do not know why mimosa might be unpalatable to other ruminant species (such as feral buffalo and deer). Even among ruminants, however, different species, populations, and individuals possess varying abilities to cope with chemical defenses[64]. For example, the encroaching shrub *Solanum campylacanthum* in Kenya is highly toxic and potentially lethal to sheep[66], but is intensively browsed and suppressed by wild antelopes[67].

These considerations highlight important questions for future research on trophic rewilding and for debates over 'novel ecosystems'[68]: to what extent are the effects of different megafaunal species functionally redundant[67], and what does that imply about the order and timing of species reintroductions needed to achieve management objectives[17,69]? We found that the contemporary LMH assemblage in Gorongosa was able to restore biotic resistance to shrub encroachment despite a radical shift in LMH species composition and size structure relative to the pre-war baseline. However, the specific mechanisms of control may have differed between these periods. Tinley[38] described elephant as major consumers of mimosa in the floodplain historically, whereas we find exceedingly infrequent floodplain utilization and mimosa consumption by elephants in the post-war era[58,70]. It is possible that trampling by megaherbivores (elephant, hippo) and large, herd-forming grazers (buffalo, zebra, wildebeest) was more important historically than in the current assemblage, which is dominated by smaller, less gregarious ungulates. Yet these smaller, more selectively feeding species might be more efficient at controlling mimosa at early growth stages (see, for example, Supplementary Videos 1 and 2), which might compensate for any reduction in trampling and for the ability of larger-bodied species such as elephant to kill large plants. We also note that the net-negative effect of the LMH assemblage as a whole might obscure species-specific effects that differ in magnitude or even direction. For example, strict grazers such as warthog (Extended Data Fig. 1) might have a facilitative effect on mimosa (for example, by suppressing competing grasses such as *C. dactylon*) that is outweighed by the stronger suppressive effects of other species. Historically, hippo ate large quantities of *C. dactylon*[38] and might likewise have mitigated the competitive effects of this abundant grass. Ultimately, whereas we have demonstrated that trophic rewilding can rapidly restore a key ecosystem function despite a major change in the animal assemblage, we can only speculate about the contributions of particular species and the relative importance of complementary mechanisms such as consumption and trampling. Parsing these nuances would enable more fine-grained insights into the degree of functional redundancy in diverse megafaunal assemblages[67], and how restoration can be tailored to achieve particular management objectives—central foci of research on both trophic rewilding[17,69] and novel ecosystems[68]. For example, longer-term monitoring of mimosa could illuminate the effects of trampling and how the strength of biotic resistance changes as Gorongosa's megaherbivores continue to recover, while species-specific effects could be evaluated using size-selective exclosures[67,71–74]. Similar approaches could be used in other systems to understand the extent to which livestock are functional analogues of wild LMH (although this is not a pertinent issue in Gorongosa or in many other parts of Africa where livestock are kept at negligible densities owing to tsetse fly and trypanosomiasis[75]).

Our results do suggest one general lesson for efforts to restore vegetation structure via trophic rewilding. In Gorongosa, three large-carnivore species (leopard, wild dog, and hyena) were extirpated before post-war recovery began. Lions persisted, but occurred at roughly one-third of their pre-war abundance in 2017[36,37]. Active reintroduction of large carnivores (starting with 14 wild dogs translocated from South Africa) was initiated only in 2018, by which time LMH biomass had recovered to nearly pre-war levels[35]. Although it would have been possible to begin carnivore restoration at an earlier date, the delay provided populations of mid-sized herbivores—which are predator-limited in more-intact systems[76]—with a sufficient head start to reverse shrub encroachment in the floodplain. Moreover, the extended relaxation of predation risk enabled ordinarily forest-dwelling species such as bushbuck (*Tragelaphus sylvaticus*) to expand into the floodplain, where they accounted for only 0.3% of total floodplain LMH biomass but consumed diets comprising 74% mimosa[77]. We therefore hypothesize that the efficiency of trophic rewilding might be maximized by postponing carnivore reintroductions until after herbivore populations have begun to strain carrying capacity. Continued monitoring will tell whether the return of apex predators in Gorongosa weakens biotic resistance via a trophic cascade, or whether herbivores maintain control over invasive shrubs even in the presence of a functionally intact carnivore guild (as was the case historically[38]).

Conclusion

By combining historical and contemporary monitoring data, diet and forage-quality analyses, and a multiyear field manipulation, we have provided evidence (1) that war-induced loss of native large herbivores disrupted a key ecosystem function (biotic resistance to shrub invasion), leading to a degraded ecosystem structure (woody encroachment in floodplain grasslands); and (2) that the restoration of native megafauna revived this function and reversed the degradation to a state resembling the pre-war baseline. These results underscore the resilience of ecosystems in the face of decades of defaunation, provide empirical support for the efficacy of trophic rewilding in restoring top-down interactions and associated functions[15], and suggest a generalizable suite of methods that can be used to benchmark rewilding progress[20]. Locally, our findings obviate the need for the aggressive and expensive management interventions that had been proposed to control mimosa in Gorongosa[39], such as exotic biocontrol agents (which would risk novel invasions) and aerial herbicide application (which would risk threats to human health in downstream communities that rely on Lake Urema's outflow for water supply). More broadly, our results highlight the potential utility of trophic rewilding for reversing a common form of environmental degradation on relatively rapid ecological timescales in Africa's protected areas.

Methods

Focal species. The shrub *M. pigra* is native to tropical America and spread globally during the 1800s as an ornamental and a botanical curiosity, owing to its touch-sensitive (thigmonastic) leaves[47,78,79]. In Africa, mimosa was first recorded in Egypt in 1826 and is thought to have spread along river systems; it was collected by botanists in Rwanda in 1932 but is likely to have arrived there by the mid-1800s[80]. Mimosa was likewise recorded throughout East Africa and much of West Africa in floras published in the 1950s[81]. Mimosa has several traits that make it an aggressive invader. First, its floating seeds enable it to disperse widely and rapidly[63]. Second, it can grow and reproduce quickly, reaching maturity within 120 days and reproducing year-round[47]. Third, it can re-sprout from root stock and regenerate from dense soil seed banks[48]. It is defended by short prickles and has been found to produce at least low levels of the toxic amino acid mimosine[40]. Mimosa is considered a major threat to wetland biodiversity, ecosystem services, and agriculture; infestations have imposed diverse ecological and economic costs in ecosystems worldwide[49,81–83]. Mimosa remains poorly studied in Africa (but see refs. [56,80,82]), where it now occurs in at least 42 countries[81]. Mimosa-control strategies developed in Australia include cutting, burning, herbicide, bulldozing, and at least 15 introduced insect and fungal biocontrol agents[84–87]. These measures are costly: Australia spent AU$500,000 annually trying to eradicate mimosa in Kakadu National Park[88], and countrywide costs were estimated at US$20 million over 24 years[89]. Despite these efforts, mimosa has continued to spread in Australia[88,90].

Little is known about how LMH interact with mimosa in either its native or invasive range. Studies from Australia have generally argued either that feral ungulates and macropods facilitate mimosa (H_2) by overgrazing native competitors, dispersing seeds, and disturbing soil[47–50], or that LMH interact weakly with mimosa (H_1) because of its ostensibly unpalatable foliage[40,41] and thus have neutral effects on the plant[63]. Yet these inferences are based on limited empirical evidence; to our knowledge, interactions between LMH and mimosa have not been intensively studied anywhere.

Geographical and historical context. Gorongosa National Park occupies roughly 4,000 km² of central Mozambique (18° 53′ S, 34° 26′ E), most of it within the Great Rift Valley (Fig. 1). The warm wet season spans November to April, and a cool dry season occurs from May to October. The mean annual precipitation (±1 s.e.m.) in the Rift Valley, measured at the park headquarters at Chitengo, was 842.6 ± 51.9 mm over 26 years between 1957 and 2011 (no data are available for 1970 to 1998). The mean annual rainfall from 2012 to 2018 (the period bracketing our fieldwork) was 937.4 ± 154.5 mm (Fig. 2c). A previous study found no directional trend in annual rainfall from 1951 to 2012 within a roughly 20 × 20 km² grid around this area, using data from the African Flood and Drought Monitor[46].

Near the centre of the park is the shallow (<2 m) perennial Lake Urema[91] (Fig. 1a,b). During the wet season, Lake Urema collects rainfall and runoff from the rift escarpments[92], flooding up to 780 km² of low-lying area in the Rift Valley portion of the park[93] (Fig. 1e,h). The receding floodwaters unveil a productive floodplain (Fig. 1f), historically characterized[38] as a grassy lawn with sparse forbs, dissected by drainage channels and mudflats, with large areas dominated by grasses such as *C. dactylon* and *D. swazilandensis* (syn. *D. didactyla*). In the early 1970s, this floodplain supported large aggregations of buffalo (*Syncerus caffer*), hippo (*Hippopotamus amphibius*), zebra (*Equus quagga*), wildebeest (*Connochaetes taurinus*), and waterbuck (*Kobus ellipsiprymnus*), with local biomass densities estimated to be >200,000 kg km⁻² in places[38].

The Mozambican Civil War (1977–1992) devastated Gorongosa's wildlife[94], with >90% declines in abundance among large-bodied herbivore species[35]. Among top carnivores, only lions (*Panthera leo*) persisted, but in much lower numbers than the historical estimate[38] of ~200 individuals; 104 lions were documented between 2012 and 2016[37], and ~65 individuals were thought to be alive in 2017[36]. Leopards (*P. pardus*), hyenas (*Crocuta crocuta*), and African wild dogs (*Lycaon pictus*) were all functionally extirpated[35]. The Gorongosa Project, a public–private partnership, was launched in 2007 with the mission of restoring ecological integrity while simultaneously alleviating poverty in the park's buffer zone via ecotourism and other enterprises[36]. The ecosystem management strategy to achieve these objectives has focused on the recovery and reintroduction of native megafauna[35–37]. The reinstatement of effective conservation law enforcement, coupled with efforts to mitigate human–wildlife conflict, has facilitated the recovery of remnant ungulate and lion populations[35–37,70]. In addition, 451 individuals of six LMH species (elephant, hippo, buffalo, zebra, eland, and wildebeest) were translocated into Gorongosa from elsewhere in southern Africa between 2007 and 2014, and a founding pack of 14 wild dogs was introduced from Kwazulu-Natal in 2018[35]. Future reintroductions of wild dogs, leopards, and hyenas are planned[35,36,77]. Thus, the Gorongosa Project is a large-scale trophic-rewilding effort that blends both 'passive' and 'active' rewilding (sensu ref. [17]). By 2018, the total biomass density of all LMH species in Gorongosa was ~95% of pre-war estimates (although note that the pre-war counts included only large-bodied species; see Estimation of large-herbivore biomass density in the Urema floodplain), but species' abundances were heavily skewed relative to the pre-war baseline[35]. The formerly dominant largest-bodied species remain relatively rare, whereas mid-sized ungulates—waterbuck, reedbuck (*Redunca arundinum*), impala (*Aepyceros melampus*), oribi (*Ourebia ourebi*), and warthog (*Phacochoerus africanus*)—now account for the vast majority of LMH biomass[35].

Mimosa is the only alien invasive shrub known to occur in the core of Gorongosa National Park. It is also one of the only woody plant species of any kind that occurs in the Urema floodplain. Although we know of no evidence on the date of arrival of mimosa in Mozambique, data from other countries (including neighbouring Tanzania) suggest that it was present for at least several decades and perhaps a century or more before Tinley's[38] pre-war surveys in Gorongosa. Tinley[38] found that mimosa accounted for 95% of all woody plants in the floodplain in 1972, but also noted that "mimosa is a favored browse food and only attains shrub growth form during inundations; the remainder of the time it assumes a prostrate growth form in response to heavy utilization by herbivores." In 2007, however, after defaunation and before substantial LMH recovery, Beilfuss[39] found "no evidence of significant herbivory on mimosa" and advocated exploration of multiple control strategies, including fire, herbicide, manual removal, and introduction of insect and fungal enemies.

Estimation of LMH biomass density in the Urema floodplain. We assembled data from three pre-war (1969–1972) and twelve post-war (1994–2018) aerial wildlife counts to estimate the biomass density of LMH in the Urema floodplain. The full methodology for these aerial counts has been published, along with the results for a 1,832-km^2 survey block in the core of the park[35]. This block encompasses various grassland, savanna, and forest landscape types. Here, we used this dataset to extract only the records that occurred within the 713-km^2 floodplain portion of the survey block; this portion represents 91.4% of the total 780-km^2 floodplain landscape in Gorongosa[93] (Fig. 1h). Raw count data were converted into biomass densities based on the area of floodplain surveyed in each year, following ref. [35], to account for the variable areal coverage of the surveys conducted before 2014. These data underestimate the true LMH biomass density in the floodplain from 1969 to 1972, because pre-war counts included only nine of the largest-bodied (≥170 kg) species[38]—elephant (*Loxodonta africana*), hippo, buffalo, eland (*Taurotragus oryx*), zebra, sable (*Hippotragus niger*), waterbuck, wildebeest, and hartebeest (*Alcelaphus buselaphus*)—whereas post-war counts included all species ≥10 kg (ref. [35]). Accordingly, we do not know the pre-war densities of currently abundant mid-sized species such as warthog, impala, reedbuck, and oribi. However, the overall shift in assemblage size structure from larger- to smaller-bodied species can be gauged by comparing the relative densities of just the nine species that were counted in both pre- and post-war surveys; waterbuck alone accounted for roughly the same proportion of biomass in the floodplain in 2018 as did elephant, hippo, and buffalo together in 1972 (see Results).

Population trends of *M. pigra* in the Urema floodplain (p_1). In April 1972, Tinley[38] surveyed 18 1-ha plots in the floodplain, which were situated along three parallel transects extending outwards from Lake Urema (Fig. 1b). In each of 30 1-m^2 quadrats in each plot (540 total quadrats), Tinley recorded the presence of all plant species. We replicated these surveys nine times from 2015 to 2017, randomizing quadrat locations within each plot in each survey by selecting a random compass orientation and a random number of steps from the plot centre. In each quadrat, we recorded whether mimosa was present (1) or absent (0), distinguishing seedlings (individuals <15 cm in length with herbaceous stems) from recruits (≥15 cm total stem length, when stems begin to lignify). For analysis, we focused on the proportion of 1-m^2 quadrats in each plot that contained recruits ≥15 cm, as large numbers of seedlings emerge after wet periods but die before reaching reproductive size[40]. In each year, we conducted surveys in both the early and late dry season (the floodplain is typically underwater and thus cannot be surveyed during the wet season), although the timing of the surveys and the accessibility of particular plots varied depending on the spatio-temporal distribution of rainfall and flooding. The 2015 surveys were conducted in July (18 plots, 12–15 quadrats per plot, 267 total quadrats) and November (8 plots, 10–15 quadrats per plot, 94 total quadrats). The 2016 surveys were conducted in March (18 plots, 15 quadrats per plot, 270 total quadrats), May (15 plots, 15 quadrats per plot, 225 total quadrats), August (17 plots, 15 quadrats per plot, 255 total quadrats), and November (18 plots, 15 quadrats per plot, 270 total quadrats). The 2017 surveys were conducted in June (8 plots, 15 quadrats per plot, 120 total quadrats), September (17 plots, 15 quadrats per plot, 255 total quadrats), and December (17 plots, 15 quadrats per plot, 255 total quadrats).

To quantify trends in mimosa occurrence through time, we treated the 18 1-ha plots as the units of analysis. To account for the variation in the number and identity of plots included in each survey and to minimize sampling artefacts, we first averaged the proportion of quadrats in each plot that contained mimosa across all surveys of that plot conducted within each year, generating a single mean value for each plot in each year. Thus, each data point in Fig. 2b and in the associated statistical analyses represents a plot-level average of one-to-four surveys of that plot in a given year, with a sample size of $n = 18$ plots in 1972, 2015, and 2016, and $n = 17$ plots in 2017. This treatment of the repeated-measures data is statistically conservative in that it does not assume independence of surveys of a given plot within the same year (between floods), and it balanced the dataset and maximized comparability by ensuring that at least 17 of the 18 plots were represented in each year being compared. We analysed these proportional data by fitting a binomial GLM with logit-link function (estimated using maximum likelihood in JMP Pro v.13.0), with year and plot identity as categorical predictors. We tested our prediction (p_1) that mimosa occurrence increased from 1972 to 2015 and decreased from 2015 to 2017 by conducting pairwise contrasts between years, using likelihood-ratio χ^2 tests.

We had also surveyed all 18 of these plots in July 2013 (30 quadrats per plot, 540 total quadrats) and recorded mimosa in 53.0% ± 6.7% of quadrats per plot, which is 2.7-fold higher than the value recorded in July 2015. Later, in the process of constructing a taxonomically verified local plant reference database for DNA metabarcoding[58], we learned that we had mistakenly conflated *M. pigra* with a similar-looking mimosoid plant, *Neptunia oleracea* (water mimosa), in this survey—meaning that 53% represents the upper bound of true mimosa occurrence in 2013. However, mimosa was fourfold more common than *N. oleracea* in 2015, which suggests that true mimosa occurrence in 2013 was almost certainly higher than the highest value shown in Fig. 2b—and thus that the decline of mimosa in these plots spanned at least 2013 to 2017. We conservatively omitted this datum from graphical presentation and statistical analyses, but we consider it an informative reference point and therefore included a dashed line in Fig. 2b to reflect the likelihood that the mimosa decline began before 2015.

Because our survey data from these 18 plots from 2015 to 2017 may be insufficient to characterize long-term trends in woody-plant occurrence, and because these 3 years coincided with below-average rainfall in the park (respectively 18%, 10%, and 36% lower than the long-term average), we assembled data on mimosa density from an independent set of four floodplain plots (locations in Fig. 1b) that were monitored at intervals between 2011 and 2019. This longer timespan encompassed both above-average (2013, 2014, 2018, and 2019) and below-average (2012, 2015, 2016, and 2017) rainfall years (Fig. 2c). In these plots, all woody plants of all sizes were counted within four 2 × 25 m^2 belt transects on each side of a 625-m^2 square. The mimosa density in each plot was calculated for the 200 m^2 encompassed by these transects (Fig. 2d).

Diet analysis (p_2). To test p_2, that Gorongosa's LMH feed heavily on mimosa, we assessed the diet composition of six dominant floodplain ungulate species, using DNA metabarcoding[62,95,96] of faecal samples collected in the early dry season (June–August) between 2013 and 2018. This period encompassed both above-average (2013 and 2018) and below-average (2015, 2016, and 2017) rainfall years (no samples were collected in 2014). In addition, we analysed a set of samples collected in the late dry season (October–November) of 2017 and 2018 to gauge the sensitivity of mimosa consumption to declining moisture availability. We collected fresh samples exclusively from the floodplain, typically after observing defaecation. Warthog and waterbuck were sampled in all 5 years; reedbuck, impala, and oribi were sampled in 4 years (2015–2018); and buffalo were sampled only in 2015 (because buffalo remain relatively rare and cannot always be found in the floodplain). Our primary analyses are based on a total of 419 faecal samples from the early dry season, representing warthog ($n = 80$), waterbuck ($n = 178$), reedbuck ($n = 48$), impala ($n = 45$), oribi ($n = 41$), and buffalo ($n = 27$), with a minimum of $n = 5$ samples per species in any given year (Fig. 3 and Extended Data Fig. 1). The intra-annual contrasts incorporated an additional 50 samples from the late dry season (Extended Data Fig. 2).

The metabarcoding method targets a short and variable fragment of plant DNA, the P6 loop of the chloroplast *trn*L intron[95], which enables us to (1) identify food-plant taxa by comparing plant DNA in faecal samples with reference databases, and (2) estimate the proportional representation of each plant taxon in each LMH species' diet, based on the RRA of DNA sequences in each sample[59]. Mimosa had a unique P6 barcode in our local plant reference database[58] and exhibited low similarity (<92%) with the only other common floodplain plant in the same subfamily (*N. oleracea*, for which we also obtained a 100% match in herbivore diets), making it highly likely that our detections of mimosa are accurate.

All sample-collection, DNA-extraction, PCR, and sequencing procedures followed established methods that we have used previously in this system[58,70,77] and others[62]. The sequence data from 2016 are a subset of those generated during a broader synoptic study of LMH diets in Gorongosa[58]. We first provide a high-level overview of our workflow before presenting detailed methods over the next several paragraphs. DNA was extracted from each sample individually using commercial faecal-DNA extraction kits. Standard methods were employed to amplify the P6 marker, a conventional metabarcode for vascular plants[58,60–62,95,97,98]. Extraction and PCR controls were included in all years, and from 2015 to 2018 we also performed PCR replicates for each sample. Plant amplicons were purified and later sequenced on an Illumina HiSeq platform. Sequence data were curated using OBITools v.1.2 software[99]. Taxonomic assignments of unique sequences (molecular operational taxonomic units, mOTUs) were made by comparison to a local database of taxonomically verified plant vouchers[58] and a global database generated by in silico PCR from the European Molecular Biology Laboratory database. To quantify the contribution of mimosa to LMH diets, we first rarefied the mOTUs-by-samples matrices to 3,000 reads per sample and converted these matrices into proportions to obtain the RRA of each plant mOTU per sample. We then extracted the RRA of sequences that matched perfectly (100% identity) with *M. pigra* sequences in our local reference database and averaged across samples to determine the mean RRA of mimosa sequences in the diet of each LMH species in each year (or season). We interpret RRA as the approximate proportional contribution of mimosa to each species' diet[59,61,62]. However, because RRA may not always be a reliable proxy for quantitative consumption[59], we also conducted a complementary analysis based on the frequency of occurrence (presence–absence) of plant taxa in each sample. Together, these two analyses constitute a robust test of our prediction (p_2) that mimosa is a frequent and abundant component of LMH diets in Gorongosa, notwithstanding potential recovery biases and other sources of uncertainty inherent in dietary analysis using DNA metabarcoding[59].

Samples from each year were processed, sequenced, and analysed independently from one another; samples from the early versus late dry season in 2018 were also sequenced separately. Owing to subtle differences in the pipeline in different sampling periods, which are described below, direct quantitative comparisons of results between years (and seasons, for 2018) should be interpreted cautiously. We emphasize that the objective of these analyses was to test whether (and which) large herbivores consumed mimosa in substantial quantities within any given sampling period, and not to make inferences about temporal trends in consumption. In all years, samples were collected from faecal piles in unused plastic bags, immediately placed on ice, and later homogenized by kneading the bag. In 2013, samples were preprocessed using the Omega E.Z.N.A. Stool DNA kit (Omega Bio-Tek); approximately 100–200 mm^3 of sample was added to a cryogenic tube containing ~200 mg of glass beads and 540 µl of SLX-Mlus buffer, homogenized on a flatbed vortex, subjected to antiviral treatment (see below), and frozen for transport to Princeton University. In 2015–2018, samples were preprocessed as follows: approximately 100–200 mm^3 of sample was transferred into tubes containing silica beads and a DNA stabilization/lysis buffer (Zymo Xpedition Stabilization/Lysis Solution, Zymo Research); tubes were vortexed for 30 s to lyse cells and then frozen. Before transport to the United States, all samples were subjected to one of the following antiviral treatments mandated by the US Department of Agriculture's Animal and Plant Health Inspection Service (permit numbers 122489, 123156, and 130123). In 2013 and 2015, we applied a chemical-and-heat treatment wherein samples were treated with proteinase K, heated to 95 °C for 15 min, and then treated with RNase A. In 2016–2018, following the issuance of revised regulations, we used a heat-only treatment of 72 °C for 30 min. On arrival at Princeton University, samples were stored at −80 °C and later extracted in a facility dedicated to faecal DNA analysis. Faecal samples were extracted per the manufacturer's instructions using E.Z.N.A. Stool DNA kits in 2013, and using Zymo Xpedition Soil/Fecal DNA MiniPrep kits in 2015–2018.

To amplify plant DNA contained in faecal samples, we targeted a short and variable region of the chloroplast genome, the P6 loop of the *trn*L (UAA) intron[95], using PCR primers g (forward: 5′-GGGCAATCCTGAGCCAA-3′) and h (reverse: 5′-CCATTGAGTCTCTGCACCTATC-3′). Tags consisting of eight base pairs (bp) (each differing by at least four nucleotides) were added to the 5′ end of each primer to enable PCR products to be multiplexed and sequenced within a single high-throughput sequencing run[96,100]. PCR mixtures contained 1X GenAmp PCR buffer II; 2.5 mM of $MgCl_2$ (Applied Biosystems); 0.2 mM each of dNTP; 0.1 mg ml^{-1} of BSA (New England Biolabs); 0.2 µM each of primer; 4% dimethyl sulfoxide (Sigma-Aldrich); 0.5 U AmpliTaq Gold DNA Polymerase; and 2 µl of DNA extract, in a final reaction volume of 12.5 µl in 2013 and 20 µl in 2015–2018. Thermocycling conditions included initial denaturing at 95 °C for 10 min, followed by 35 cycles of denaturing at 95 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 30 s, and a final elongation step at 72 °C for 2 min. Multiple extraction controls (sample-free extracts), PCR controls (nuclease-free water), and positive controls were included in the analyses. For 2015–2018 samples, we performed multiple PCR replicates (two or three per extract in 2015 and 2016, three per extract in 2017 and 2018) to monitor the reproducibility of results and any effects of variation in sample processing[97,101]. PCR products from 2013 and 2015 were purified using a SequalPrep Normalization Plate Kit (Applied Biosystems), and those from 2016 to 2018 with a MinElute PCR Purification Kit (Qiagen). Libraries from 2013, 2015, and 2018 were prepared using a PCR-based approach, whereas a PCR-free approach was used for 2016 and 2017 libraries. All libraries were sequenced on the Illumina HiSeq 2500 platform (170-bp single-end sequencing for 2013 libraries and 2 × 150-bp paired-end sequencing for 2015–2018 libraries) at Princeton's Lewis-Sigler Institute for Integrative Genomics.

The filtering procedures in OBITools were as follows. (1) Paired-end reads (that is, those from the 2015–2018 libraries) were aligned and assembled using the illuminapairedend command. (2) Sequences were assigned to their original samples, on the basis of the tags fixed to the primers, using the ngsfilter command (allowing zero errors on tags and a maximum of two errors on primers). (3) Identical sequences were merged using the obiuniq command. (4) Low-quality sequences were discarded, including sequences with a low alignment-quality score (<40, the value corresponding to perfect alignment between the last 10 bases of each read), those with an unexpected length (<8 bp or >180 bp, outside of the P6 barcode length range), those containing ambiguous nucleotides, and those represented by only one read in entire dataset. (5) Sequences were assigned to a plant taxon (ecotag command) by comparison with two different reference databases: a local plant reference database[58] and a global reference database generated by in silico PCR (ecoPCR program[102]) from the European Molecular Biology Laboratory's Nucleotide Sequence Database (Release 130 for 2013–2016, Release 134 for 2017–2018; ftp://ftp.ebi.ac.uk/pub/databases/embl/release). (6) The obiclean command (with parameters $d = 1$ and $r = 0.25$) was used to detect sequences potentially resulting from amplification or sequencing errors; for each sample, the program determines whether a sequence is more likely to be a true sequence (head) from which others are derived, a sequence that is derived from another (internal), or a sequence from which no other sequence is derived and is itself not derived from another (singleton). This information was used later in the filtering process to remove sequences likely to have resulted from PCR or sequencing errors[58]. (7) Files were converted into mOTUs-by-samples tables and analysed using R v.3.5.3 (ref. [103]).

By default, sequences were first assigned to the local reference database[58]. However, if the local database assignment score was <98%, and if the global database score was greater than the local database score, then the sequence was reassigned to the global database. To remove sequences likely to have resulted from PCR or sequencing errors, we discarded all mOTUs that both (1) did not perfectly match any sequence from the local reference database and (2) were more frequently considered to be errors (internal) than true sequences (head or singleton) in the obiclean analysis[99]. We also filtered out low-quality mOTUs (putative contaminants, chimaeras, and highly degraded sequences) as follows. If an mOTU had its maximal average RRA in negative controls, then it was considered a potential contaminant and removed from all samples. Likewise, mOTUs that displayed low similarity (<80% identity) with their closest match were considered likely to be chimaeras and/or highly degraded sequences and were excluded.

To assess the reproducibility of results from 2015, 2016, 2017, and 2018, we employed a graph-partitioning approach (using the igraph package[104] in R) to identify outlying PCR replicates—that is, replicates that were substantially different from other replicates of the same DNA extract[105]. To do this, we first calculated the Bray–Curtis dissimilarity between each pair of PCR products on the basis of their sequence composition and then clustered together those with Bray–Curtis dissimilarities <0.3 for 2015, 2016, and 2017 and <0.2 for 2018 (empirical values determined from the distribution of pairwise Bray–Curtis dissimilarities between replicates and between samples). In the resulting graph, PCR replicates that did not cluster with other replicates of the same DNA extracts were considered to be outliers. Similarly, replicates that clustered with control samples were considered to be contaminated PCR products. This last filtering step was not applied for the 2018 data because the sequence data from the early dry season samples were of comparatively low quality, with a large number of tag-jumps[106,107] between samples and controls causing an artificially high number of PCR products to be clustered with controls. Omitting this filtering step allowed us to retain more samples for analysis and did not qualitatively alter the results (which we compared using both approaches). PCR products with a low number of reads (based on the distribution of the numbers of reads in samples versus controls) were also removed at this stage. Next, the number of reads was averaged among the remaining technical replicates of each sample. In an effort to reduce the impact of low-abundance false positives that can arise from tag-jumps during Illumina sequencing, we removed sequences representing <1% of RRA within samples. Finally, the mOTUs-by-samples matrices were rarefied to 3,000 reads per sample and used to calculate RRA, as described above. Analyses based on frequency of occurrence (Fig. 3b) counted plant mOTUs as present in a sample if they accounted for at least 1% of RRA[59].

M. pigra had a unique P6 barcode in our local plant reference database. To evaluate the likelihood that primer biases might have resulted in an overrepresentation of *M. pigra* sequences in our dataset, we conducted an analysis of potential primer biases among the ten most abundant plant taxa in the Gorongosa floodplain (based on our surveys of the 18 long-term monitoring plots). This analysis revealed that the binding site of the reverse P6 primer in *M. pigra* contained one mismatch with the primer sequence, located on the 5′ end (third position, 20 bases from the 3′ end). We observed the same pattern for two other taxa, Cyperaceae spp. (also third position) and *Ambrosia* sp. (fifth position). The other eight most common taxa exhibited no mismatch on any primer. Thus, we found no evidence for a positive amplification bias towards *M. pigra*.

Relative forage quality. To assess the forage quality of mimosa relative to other abundant floodplain plants, we measured crude-protein content for mimosa, along with the two most abundant grass species (*C. dactylon* and *D. swazilandensis*), the most abundant forb species (*H. ovalifolium*), and another leguminous woody plant species (*A. xanthophloea*) that occurs occasionally in the floodplain[38] and abundantly at the boundary between the floodplain and the adjoining savanna. We collected >5 g of the youngest fully opened leaves, pooling foliage from ≥3 individuals for analysis. Samples were dried to constant weight at 60 °C and sent to Dairy One Cooperative, Inc., where nitrogen concentrations were determined via combustion (AOAC method 990.03). Crude protein was estimated as 6.25 × N.

Responses of mimosa to experimental large-herbivore exclusion (p_3). To test p_3, that experimental LMH exclusion releases mimosa from top-down control, we constructed six hexagonal fenced large-herbivore-exclusion plots (260 m^2) in September 2015. Each exclosure was adjacent to one of the 1-ha long-term monitoring plots (Fig. 1b), and paired unfenced control plots of equal size were delineated within the monitoring plots. The exclosures were initially constructed using 3 m metal posts and square-mesh wire fencing. During the first year of the experiment, there was a 40 cm gap beneath the fence; in September 2016, new fences were erected outside the originals (which had warped during the flood) using steel-frame panels with an iron grid that eliminated the gap (Fig. 1f). Ungulates >20 kg were excluded throughout the 3-year experiment, aside from rare temporary incursions, as verified by dung counts conducted during each survey along with intermittent camera trapping.

Shortly after exclosure construction (November 2015), we individually tagged all of the mimosa plants in five of the exclosure–control pairs (controls: range 5–60 individuals per plot, mean ± s.e.m. 20 ± 10; exclosures: range 0–15 individuals per plot, mean ± s.e.m. 7 ± 3). In the sixth exclosure–control pair, we tagged all individuals in one-third of each plot ($n = 66$ plants in the control, 115 in the exclosure). For each tagged plant, we measured (1) plant height; (2) canopy dimensions (the width of the longest axis and its perpendicular), which we converted into canopy area using the formula for an ellipse; and (3) reproductive output, separately counting immature floral buds, mature flowers, immature (green) fruits, and mature (brown) seed-pods. We surveyed the plots in November 2015, May 2016, August 2016, June 2017, September 2017, and August 2018. Newly established mimosa plants were tagged when they reached the 15 cm stem-length threshold corresponding to recruitment out of the seedling stage. We quantified the mortality of tagged individuals after the 2016–2017 and 2017–2018 floods (that is, from survey 3 to survey 5 and from survey 5 to survey 6, respectively). In the fifth survey (September 2017), we quantified recruitment by counting all new plants (distinguishing seedlings from recruits with ≥15 cm stem length). In the final survey, in August 2018, we counted all plants ≥15 cm stem length to determine the total density and biomass of mimosa in each plot.

The biomass of mimosa was estimated from a regression of dry mass as a function of plant dimensions. We chose 34 mimosa plants in the Gorongosa floodplain, deliberately selecting individuals that encompassed a wide range of sizes. For each of these plants, we measured height (range 3–204 cm), the widest canopy axis (range 5–370 cm), and the orthogonal short axis (range 3–265 cm). We estimated plant volume from these measurements, assuming that shrubs had an ellipsoidal shape. We then measured the aboveground biomass for each of these plants by clipping all stems at ground level, drying to constant weight at 70 °C, and weighing to the nearest milligram (range 0.062–2,454 g). Plant volume explained >96% of the variance in dry biomass (Extended Data Fig. 4), and this regression equation was used to estimate the summed aboveground biomass of living plants in each experimental plot from height and canopy measurements (Fig. 5b).

We treated experimental plots as the units of statistical analysis. Owing to variation in flooding and in the abundance of mimosa in each plot, the number of plots available for any given analysis ranged from 7 to 12 (but always included $n \geq 3$ plots of each treatment; see specific sample sizes in Figs. 4 and 5). Before the analysis, we calculated the means of all individual-level responses in each plot in each survey. We analysed the mean net change in height and canopy area per plot of plants that had been tagged in survey 1 and survived through survey 5 using one-way ANOVA as a function of experimental treatment. To assess treatment effects on recruitment between surveys 3 and 5, we analysed the total number of new plants in each plot (separately for seedlings and for recruits ≥15 cm) using one-way ANOVA on square-root-transformed count data. To assess mortality, we analysed the proportion of tagged individuals in each plot that died between surveys 3–5 and 5–6, using a binomial GLM with exclosure treatment as the predictor. The density and biomass of mimosa per plot were compared using one-way ANOVA as a function of treatment. All descriptive statistics are given as mean ± 1 s.e.m.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The field data are provided in Supplementary Data 1–8. The field data along with raw dietary sequence data and metadata from 2013, 2015, 2017, and 2018 are available via Dryad (https://doi.org/10.5061/dryad.sxksn02zc). Dietary sequence data and metadata from 2016, along with the local plant reference database, are available via Dryad (https://doi.org/10.5061/dryad.63tj806).

Received: 23 April 2019; Accepted: 20 November 2019;

References

1. Estes, J. A. et al. Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011).
2. Ripple, W. J. et al. Collapse of the world's largest herbivores. *Sci. Adv.* **1**, e1400103 (2015).
3. Malhi, Y. et al. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl Acad. Sci. USA* **113**, 838–846 (2016).
4. Dirzo, R. et al. Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
5. Smith, F. A., Elliott Smith, R. E., Lyons, S. K. & Payne, J. L. Body size downgrading of mammals over the Late Quaternary. *Science* **360**, 310–313 (2018).
6. Barnosky, A. D. Assessing the causes of late Pleistocene extinctions on the continents. *Science* **306**, 70–75 (2004).
7. Ceballos, G. et al. Accelerated modern human–induced species losses: entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253 (2015).
8. Daskin, J. H. & Pringle, R. M. Warfare and wildlife declines in Africa's protected areas. *Nature* **553**, 328–332 (2018).
9. Pringle, R. M., Palmer, T. M., Goheen, J. R., McCauley, D. J. & Keesing, F. Ecological importance of large herbivores in the Ewaso ecosystem. *Smithson. Contrib. Zool.* **632**, 43–54 (2011).
10. Johnson, B. E. & Cushman, J. H. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. *Conserv. Biol.* **21**, 515–526 (2007).
11. Cromsigt, J. P. G. M. & te Beest, M. Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. *J. Ecol.* **102**, 566–575 2014).
12. Cromsigt, J. P. G. M., Kemp, Y. J. M., Rodriguez, E. & Kivit, H. Rewilding Europe's large grazer community: how functionally diverse are the diets of European bison, cattle, and horses? *Restor. Ecol.* **26**, 891–899 (2018).
13. Zamboni, T., Di Martino, S. & Jiménez-Pérez, I. A review of a multispecies reintroduction to restore a large ecosystem: the Iberá Rewilding Program (Argentina). *Perspect. Ecol. Conserv.* **15**, 248–256 (2017).
14. Svenning, J.-C. et al. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proc. Natl Acad. Sci. USA* **113**, 898–906 (2016).
15. Bakker, E. S. & Svenning, J.-C. Trophic rewilding: impact on ecosystems under global change. *Phil. Trans. R. Soc. Lond. B* **373**, 20170432 (2018).
16. Pettorelli, N., Durant, S. M. & du Toit, J. (eds) *Rewilding* (Cambridge Univ. Press, 2019).
17. Svenning, J.-C., Munk, M. & Schweiger, A. in *Rewilding* (eds Pettorelli, N. et al.) 73–98 (Cambridge Univ. Press, 2019).
18. Sinclair, A. R. E. et al. Predicting and assessing progress in the restoration of ecosystems. *Conserv. Lett.* **11**, e12390 (2017).
19. Schweiger, A. H., Boulangeat, I., Conradi, T., Davis, M. & Svenning, J.-C. The importance of ecological memory for trophic rewilding as an ecosystem restoration approach. *Biol. Rev.* **41**, 571 (2018).
20. Torres, A. et al. Measuring rewilding progress. *Phil. Trans. R. Soc. Lond. B* **373**, 20170433 (2018).
21. Fuhlendorf, S. D., Davis, C. A., Elmore, R. D., Goodman, L. E. & Hamilton, R. G. Perspectives on grassland conservation efforts: should we rewild to the past or conserve for the future? *Phil. Trans. R. Soc. Lond. B* **373**, 20170438 (2018).
22. Stevens, N., Lehmann, C. E. R., Murphy, B. P. & Durigan, G. Savanna woody encroachment is widespread across three continents. *Glob. Change Biol.* **23**, 235–244 (2016).
23. Ratajczak, Z., Nippert, J. B. & Collins, S. L. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* **93**, 697–703 (2012).
24. Honda, E. A. & Durigan, G. Woody encroachment and its consequences on hydrological processes in the savannah. *Phil. Trans. R. Soc. Lond. B* **371**, 20150313 (2016).
25. Stevens, N., Erasmus, B. F. N., Archibald, S. & Bond, W. J. Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock? *Phil. Trans. R. Soc. Lond. B* **371**, 20150437 (2016).
26. Hempson, G. P., Archibald, S. & Bond, W. J. The consequences of replacing wildlife with livestock in Africa. *Sci. Rep.* **7**, 17196 (2017).
27. Archer, S. R. et al. in *Rangeland Systems* (ed. Briske, D. D.) 25–84 (Springer, 2017).
28. Zavaleta, E. The economic value of controlling an invasive shrub. *Ambio* **29**, 462–467 (2000).
29. Lowe, S., Browne, M., Boudjelas, S. & De Poorter M. *100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database* (Invasive Species Specialist Group of the Species Survival Commission of the World Conservation Union, 2004).
30. Ratajczak, Z., Nippert, J. B., Hartman, J. C. & Ocheltree, T. W. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. *Ecosphere* **2**, 121 (2011).
31. Olofsson, J. & Post, E. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Phil. Trans. R. Soc. Lond. B* **373**, 20170437 (2018).
32. Derham, T. T., Duncan, R. P., Johnson, C. N. & Jones, M. E. Hope and caution: rewilding to mitigate the impacts of biological invasions. *Phil. Trans. R. Soc. Lond. B* **373**, 20180127 (2018).
33. Vavra, M., Parks, C. G. & Wisdom, M. J. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *For. Ecol. Manage.* **246**, 66–72 (2007).
34. Maron, J. L. & Vilà, M. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* **95**, 361–373 (2001).

35. Stalmans, M. E., Massad, T. J., Peel, M. J. S., Tarnita, C. E. & Pringle, R. M. War-induced collapse and asymmetric recovery of large-mammal populations in Gorongosa National Park, Mozambique. *PLoS ONE* **14**, e0212864 (2019).
36. Pringle, R. M. Upgrading protected areas to conserve wild biodiversity. *Nature* **546**, 91–99 (2017).
37. Bouley, P., Poulos, M., Branco, R. & Carter, N. H. Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biol. Conserv.* **227**, 233–242 (2018).
38. Tinley, K. L. *Framework of the Gorongosa Ecosystem, Mozambique*. PhD thesis, Univ. Pretoria (1977).
39. Beilfuss, R. *Adaptive Management of the Invasive Shrub* Mimosa pigra *at Gorongosa National Park* (Gorongosa National Park Department of Scientific Services, 2007).
40. Lonsdale, W. M. in *A Guide to the Management of* Mimosa pigra (ed. Harley, K. L. S.) 8–32 (CSIRO, 1992).
41. Janzen, D. H. in *Costa Rican Natural History* (ed. Janzen, D. H.) 277–278 (Univ. Chicago Press, 1983).
42. Keane, R. M. & Crawley, M. J. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17**, 164–170 (2002).
43. Levine, J. M., Adler, P. B. & Yelenik, S. G. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* **7**, 975–989 (2004).
44. Parker, J. D., Burkepile, D. E. & Hay, M. E. Opposing effects of native and exotic herbivores on plant invasions. *Science* **311**, 1459–1461 (2006).
45. Cerling, T. E., Harris, J. M. & Passey, B. H. Diets of East African Bovidae based on stable isotope analysis. *J. Mammal.* **84**, 456–470 (2003).
46. Daskin, J. H., Stalmans, M. & Pringle, R. M. Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *J. Ecol.* **104**, 79–89 (2016).
47. Attard, E., Chopping, C., Austin, P., Williams, J. & Pople, T. *Minimising the Risk of Spread of* Mimosa pigra *from Peter Faust Dam, Proserpine* (State of Queensland Department of Natural Resources and Water, 2006).
48. Lonsdale, W. M., Harley, K. & Gillett, J. D. Seed bank dynamics in *Mimosa pigra*, an invasive tropical shrub. *J. Appl. Ecol.* **25**, 963–976 (1988).
49. Braithwaite, R. W., Lonsdale, W. M. & Estbergs, J. A. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biol. Conserv.* **48**, 189–210 (1989).
50. Cook, G. D., Setterfield, S. A. & Maddison, J. P. Shrub invasion of a tropical wetland: implications for weed management. *Ecol. Appl.* **6**, 531–537 (1996).
51. Perino, A. et al. Rewilding complex ecosystems. *Science* **364**, eaav5570 (2019).
52. Dublin, H. T., Sinclair, A. & McGlade, J. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J. Anim. Ecol.* **59**, 1147–1164 (1990).
53. Hirota, M., Holmgren, M., van Nes, E. H. & Scheffer, M. Global resilience of tropical forest and savanna to critical transitions. *Science* **334**, 232–235 (2011).
54. Staver, A. C., Archibald, S. & Levin, S. A. The global extent and determinants of savanna and forest as alternative biome states. *Science* **334**, 230–232 (2011).
55. Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A. S. High-resolution mapping of global surface water and its long-term changes. *Nature* **540**, 418–422 (2016).
56. Mumba, M. & Thompson, J. R. Hydrological and ecological impacts of dams on the Kafue Flats floodplain system, southern Zambia. *Phys. Chem. Earth* **30**, 442–447 (2005).
57. Codron, D. et al. Diets of savanna ungulates from stable carbon isotope composition of faeces. *J. Zool.* **273**, 21–29 (2007).
58. Pansu, J. et al. Trophic ecology of large herbivores in a reassembling African ecosystem. *J. Ecol.* **107**, 1355–1376 (2019).
59. Deagle, B. E. et al. Counting with DNA in metabarcoding studies: how should we convert sequence reads to dietary data? *Mol. Ecol.* **28**, 391–406 (2019).
60. Craine, J. M., Towne, E. G., Miller, M. & Fierer, N. Climatic warming and the future of bison as grazers. *Sci. Rep.* **5**, 16738 (2015).
61. Willerslev, E. et al. Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* **506**, 47–51 (2014).
62. Kartzinel, T. R. et al. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proc. Natl Acad. Sci. USA* **112**, 8019–8024 (2015).
63. Lonsdale, W. M. Rates of spread of an invading species—*Mimosa pigra* in northern Australia. *J. Ecol.* **81**, 513–521 (1993).
64. Freeland, W. J. & Janzen, D. H. Strategies in herbivory by mammals: the role of plant secondary compounds. *Am. Nat.* **108**, 269–289 (1974).
65. Dearing, M. D., Foley, W. J. & McLean, S. The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **36**, 169–189 (2005).
66. Thaiyah, A. G. et al. Acute, sub-chronic and chronic toxicity of *Solanum incanum* L in sheep in Kenya. *Kenya Vet.* **35**, 1–8 (2011).
67. Pringle, R. M. et al. Low functional redundancy among mammalian browsers in regulating an encroaching shrub (*Solanum campylacanthum*) in African savannah. *Proc. R. Soc. B* **281**, 20140390 (2014).
68. Seastedt, T. R., Hobbs, R. J. & Suding, K. N. Management of novel ecosystems: are novel approaches required? *Front. Ecol. Environ.* **6**, 547–553 (2008).
69. Bakker, E. S. et al. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proc. Natl Acad. Sci. USA* **113**, 847–855 (2016).
70. Branco, P. S. et al. Determinants of elephant foraging behavior in a coupled human-natural system: is brown the new green? *J. Anim. Ecol.* **88**, 780–792 (2019).
71. Goheen, J. R. et al. Piecewise disassembly of a large-herbivore community across a rainfall gradient: the UHURU experiment. *PLoS ONE* **8**, e55192 (2013).
72. Pringle, R. M., Prior, K. M., Palmer, T. M., Young, T. P. & Goheen, J. R. Large herbivores promote habitat specialization and beta diversity of African savanna trees. *Ecology* **97**, 2640–2657 (2016).
73. Coverdale, T. C. et al. Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecology* **97**, 3219–3230 (2016).
74. Goheen, J. R. et al. Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU, and GLADE experiments. *Ann. N.Y. Acad. Sci.* **1429**, 31–49 (2018).
75. Carter, N. H. et al. Climate change, disease range shifts, and the future of the Africa lion. *Conserv. Biol.* **32**, 1207–1210 (2018).
76. Sinclair, A. R. E., Mduma, S. & Brashares, J. S. Patterns of predation in a diverse predator-prey system. *Nature* **425**, 288–290 (2003).
77. Atkins, J. L. et al. Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* **364**, 173–177 (2019).
78. Miller, I. L. & Lonsdale, W. M. Early records of *Mimosa pigra* in the Northern Territory. *Plant Prot. Q.* **2**, 140–142 (1987).
79. Zedler, J. B. & Kercher, S. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Crit. Rev. Plant Sci.* **23**, 431–452 (2004).
80. Seburanga, J. L., Kaplin, B. A., Bizuru, E. & Mwavu, E. N. The folk biology of South American–native shrub, *Mimosa pigra* L. [Leguminosae] and its invasive success in Rwanda. *Int. J. Biodiv. Conserv.* **5**, 486–497 (2013).
81. CABI *Mimosa pigra* (giant sensitive plant) [original text by Rojas-Sandoval, J. & Acevedo-Rodríguez, P.] in *Invasive Species Compendium* (CAB International, 2019); https://www.cabi.org/isc
82. Shanungu, G. K. Management of the invasive *Mimosa pigra* L. in Lochinvar National Park, Zambia. *Biodiversity* **10**, 56–60 (2009).
83. Rijal, S. & Cochard, R. Invasion of *Mimosa pigra* on the cultivated Mekong River floodplains near Kratie, Cambodia: farmers' coping strategies, perceptions, and outlooks. *Reg. Environ. Change* **16**, 681–693 (2015).
84. Paynter, Q. Evaluating the impact of biological control against *Mimosa pigra* in Australia: comparing litterfall before and after the introduction of biological control agents. *Biol. Control* **38**, 166–173 (2006).
85. Paynter, Q. & Flanagan, G. J. Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, *Mimosa pigra*. *J. Appl. Ecol.* **41**, 615–629 (2004).
86. Ostermeyer, N. & Grace, B. S. Establishment, distribution and abundance of *Mimosa pigra* biological control agents in northern Australia: implications for biological control. *BioControl* **52**, 703–720 (2007).
87. Lonsdale, W. M. & Miller, I. L. Fire as a management tool for a tropical woody weed: *Mimosa pigra* in northern Australia. *J. Environ. Manage.* **39**, 77–87 (1993).
88. Adams, V. M., Setterfield, S. A., Douglas, M. M., Kennard, M. J. & Ferdinands, K. Measuring benefits of protected area management: trends across realms and research gaps for freshwater systems. *Phil. Trans. R. Soc. Lond. B* **370**, 20140274 (2015).
89. Heard, T. A. & Paynter, Q. in *Biological Control of Tropical Weeds Using Arthropods* (eds Muniappan, R. et al.) 256–273 (Cambridge Univ. Press, 2009).
90. Cook, D. C., Sheppard, A., Liu, S. & Lonsdale, W. M. in *Pest Risk Modelling and Mapping for Invasive Alien Species* (ed. Venette, R. C.) 145–161 (CABI, 2015).
91. Böhme, B., Steinbruch, F., Gloaguen, R., Heilmeier, H. & Merkel, B. Geomorphology, hydrology, and ecology of Lake Urema, central Mozambique, with focus on lake extent changes. *Phys. Chem. Earth* **31**, 745–752 (2006).
92. Steinbruch, F. & Weise, S. M. Analysis of water stable isotopes fingerprinting to inform conservation management: Lake Urema wetland system, Mozambique. *Phys. Chem. Earth* **72-75**, 13–23 (2014).
93. Stalmans, M. & Beilfuss, R. *Landscapes of the Gorongosa National Park* (Gorongosa National Park Department of Scientific Services, 2008).
94. Convery, I. & Morley, R. in *Displaced Heritage: Responses to Disaster, Trauma, and Loss* (eds Convery, I. et al.) 129–142 (Boydell, 2014).

95. Taberlet, P. et al. Power and limitations of the chloroplast *trn*L (UAA) intron for plant DNA barcoding. *Nucl. Acids Res.* **35**, e14 (2007).
96. Valentini, A. et al. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the *trn*L approach. *Mol. Ecol. Res.* **9**, 51–60 (2009).
97. Pansu, J. et al. Reconstructing long-term human impacts on plant communities: an ecological approach based on lake sediment DNA. *Mol. Ecol.* **24**, 1485–1498 (2015).
98. Taberlet, P., Bonin, A., Zinger, L. & Coissac, E. *Environmental DNA for Biodiversity Research and Monitoring* (Oxford Univ. Press, 2018).
99. Boyer, F. et al. obitools: a Unix-inspired software package for DNA metabarcoding. *Mol. Ecol. Res.* **16**, 176–182 (2016).
100. Binladen, J. et al. The use of coded PCR primers enables high-throughput sequencing of multiple homolog amplification products by 454 parallel sequencing. *PLoS ONE* **2**, e197 (2007).
101. Ficetola, G. F. et al. Replication levels, false presences and the estimation of the presence/absence from eDNA metabarcoding data. *Mol. Ecol. Res.* **15**, 543–556 (2014).
102. Ficetola, G. F. et al. An in silico approach for the evaluation of DNA barcodes. *BMC Genomics* **11**, 434 (2010).
103. R Development Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2016).
104. Csárdi, G. & Nepusz, T. The igraph software package for complex network research. *InterJournal Complex Systems*, 1695 (2006).
105. Zinger, L. et al. Extracellular DNA extraction is a fast, cheap and reliable alternative for multi-taxa surveys based on soil DNA. *Soil Biol. Biochem.* **96**, 16–19 (2016).
106. Carlsen, T. et al. Don't make a mista(g)ke: is tag switching an overlooked source of error in amplicon pyrosequencing studies? *Fungal Ecol.* **5**, 747–749 (2012).
107. Schnell, I. B., Bohmann, K. & Gilbert, M. T. P. Tag jumps illuminated—reducing sequence-to-sample misidentifications in metabarcoding studies. *Mol. Ecol. Res.* **15**, 1289–1303 (2015).

Acknowledgements

We thank Parque Nacional da Gorongosa and the government of Mozambique for permission to conduct this research. We thank the Gorongosa Project for facilitating scientific research, with special thanks to M. Marchington, F. Moniz, A. Dos Santos, T. Massad, and G. Carr. The Gorongosa Project had no role in the conceptualization, design, data collection, data analysis, manuscript preparation, or decision to publish. We are indebted to K. Tinley for his pioneering research[38] on Gorongosa's pre-war ecology. Supplementary Video 1 was produced in collaboration with National Geographic Labs Crittercam. Funding was provided by National Geographic Young Explorers Grant no. 9459-14; the US National Science Foundation (grant no. IOS-1656527 and the Graduate Research Fellowship Program); the Princeton Environmental Institute's Grand Challenges programme; the Randall and Mary Hack '69 Award for Water and the Environment; Princeton University's Institutes for African Studies and International and Regional Studies; the Greg Carr Foundation; the Cameron Schrier Foundation; the Sherwood Foundation; and Princeton's Innovation Fund for New Ideas in the Natural Sciences.

Author contributions

J.A.G. and R.M.P. conceived and designed the research. J.A.G. conducted the primary plant surveys and the exclosure experiment, and collected specimens for the plant reference database. J.P., M.C.H., and T.R.K. conducted the DNA metabarcoding analyses. J.P. analysed the dietary data. A.B.P. contributed the forage-quality data. M.J.S.P. contributed additional plant-survey data. M.E.S. contributed the wildlife-count data. J.A.G., J.P., M.C.H., T.R.K., T.C.C., J.H.D., A.G.C., and R.M.P. collected samples and field data. J.A.G. and R.M.P. analysed the field data. J.A.G., J.P., and R.M.P. wrote the manuscript. All authors made revisions and approved the final draft.

Competing interests

A.G.C. and M.E.S. were employed by the Gorongosa Project, a non-profit organization that co-manages conservation and restoration in Gorongosa National Park in partnership with the government of Mozambique. M.J.S.P. was contracted by the Gorongosa Project to conduct vegetation surveys. R.M.P. was an unpaid member on the board of directors of the Gorongosa Project. All other authors have no competing interests.

Additional information

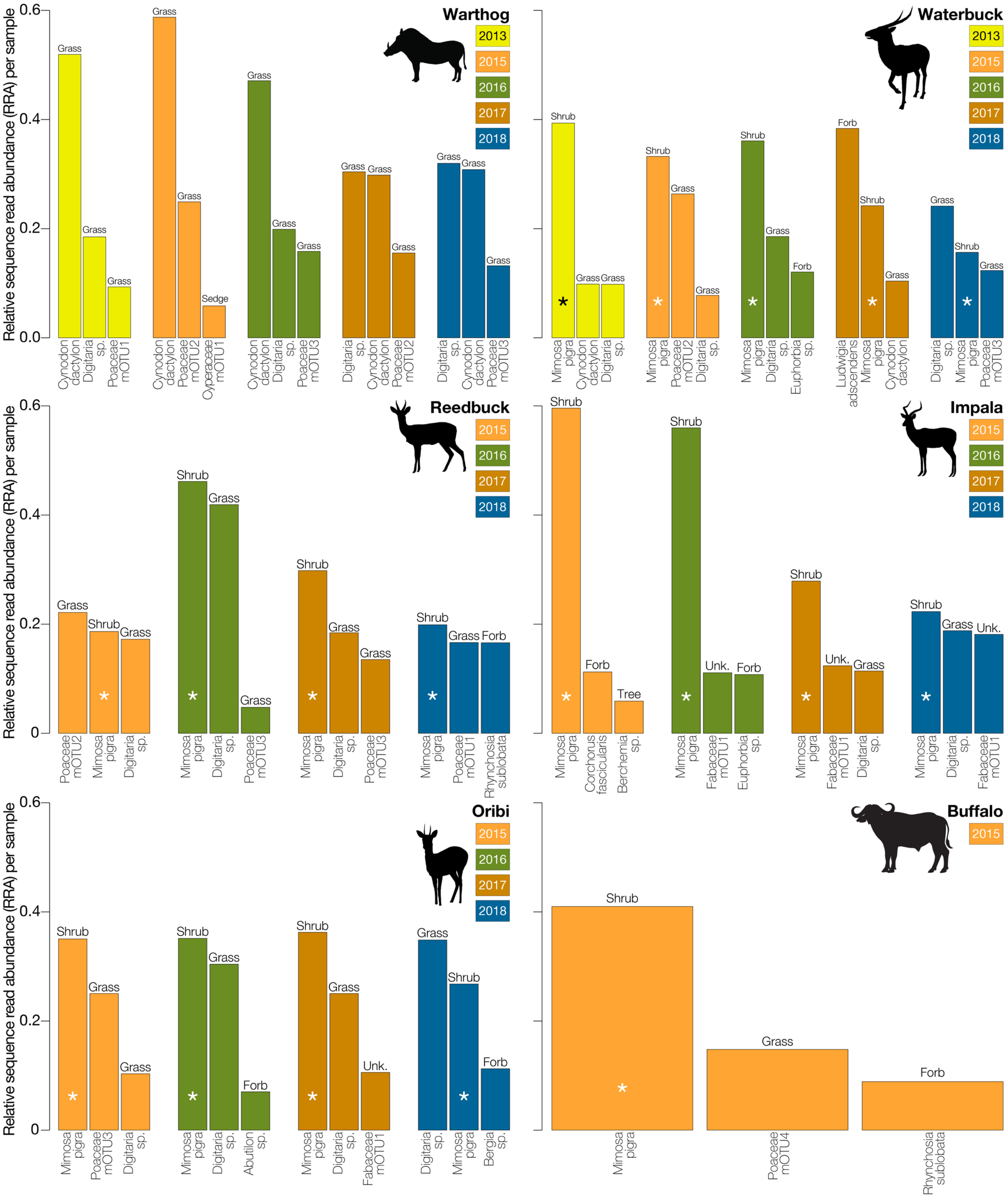
Extended data is available for this paper at https://doi.org/10.1038/s41559-019-1068-y.

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-1068-y.

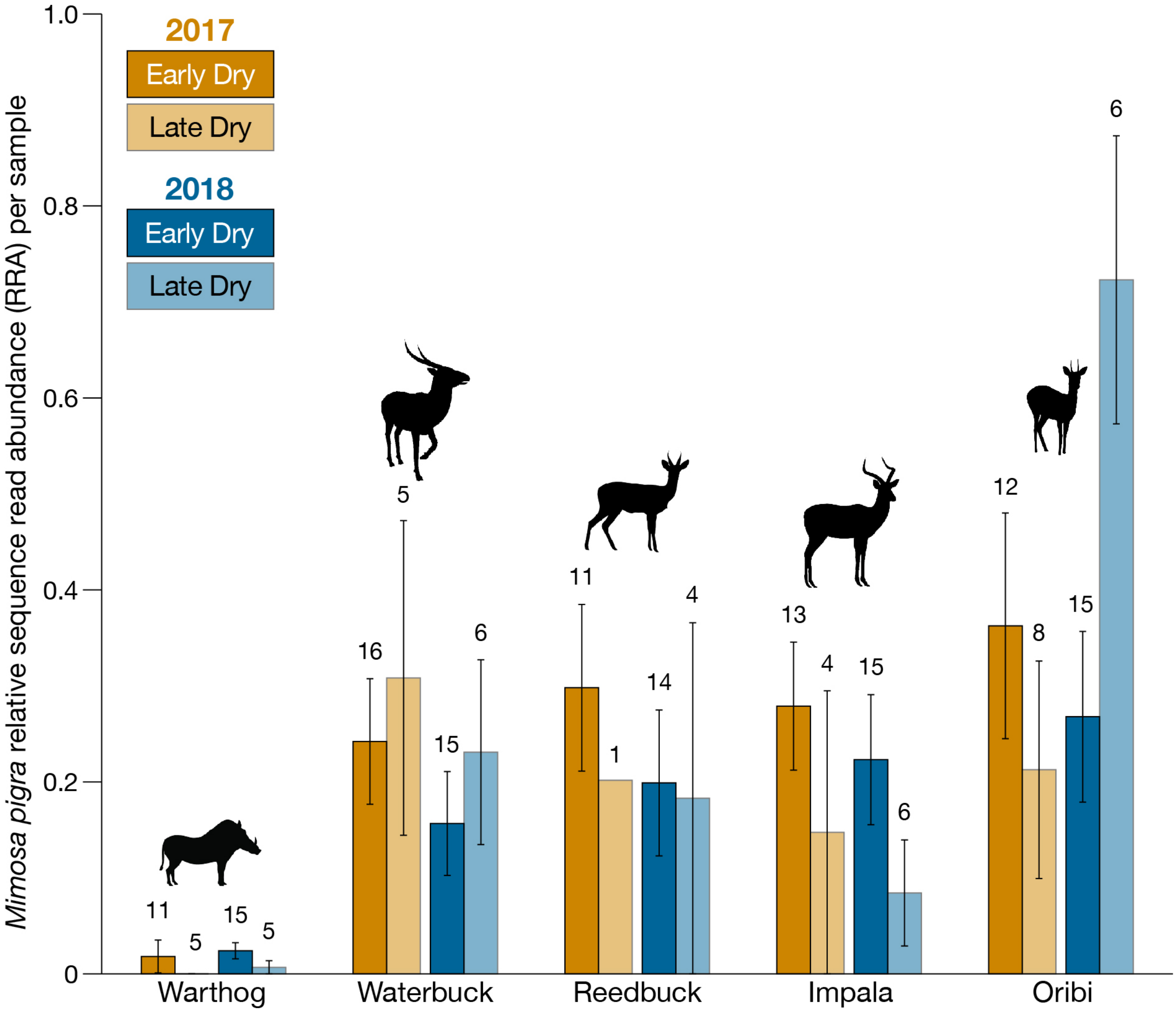
Correspondence and requests for materials should be addressed to R.M.P.

Reprints and permissions information is available at www.nature.com/reprints.

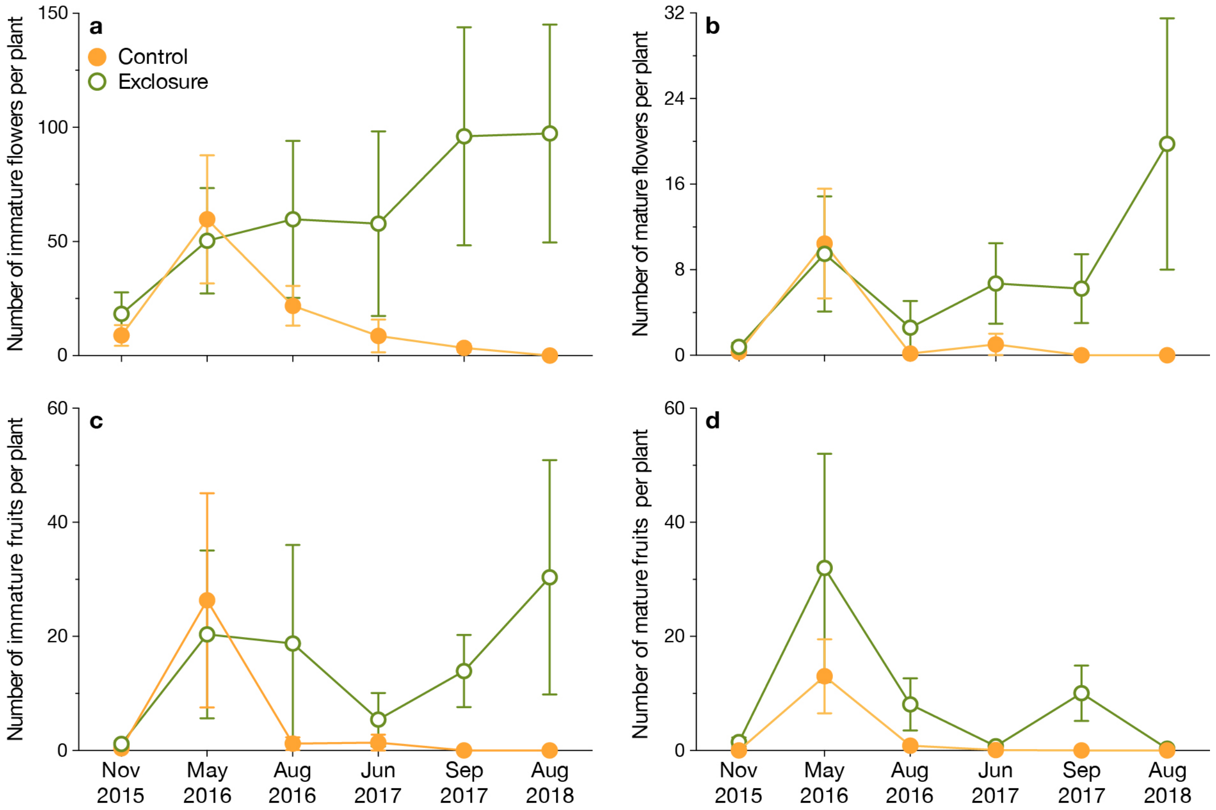
Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



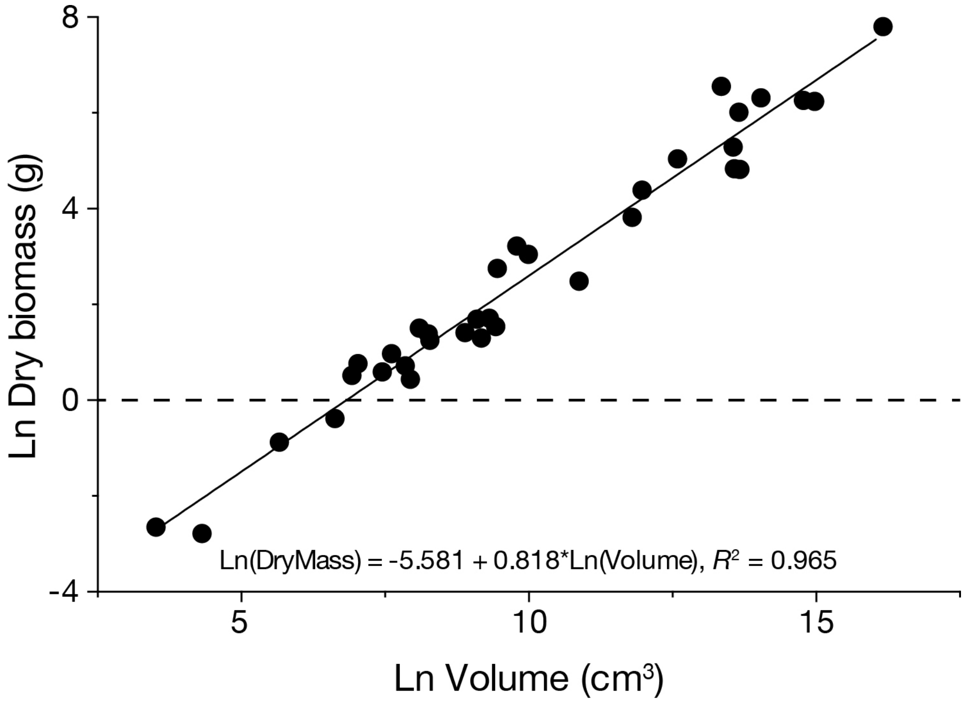
Extended Data Fig. 1 | Top food plants for six dominant ungulates in the Urema floodplain between 2013 and 2018. Bars show the mean relative read abundance of each plant taxon across all fecal samples in each year for each species. Sample sizes for each species in each year are shown in Fig. 3a. The best possible taxonomic identification for each plant (see Methods) is provided beneath each bar, and the corresponding plant life-form (grass, shrub, tree, or forb) is listed above each bar. Stars within bars denote *Mimosa pigra* (the first or second most abundant food for all ruminant species in all years).



Extended Data Fig. 2 | Mimosa consumption in early (June–August) versus late (October–November) dry season of 2017 (below-average rainfall year) and 2018 (above-average rainfall year). Bars show the mean (±1 s.e.m.) relative read abundance of *Mimosa pigra* across all fecal samples in each season for each species. Sample sizes for each species in each season are shown above bars. As for Fig. 3, quantitative comparisons between years (and between seasons for 2018) should be interpreted cautiously (see Methods). Although sample sizes are limited for some species in some seasons, the data show that antelope species consumed mimosa in appreciable quantities throughout the dry season.



Extended Data Fig. 3 | Suppression of *Mimosa pigra* reproduction by large herbivores. Here, the results in Fig. 4c, d are broken down to show independent trends in immature floral buds (**a**) and mature flowers (**b**), along with immature green fruits (**c**) and mature brown seed pods (**d**) in the experimental exclosure and control plots. Points show the mean (±1 s.e.m.) number of reproductive structures per plant in each treatment over three years. As in Fig. 4a–d, measurements at the level of individual plants were averaged at the plot level before the analysis (from left to right in each panel, $n = 12, 6, 12, 9, 10$, and 9 plots per survey). These data show that large herbivores have essentially eliminated reproductive output by mimosa in Gorongosa: few reproductive structures at any stage of development were recorded in the control plots as of 2017, and none at all were found in 2018.



Extended Data Fig. 4 | Estimation of aboveground dry biomass from field measurements of plant volume. Plant volume was calculated using measurements of height and canopy dimensions for each of 34 *Mimosa pigra* individuals, assuming an ellipsoidal shrub shape, and regressed against the dry aboveground biomass measured for each of the same plants (see Methods). The regression equation shown was used to estimate the aboveground biomass of standing plants in each experimental exclosure and control plot in 2018 (see Fig. 5b).

Extended Data Fig. 5 | Rapid recruitment and growth of *Mimosa pigra* inside, but not outside, experimental herbivore exclosures. All photos are from the same exclosure-control pair (in long-term monitoring plot 16). **a**, Panoramic photograph of the control plot in 2018, showing floodplain dominated by grasses (mostly *Cynodon dactylon*) and forbs (mostly *Heliotropium* spp.); a total of 13 mimosa plants were recorded in this 260-m^2 plot in 2018, none taller than 43 cm. The exclosure plot is visible at top center. **b**, Forb-dominated understory in the exclosure plot in September 2017, when a total of 57 small mimosa plants were recorded, none taller than 31 cm (up from just one individual recorded in September 2016). **c**–**e**, Three views of the same exclosure plot in August 2018, when 661 mimosa plants of at least 15-cm stem length were recorded, including individuals up to 158-cm tall.

nature research

Corresponding author(s): Robert Mitchell Pringle

Last updated by author(s): Oct 26, 2019

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software or computer code was used in data collection.
Data analysis	Observational and experimental field data were analyzed using the commercial statistical software package JMP Pro versions 13.0 and 14.0. DNA- metabarcoding data were analyzed in R version 3.5.3 using the open-source software packages obitools (Boyer et al. 2016) and igraph (Csárdi & Nepusz 2006). Graphs were made in Prism version 6.0h.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The field data that support the findings of this study are available in Supplementary Data 1–8. Dietary sequence data and metadata from 2016, along with the local plant reference database, had previously been deposited in Dryad (doi:10.5061/dryad.63tj806). Dietary sequence data and metadata from 2013, 2015, 2017, and 2018 are also deposited in Dryad (doi pending).

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The study comprises three major components. (1) Long-term observational monitoring of Mimosa pigra plants in 18 one-hectare monitoring plots and four 200-m2 plots, and of large mammalian herbivores throughout the Urema floodplain of Gorongosa National Park. (2) DNA metabarcoding analysis of 469 large-herbivore fecal samples collected within the Urema floodplain. (3) An experiment comprising 6 fenced large-herbivore exclosures and 6 paired unfenced control plots to which large herbivores had unfettered access (n = 12 plots total).
Research sample	The primary research sample comprises a population of the invasive shrub Mimosa pigra within the 780-km2 Urema floodplain landscape in Gorongosa National Park. This population was analyzed using observational and experimental methods. Mimosa pigra was the focal species because it is a noxious pan-tropical invasive shrub, and the only non-native invasive woody plant species known from within the core of Gorongosa National Park. A secondary research sample comprised fecal samples from the six most abundant large mammalian herbivore species within the Urema floodplain. This sample of species was selected because it collectively represents the overwhelming majority of large-herbivore biomass in this ecosystem (>80%) and includes both the single most-abundant pre-war species (buffalo) and the single most-abundant post-war species (waterbuck). A tertiary research sample comprised measurements of foliar crude-protein content for a total of six plant species. These six species were selected because they include the most abundant species of each major plant life-form (grasses, forbs, and woody plants) within the Urema floodplain.
Sampling strategy	No statistical methods were used to predetermine sample sizes. The sample of 18 one-hectare monitoring plots (Fig. 2b) was pre-determined because this was the sample for which pre-war data from 1972 were available. These plots were surveyed (by recording Mimosa pigra presence/absence in between 10 and 30 randomly placed 1-m2 quadrats per plot) several times per year from 2015 to 2017, and data were averaged for each plot within each year (i) to account for our inability to access some plots in certain surveys because they were flooded and (ii) to minimize the effects of any sampling artifacts within any given survey (for example, variation arising from random placement of quadrats within each plot in each survey. The sample of Mimosa pigra densities in four 200-m2 plots from 2011-2019 (Fig. 2d) is part of an independent network of vegetation monitoring plots maintained by Gorongosa National Park; we analyzed data from four plots that were located in the floodplain close to the other 18 monitoring plots and contained Mimosa pigra. The sample of 469 large-herbivore fecal samples (representing between 27 and 189 samples per species, and between 1 and 80 samples per species per sampling bout; Fig. 3 and Extended Data 1, 2) was collected opportunistically and represented the maximum possible sample size per species per season given logistical and time constraints. The sample of 12 experimental plots (6 exclosures and 6 controls; Figs. 4, 5 and Extended Data 3) was the maximum number that we were able to construct given logistical, time, and financial constraints; prior work by the senior author using large-herbivore exclosures in African ecosystems led us to believe that six replicates of each treatment would provide adequate statistical power to detect any biologically meaningful effects.
Data collection	Data on Mimosa pigra plants from the 18 one-hectare monitoring plots and the 12 exclosure/control plots were recorded by J.A.G., with the assistance of A.G.C., except for data from 1972, which were recorded by K.L. Tinley and published in his PhD Thesis (Tinley 1977, University of Pretoria). Data on mimosa densities in the four 200-m2 monitoring plots were recorded by M.J.S.P. Data from pre-war aerial wildlife counts were recorded by K.L. Tinley and derived from his 1977 PhD thesis; data from post-war aerial wildlife counts were recorded by M.E.S. and M.J.S.P.; M.E.S. curated and analyzed the data from both pre- and post-war intervals. DNA metabarcoding data were generated by J.P., M.C.H., and T.R.K. and were curated and analyzed by J.P. Data on Mimosa pigra dry biomass were generated and recorded by M.C.H. Data on plant crude- protein contents were generated by A.B.P. based on samples submitted to a commercial laboratory facility.
Timing and spatial scale	Pre-war data were recorded by K.L. Tinley (PhD Thesis, 1977, University of Pretoria) from 1969-1972. Post-war data were collected from 2011 to 2019. Rainfall data were collected from 1957-1969 and 1999-2019. Observational surveys of the 18 one-hectare long-term monitoring plots were conducted each year from 2015 to 2017, to monitor inter-annual variation; moreover, these surveys were replicated at least twice (and maximally four times) within each year to ensure that we collected data from both the early dry season (i.e., immediately post-flood) and late dry season in each year. Although we did not select the spatial scale of these 18 one-hectare plots, which were established by Tinley in 1972, we believe that this spatial scale (including a gradient of distance away from Lake Urema; see Fig. 1b) is adequate for inferring landscape-wide dynamics. Samples for DNA metabarcoding were collected during the early-to-mid dry season in each of five years (2013, 2015-2018) and the late dry season in each of two years (2017, 2018) to ensure that our results were reproducible across years of the study and to test for any pronounced intra-annual variation. The herbivore-exclusion experiment was maintained and surveyed at least once (and sometimes twice) in each year from 2015 to 2018 to monitor temporal dynamics. The spatial scale of the experimental plots (260 m2) was chosen semi-arbitrarily to be (i) large enough to have a high likelihood of containing a reasonable sample size of Mimosa pigra plants in each plot and (ii) small enough for investigators to sample comprehensively in a feasible amount of time.
Data exclusions	We collected survey data from the 18 one-hectare monitoring plots in 2013, but we did not plot these data graphically or include them in statistical analyses because we later learned that we had conflated Mimosa pigra with a similar looking and closely related plant (Neptunia oleracea), meaning that we could not rigorously calculate the true frequency-of-occurrence for Mimosa pigra in that survey. We do allude to these 2013 data in the manuscript and in Fig. 2b; formally including these data would merely strengthen our conclusions. Illumina sequence data from DNA-metabarcoding analyses were discarded when standard quality- control filtering

	procedures suggested that the data were of poor quality or represented potential contamination (as described in detail in the Methods). These are standard bioinformatics procedures for DNA-metabarcoding data. No other data were excluded from analysis. In individual surveys of long-term monitoring and experimental plots, it was not always possible to access all plots, meaning that no data were obtained for particular plots in particular surveys.
Reproducibility	The large-herbivore experiment was not replicated in time. It was however maintained and monitored repeatedly through time over three years, and the temporal trends in the data are consistent with high data fidelity.
Randomization	The locations of the 18 one-hectare monitoring plots were established by Tinley (1977) at regular distances along three transects extending outwards from Lake Urema. The locations of these plots were therefore not randomized, but were spatially representative. In surveying these plots from 2015-2017, we fully randomized the position of each sampling quadrat, by selecting random numbers of steps and random compass orientations from the center of the plot. The four 200-m2 monitoring plots are part of a larger network of plots, the locations of which were chosen nonrandomly to encompass the range of vegetation types in Gorongosa National Park. Each of these plots was sampled comprehensively to determine the density of Mimosa pigra. To maximize consistency with data from the 18 long-term monitoring plots, we situated experimental plots adjacent to each of six of the 18 long-term monitoring plots; these six were chosen haphazardly from the 18 available and represented a gradient of distance from Lake Urema (Fig. 1b), to ensure representative coverage of vegetation zones (areas farther from the lake have more continuous grass cover, whereas areas closer to the lake have more bare ground and comparatively greater forb cover). The specific locations of the 260-m2 experimental plots were selected haphazardly and without reference to the focal species, Mimosa pigra; the control plots were situated within the long-term monitoring plot at each location, and the exclosures were situated between 100 and 300 m from the plot edge. The only constraint in selecting plot locations was to avoid areas adjacent to drainage channels and associated mudflats. In monitoring specific Mimosa pigra individuals within experimental plots, we made an effort to be comprehensive, tagging and monitoring all individuals rather than selecting a subset (with one exception described in the Methods, in which we tagged all individuals within one-third of one pair of exclosure and control plots owing to exceptionally high density of Mimosa pigra in that location).
Blinding	Blinding was not possible in the context of our study, because investigators are inevitably aware of the context in which they are working (for example, within fenced experimental exclosures or unfenced control plots).

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Field work was conducted throughout the dry seasons of 2013 and 2015 to 2019. Field work is not possible in this site during the wet season, when the study area is flooded (see Fig. 1e). Mean annual rainfall from 2012 to 2018 was 937 mm ± 154 s.e., which is comparable to the previously published historical estimate from this site of 840 mm per year (Tinley 1977).
Location	All data were collected from the 780-m2 Lake Urema floodplain in Gorongosa National Park Mozambique. The observational and experimental vegetation monitoring plots were located in the southern part of this floodplain landscape (Northern bound: -18.8703 34.4346; Southern bound -18.9012 34.4382; Western bound -18.8837 34.4146; Eastern bound -18.8884 34.4588).
Access and import/export	Research was conducted under permits granted by the Department of Scientific Services of Gorongosa National Park. Fecal samples were imported into the United States under permits from the United States Department of Agriculture, Animal and Plant Health Inspection Service (permit numbers 122389, 123156, 130123)
Disturbance	The only disturbance to the site involved the addition of metal tags to Mimosa pigra plants and the construction of six fenced exclosure plots.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology
☒	☐	Animals and other organisms
☒	☐	Human research participants
☒	☐	Clinical data

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging