COMMUNITY ECOLOGY – ORIGINAL RESEARCH

# Diverse effects of the common hippopotamus on plant communities and soil chemistry

Douglas J. McCauley[1] · Stuart I. Graham[2] · Todd E. Dawson[3,4] · Mary E. Power[4] · Mordecai Ogada[5] · Wanja D. Nyingi[6] · John M. Githaiga[7] · Judith Nyunja[8] · Lacey F. Hughey[1] · Justin S. Brashares[3]

## Abstract

The ecological importance of the common hippopotamus (*Hippopotamus amphibius*) in aquatic ecosystems is becoming increasingly well known. These unique megaherbivores are also likely to have a formative influence on the terrestrial ecosystems in which they forage. In this study, we employed a novel exclosure design to exclude *H. amphibius* from experimental plots on near-river grasslands. Our three-year implementation of this experiment revealed a substantial influence of *H. amphibius* removal on both plant communities and soil chemistry. *H. amphibius* significantly reduced grassland canopy height, increased the leafiness of common grasses, reduced woody plant abundance and size, and increased the concentrations of several soil elements. Many of the soil chemistry changes that we experimentally induced by exclusion of *H. amphibius* were mirrored in the soil chemistry differences between naturally occurring habitats of frequent (grazing lawns) and infrequent (shrub forest) use by *H. amphibius* and other grazing herbivores. In contrast to existing hypotheses regarding grazing species, we found that *H. amphibius* had little effect on local plant species richness. Simultaneous observations of exclosures designed to remove all large herbivores revealed that *H. amphibius* removal had ecologically significant impacts, but that the removal of all species of large herbivores generated more pronounced impacts than the removal of *H. amphibius* alone. In aggregate, our results suggest that *H. amphibius* have myriad effects on their terrestrial habitats that likely improve the quality of forage available for other herbivores. We suggest that ongoing losses of this vulnerable megaherbivore are likely to cause significant ecological change.

Communicated by Joanna E. Lambert.

Douglas J. McCauley and Stuart I. Graham contributed equally.

✉ Douglas J. McCauley
 douglas.mccauley@ucsb.edu

[1] Department of Ecology, Evolution and Marine Biology and the Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

[2] Department of Biology, University of Washington, Seattle, WA 98195, USA

[3] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA

[4] Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

[5] Conservation Solutions Afrika, P.O. Box 880, Nanyuki 10400, Kenya

[6] National Museums of Kenya, Ichthyology Section, P.O. Box 40658-00100, Nairobi, Kenya

[7] School of Biological Sciences, University of Nairobi, P.O. Box 30197, Nairobi, Kenya

[8] Kenya Wildlife Service, Wetlands Program, P.O. Box 40241-00100, Nairobi, Kenya

## Introduction

Prior to the late-Quaternary extinctions, megaherbivores (defined here as herbivores of mass > 1000 kg; Owen-Smith 1988) were present in most terrestrial ecosystems (Barnosky et al. 2004). Their extirpation from many systems is thought to have significantly altered the way ecosystems function

(Barnosky et al. 2016; Smith et al. 2016a; McCauley et al. 2016), with affected processes ranging from shifts in plant community composition dynamics (Bakker et al. 2016; Johnson et al. 2016), to fire regimes (Gill 2014), and biogeochemical cycling (Smith et al. 2016b). With the majority of remaining megaherbivores now either facing high extinction risk or being confined to heavily managed areas (Young et al. 2013; Ripple et al. 2015), it is imperative that we elucidate the effects of extant megaherbivores on ecosystem functioning and consequently begin to appreciate what functions are lost as they become increasingly rare.

Megaherbivores have been predicted to have disproportionately large effects on their ecosystems because their body size affords them relative immunity to non-human predation, allows them to tolerate lower quality food sources than smaller herbivores, and necessitates that they consume large quantities of forage (Owen-Smith 1988). Additionally, these large consumers have numerous non-trophic impacts on their environment (e.g., creation of game trails or channels in waterways and changing tree architecture). Consequently, megaherbivores are often identified as "ecosystem engineers" (Jones et al. 1994; Waldram et al. 2008; Hess et al. 2014).

A close relative of cetaceans, the common hippopotamus (*Hippopotamus amphibius*) joins a very small group of extant large-bodied herbivores [e.g., moose (*Alces alces*), lechwe (*Kobus leche*)] that divide their time between terrestrial and aquatic environments. *H. amphibius* spend the daylight hours resting, basking, and socializing in rivers or small pools, but at dusk they leave these aquatic refuges to feed on terrestrial vegetation (Eltringham 1999). As a large proportion of defecation occurs during the day, *H. amphibius* act as net importers of energy and nutrients to aquatic systems (Subalusky et al. 2015) and these resources have been shown to supplement aquatic food webs (McCauley et al. 2015). It has been suggested that *H. amphibius* may also play an important role in terrestrial ecosystems. The unusual feeding morphology and ecology of *H. amphibius* (i.e., extremely wide mouth and strong, horny lips that can dexterously crop short grasses) raises the possibility that they may have important effects on the plant communities that they consume. In particular, there has been speculation that *H. amphibius* may create patches of short-statured vegetation, often termed 'grazing lawns' (McNaughton 1984; Verweij et al. 2006).

Grazing lawns are known to be biotically engineered by other species of small herbivores [e.g., black brant geese (Person et al. 2003), black-tailed prairie dogs (Detling and Painter 1983)] and large herbivores [e.g., white rhino, a species that has a similar ecological feeding mode to *H. amphibius* (Cromsigt and te Beest 2014), and American bison (Knapp et al. 1999)]. These unique landscape features have captured the attention of ecologists due to their influences on plant morphology (McNaughton 1984; Hempson et al. 2015), primary productivity (McNaughton 1985; Augustine and McNaughton 2006), plant species diversity (McNaughton 1983; Belsky 1992; Karki et al. 2000), nutrient cycling rates (Ruess and Seagle 1994; Hobbs 1996; Singer and Schoenecker 2003), and their frequent use by a variety of herbivore taxa (McNaughton 1976; Waldram et al. 2008; Gosling 2014; Cromsigt et al. 2017). Specifically, intense grazing alters the morphology of grasses such that the ratio of leaf to stem tissue increases, which is thought to increase the efficiency of nutrient intake for all grazing herbivore species (McNaughton 1984; Hempson et al. 2015). Plant diversity also tends to be higher on grazing lawns because continuous cropping of taller growing plant species prevents them from outcompeting low growing species (McNaughton 1983; Belsky 1992; Karki et al. 2000). Finally, concentrated defecation has been implicated in the elevated concentrations of soil nutrients in some grazing lawns (Frank et al. 2000; but see Stock et al. 2010) and areas of intense grazing by domestic stock (Young et al. 1995).

Previous investigations of *H. amphibius* effects have been challenged by the lack of a method by which to selectively remove *H. amphibius* experimentally from study plots. Here, we attempt to overcome this challenge using a simple replicated exclosure experiment with a design that exploits the unique morphology of *H. amphibius* (e.g., wide cranium, short legged, wide body form) to exclude them from study plots while keeping these plots largely permeable to all other herbivores (Fig. 1). The permeability of these *H. amphibius* exclosures to other herbivores allowed us to sample how both floral and faunal communities interactively respond to the absence of *H. amphibius*—in effect replicating the dynamics of change as might proceed in a natural landscape from which *H. amphibius* have been lost. We maintained these exclosures for three years to investigate three hypotheses regarding the impacts of *H. amphibius* loss on terrestrial vegetation: following *H. amphibius* loss (1) the morphology of dominant grasses will change such that they become less leafy (i.e., decreasing ratio of leaf to stem tissue), (2) plant diversity will decrease, but (3) soil nutrient concentrations will not change because a large proportion of *H. amphibius* excretion occurs in their daytime aquatic refuges. Collectively, results from tests of these hypotheses enrich our view of the diverse effects that *H. amphibius* have on terrestrial ecosystems and deepen our understanding of the ecological repercussions of *H. amphibius* population decline.

## Methods

### Study area

We conducted our experiments at the Mpala Research Centre in the Laikipia District of Kenya (36°54′E, 0°19′N). We
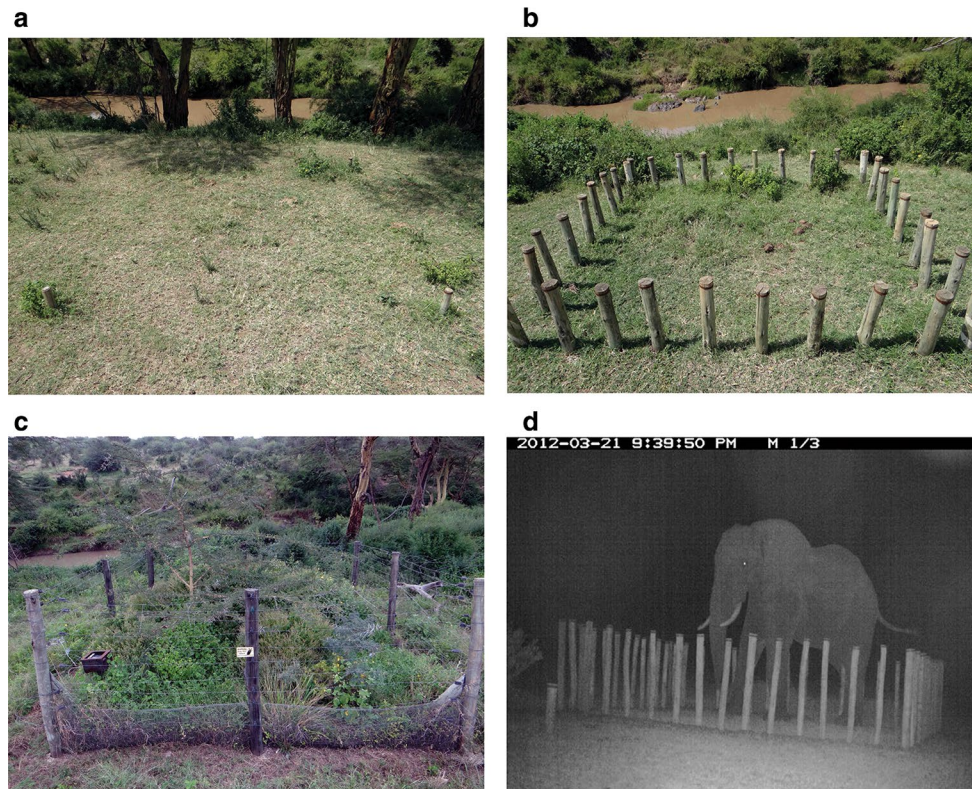
**Fig. 1** Photographs of the three exclosure treatments taken at the conclusion of the experiment: **a** Control (all herbivores present), **b** *Hippopotamus amphibius* exclosure (only *H. amphibius* excluded), **c** Total exclosure (all large/medium-sized herbivores excluded). Panel **d** shows an elephant (*Loxodonta africana*) observed in a *H. amphibius* exclosure plot during routine camera trap sampling

concentrated our field sampling in open grassland regions that bordered the Ewaso Ng'iro River and were surrounded by acacia shrub forests. Rainfall in this region is weakly trimodal with peak rainfall typically occurring in April–May, July–August, and October–November. Long-term mean annual rainfall at the study area is ~ 647 mm/year (Caylor et al. 2017). We conducted end-experiment vegetation sampling, as described below, just after a rainfall peak in October 2014 (plant morphology) and just prior to a rainfall peak in August/September 2015 (all other data).

## Exclosure design

We constructed experimental exclosure plots on *H. amphibius* grazing lawns at five field sites along a section of the Ewaso Ng'iro in June 2012. Studies tracking *H. amphibius* abundance in the largest river pool at these field sites have recorded a long-term resident population of approximately 19 individuals (McCauley et al. 2015). On-foot and aerial surveys reveal transient occupancy in other nearby pools in the same region of the experiment ranging from 1 to 8 individuals. Each experimental plot represented one of three experimental treatments: (1) Control plots—no barriers to animal movement; (2) *H. amphibius* exclosure plots—delimited by thick wooden stakes cemented

into the ground (above-ground height = $111 \pm 0.5$ cm, gap between stakes = $43 \pm 1.6$ cm; mean $\pm$ SE), and therefore, mechanically excluded *H. amphibius* because of their unique morphology and behavior (i.e., short-legged megaherbivore largely incapable of saltation) but were designed to be as permeable as possible to other large herbivores with different body morphologies; (3) Total exclosure plots—delimited by ten-strand 2.2 m-tall electric fences skirted by 70 cm of 2.0 cm mesh chicken wire that excluded all medium to large mammals (Fig. 1). Collectively, we constructed ten Control plots, ten *H. amphibius* exclosure plots, and five Total exclosure plots (higher construction and maintenance costs of Total exclosure prevented even sample sizes). Each field site contained one Total exclosure plot and, depending on the size of the site, either one (one site), two (three sites), or three (one site) plots of each of the remaining two treatments. We separated replicate plots within a site by, on average, approximately 15 m. The distance between each field site and the closest other field site ranged from 0.5 to 6.5 km. All experimental plots were 5.4 m × 5.4 m in size, which ensured a 95 cm buffer zone around a central 3.5 m × 3.5 m area. We spread our sampling, as described below, evenly across this interior zone of each plot. *H. amphibius* exclosure plots were designed to block entry only to *H. amphibius* and remain accessible to all other

herbivores. As such, *H. amphibius* exclosures record both the direct effects of *H. amphibius* removal on vegetative and soil communities as well as any additional changes that may be driven by altered abundances of other herbivores, potentially in response to the removal of *H. amphibius* (Eltringham 1974).

We used dung and camera trap surveys to track how herbivores used both *H. amphibius* exclosure plots and Control plots. Results from both methods assisted us in testing the efficacy of the *H. amphibius* exclosure plots and determining if and how the abundance of non-*H. amphibius* herbivores may have differed between *H. amphibius* exclosures and Control plots. We conducted dung surveys in all Control and *H. amphibius* exclosure plots in November 2012, January–February 2013, and August 2015 (one Control plot not surveyed in 2012). These surveys involved comprehensively searching for and counting dung piles in eight 1 m² quadrats (Young et al. 2013) evenly spaced across each plot. In each quadrat, we categorized dung piles as: domestic cattle (*Bos taurus indicus*), elephant (*Loxodonta africana*), primate [olive baboon (*Papio anubis*), vervet monkey (*Cercopithecus aethiops*)], scrub hare (*Lepus saxatilis*), large ungulate [waterbuck (*Kobus ellipsiprymnus*), greater kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*)], medium ungulate [impala (*Aepyceros melampus*)], or small ungulate [Guenther's dik dik (*Madoqua guentheri*), gray duiker (*Sylvicapra grimmia*)]. We used motion-triggered camera traps (burst of four photographs followed by a 10 s reset time; Reconyx, Hyper-Fire) to monitor herbivore activity in one Control and one *H. amphibius* exclosure plot at each field site for approximately four weeks in January–March 2016 (130 camera trap days in total). We used the obtained photographs to estimate abundance of each of the seven herbivore groups included in the dung survey and *H. amphibius* in each monitored plot. We used an estimate of abundance that reflected the time spent inside the plot by each herbivore category by counting the total number of individuals observed in each minute and summing this across all minutes in the survey period. When there were multiple photographs of the same herbivore category in a single minute, we used the largest number of individuals that occurred in the same photograph. We reviewed behaviors associated with entry of all non-*H. amphibius* mammals in these camera trap images to begin to ascertain if and how the design of the *H. amphibius* exclosures may have influenced use of these plots by these other herbivores.

## Plant and soil sampling

### Vegetation structure

To examine the effects of *H. amphibius* removal on vegetation structure, we collected data on grassland canopy height and woody plant communities. We collected grassland canopy height data in August/September 2015 at 24 sampling locations evenly spaced across each plot. To measure canopy height, we used a 20 cm diameter lightweight circular disc, which we centered over each sampling location and placed on top of the canopy (McNaughton 1976). We averaged the height above the ground of the highest and lowest points of the disc when positioned at each sampling location to obtain 24 estimates of canopy height per plot. We collected woody plant data in August/September 2015. First, we recorded the total number of woody plants in each plot during comprehensive searches of the interior sampling area of all plots. Then, we recorded species identity, height, and stem diameter at soil level for each woody plant that was encountered.

### Plant species diversity

To investigate the effect of *H. amphibius* removal on plant diversity, we collected data on plant species composition for each plot in July/August 2012 (concurrent with the time of exclosure installation) and in August/September 2015 and used these to calculate species richness and Shannon diversity. At each sampling event, we placed a rigid pin at 64 sampling locations evenly spaced across the interior of each plot and, for each contact between the pin and the vegetation, recorded the identity of the plant species. We identified plant taxa to the lowest taxonomic level possible; species level $n = 30$, genus level $n = 20$.

### Plant morphology

To determine how *H. amphibius* removal may shape the morphology of grasses, we measured key morphological attributes of the numerically dominant grass species *Cynodon plectostachyus* in October 2014. We randomly selected and measured a *C. plectostachyus* stem from each of the sampling locations used for the canopy height data, resulting in 24 sampled *C. plectostachyus* stems per plot ($n = 600$ stems in total). We measured three traits for each sampled stem: (1) stem height—measured as the distance from soil level to the base of the flag leaf; (2) number of leaves—excluding the flag leaf; (3) internode distances—measured as the distances between each consecutive pair of nodes.

### Soil chemistry: exclosure experiment

To investigate the effects of *H. amphibius* removal on soil chemistry, we took 2–3 soil samples (10 cm surface core) from all plots (except for one Total exclosure plot) in July/August 2012 ($n = 57$) and August 2015 ($n = 72$). We selected the soil sampling locations such that they were evenly spread across

the plot, that locations were not sampled twice, and that they did not overlap with any of the vegetation sampling points.

We sieved all soil samples to remove vegetative matter, dried them in a drying oven for 48 h at 40–55 °C and sent them to Brookside Laboratories (New Bremen, OH, USA) for analysis. At Brookside Laboratories, each soil sample was dried and ground to pass through a 2 mm sieve and then evaluated for: concentrations of eleven soil elements [Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, and Zn; Mehlich III extraction method (Mehlich 1984)], two forms of available nitrogen [$NO_3$ and $NH_4$; cadmium reduction method (Dahnke and Johnson 1990)], cation exchange capacity [CEC; summation method (Ross and Ketterings 1995)], organic matter content [loss on ignition method (Schulte and Hopkins 1996)], and pH.

### Soil chemistry: landscape sampling

In an attempt to increase our confidence that any changes in soil chemistry induced by our exclosures could be attributed to *H. amphibius* removal, we also conducted an observational study of how soil chemistry differed between areas frequently (grazing lawns) and rarely (surrounding acacia shrub forests) used by *H. amphibius* and other grazing herbivores. We suspected that grazing by *H. amphibius* and other herbivores is an important mechanism preventing shrub encroachment on grazing lawns and that the removal of these species may, therefore, allow encroachment and create vegetation and soil chemistry conditions similar to those of shrub forests. Additional support for an effect of *H. amphibius* removal on soil chemistry would be suggested if soil chemistry of shrub forests differed from that of grazing lawns in a manner similar to soil chemistry changes induced by experimental *H. amphibius* exclusion. We expected the removal of all herbivores (Total exclosure) to allow the most shrub encroachment and lead to soil chemistry most similar to shrub forests. We took soil samples from the center of the grazing lawns at each field site and inside adjacent shrub forest (50 m interior from grassland/shrub forest boundary) prior to exclosure construction (January 2012). We collected these soil samples at 25 m intervals along 50 m transects, resulting in three samples per transect. We sampled one or two transects (contingent on site size) within each of the five sites; $n = 48$ soil samples. We collected and analyzed these soil samples as described above. A similar observational supplement for vegetation surveys was not undertaken because our increased spatial resolution of sampling in these surveys afforded sufficient confidence in the results.

### Statistical analysis

#### Vegetation structure

We applied a natural logarithm transformation to the canopy height data prior to analysis for normalization purposes. We tested the effect of experimental treatment on canopy height using a linear mixed model (LMM) with sampling location as the unit of observation. We defined experimental treatment as the only fixed effect but included the interaction between experimental treatment and field site as a random effect to account for the interdependency of both values and the effects of treatment among measurements taken from plots at the same field site.

We statistically compared three characteristics of woody plant assemblages between plots: number of plants, plant height, and the diameter of plant stems at soil level. We analyzed the count data using a Poisson generalized linear mixed model (GLMM), which had the same fixed and random effects structure as the model used for the canopy height data but used plot as the unit of observation. To account for overdispersion in this model, we included observation identity as an additional random effect. In the analyses of woody plant height and diameter data, we used individual plant as the unit of observation. We transformed and analyzed the plant height data in exactly the same way as the canopy height data. We used Mann–Whitney tests to compare the diameter data between each experimental exclosure treatment and Control plots because a bimodal distribution prevented the use of parametric tests.

#### Plant species diversity

To compare plant species diversity between plots, we evaluated species richness and the exponential of the Shannon Index for each plot in both 2012 and 2015. The exponential of the Shannon Index (hereafter Shannon diversity) is the Hill number counterpart of the raw Shannon Index. Hill numbers are preferable to raw diversity indices because they obey the replication principle, and therefore, can be meaningfully compared between different experiments (Chao et al. 2014). The calculation of Shannon diversity required abundance data for each plant species in each plot. We calculated abundance for a specific plant species in a specific plot as the total number of sampling pins that made contact with that plant species. Due to substantial variation among plots in species richness and Shannon diversity in 2012, we calculated the change in each of these variables between 2012 and 2015, standardized by their respective 2012 values, separately for each plot and used these as the dependent variables in the analyses. We analyzed each of these two variables using a linear mixed model (LMM) which included experimental treatment and the relevant diversity value in 2012 as fixed effects. As in other models, we included the interaction between treatment and field site as a random effect to account for the interdependency of both values and the effects of treatment among plots at the same site. To examine any shifts that may have occurred in the functional composition of these vegetation communities, we compared

the change in the ratio of grass to forb abundance between experimental treatments using a Kruskal–Wallis test (distribution of data prevented use of parametric tests). We defined grasses as Graminoid plants in the families Poaceae, Cyperaceae, and Juncaceae. All other herbaceous flowering plants were classified as forbs.

### Plant morphology

We compared three morphological traits of sampled *C. plectostachyus* stems between plots: stem height, leaf: stem ratio, and mean internode distance. For each sampled stem, we calculated leaf: stem ratio as the number of leaves divided by stem height, and mean internode distance as the average of all recorded internode distances. We applied a natural logarithm transformation to each of these variables for normalization purposes before analyzing them with a LMM of the same fixed and random effects structure as the model used for the canopy height data. We used sampled stem as the unit of observation in each of these three models.

### Soil chemistry: exclosure experiment

To explore the effects of experimental treatment on soil characteristics, we compared the values of each soil parameter between treatments. We obtained a single value of each soil parameter for each plot in both 2012 and 2015 by averaging across samples. We analyzed the soil characteristics according to the LMM protocol used for plant species diversity metrics described above.

### Soil chemistry: landscape sampling

We compared grazing lawns and adjacent shrub forests for each soil variable using LMMs which included habitat (grazing lawn/shrub forest) as a fixed effect and the interaction between habitat and field site as a random effect. We used soil sample as the unit of observation in these models.

We conducted all statistical analyses in R version 3.3.2 (R Core Team 2016) and all mixed modeling used the R package lme4 (Bates et al. 2015). We tested the fixed effects of models for significance by comparing full and reduced models using likelihood ratio tests (LRTs). Model assumptions were checked using residual plots.

## Results

### Camera trap and dung surveys

Our camera trap and dung surveys demonstrated that our experimental *H. amphibius* exclosure plots were successful in excluding *H. amphibius* entirely while remaining permeable to all other herbivore groups (Table 1). The electrified Total exclosure plots were not compromised during the study period and effectively excluded all medium and large mammals detected in Control and *H. amphibius* exclosure plots. We observed a high degree of similarity in herbivore species richness (i.e., presence/absence) between Control and *H. amphibius* exclosure plots. Camera traps detected six of the seven herbivore groups in both Control and *H. amphibius* exclosure plots and did not detect the seventh group (domestic cattle) in either plot type (Table 1). Dung surveys revealed that all seven non-*H. amphibius* mammal species groups were present in both Control and *H. amphibius* exclosure plots in 2016 (Table 1), but that small ungulates were absent from both plot types in 2012 and 2013 (Table S1, S2). However, both camera trap and dung surveys revealed that the abundances of some non-*H. amphibius* herbivores were lower in *H. amphibius* exclosure plots relative to Control plots (Table 1). In the case of the camera trap surveys, this difference was only statistically significant for *L. africana* (elephants). Analysis of the dung surveys revealed these patterns of difference varied between the surveys conducted in 2012, 2013, and 2016. During the 2012 dung surveys, there were no significant differences detectable between *H. amphibius* exclosure and Control plots (Table S1). In 2013, only large ungulates had significantly lower abundance in *H. amphibius* exclosure plots (Table S2). Finally, in the 2016 dung surveys, both large ungulates and *L. saxatilis* (scrub hare) had significantly lower abundance in *H. amphibius* exclosure plots (Table 1).

### Vegetation structure

Log-transformed grassland canopy height differed significantly between the three experimental treatments [LRT, $\chi^2(2) = 19.48$, $p < 0.001$; Fig. 2]. Relative to the Control plots, the canopy was approximately twice as high in *H. amphibius* exclosure plots [$t(3.99) = 3.12$, $p = 0.036$], and over nine times higher in Total exclosure plots [$t(4.03) = 13.52$, $p < 0.001$].

Experimental treatment had a statistically significant effect on the number of woody plants [LRT, $\chi^2(2) = 6.19$, $p = 0.045$; Fig. 3a] and the log-transformed height of woody plants [LRT, $\chi^2(2) = 14.03$, $p < 0.001$; Fig. 3b]. The *H. amphibius* exclosure plots contained a similar number of woody plants as did Control plots ($Z = 1.00$, $p = 0.317$), but these plants were on average three times as tall in the exclosure plots [$t(4.70) = 3.13$, $p = 0.028$]. Total exclosure plots contained approximately three times as many woody plants as Control plots ($Z = 3.42$, $p < 0.001$) and these plants were on average over four times as tall [$t(3.10) = 7.98$, $p = 0.004$]. Relative to Control plots, the diameter of woody plant stems had a nonsignificant tendency to be larger in *H. amphibius* exclosure

**Table 1** Comparisons of herbivore abundance between Control and *Hippopotamus amphibius* exclosure plots in the third year of the experiment estimated by camera trap and dung surveys

| Taxa | Camera trap analysis | | | | Dung analysis | | | |
|---|---|---|---|---|---|---|---|---|
| | Control | *H. amphibius* exclosure | *p* value | Highest abundance | Control | *H. amphibius* exclosure | *p* value | Highest abundance |
| Domestic cattle | 0 | 0 | NA[a] | – | 2.6 (3.7) | 0.7 (1.9) | 0.09 | – |
| Elephant | 22.8 (40.7) | 0.6 (0.9) | 0.03 | Control | 2.7 (3.6) | 1.7 (2.8) | 0.52 | – |
| Primate | 5.0 (4.2) | 13.4 (21.5) | 0.67 | – | 1.0 (1.9) | 0.4 (0.7) | 0.59 | – |
| Scrub hare | 0 | 0 | NA[a] | – | 28.1 (14.6) | 11.5 (10.4) | 0.01 | Control |
| Large ungulate | 3.0 (3.7) | 2.8 (6.3) | 0.48 | – | 6.4 (6.6) | 1.0 (1.4) | 0.05 | Control |
| Medium ungulate | 4.6 (6.4) | 7.0 (15.7) | 0.80 | – | 1.7 (2.4) | 3.0 (7.1) | 0.81 | – |
| Small ungulate | 0.2 (0.5) | 0.2 (0.5) | 1.00 | – | 0.1 (0.3) | 0.1 (0.3) | 1.00 | – |
| *H. amphibius* | 1.8 (1.6) | 0 (0.0) | 0.02 | Control | 0 | 0 | NA[a] | – |

Camera trap abundance was measured for each plot as the maximum number of individuals observed in each minute summed across all minutes of the survey period. Dung abundance was measured as the number of dung piles observed in a single survey of each plot. Abundance values are presented as mean (standard deviation). Sample size was five plots per treatment for camera trap estimates and ten plots per treatment for dung estimates. The treatment in which abundance was higher is indicated for herbivore groups that showed a statistically significant difference in abundance between treatments (two-sample Wilcoxon test; $p < 0.05$). Primates were olive baboon (*P. anubis*) and vervet monkey (*C. aethiops*). Large ungulates were waterbuck (*K. ellipsiprymnus*), greater kudu (*T. strepsiceros*), eland (*T. oryx*) and giraffe (*G. camelopardalis*). Medium ungulates were impala (*A. melampus*). Small ungulates were Guenther's dik dik (*M. guentheri*) and gray duiker (*S. grimmia*)

[a] Statistical test not computed because no individuals/dung piles were observed in either treatment
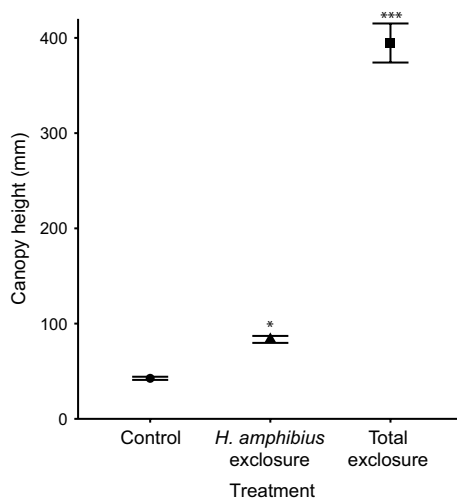


**Fig. 2** The effect of experimental treatment on plant canopy height. Points and error bars, respectively, represent means and standard errors calculated across all sampled locations. Experimental treatments are as shown in Fig. 1. Asterisks above points indicate statistical significance of differences between specific treatment and Control: *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$p < 0.001$. Statistical analyses were conducted on log-transformed data (Fig. S1)

## Plant species diversity

Experimental treatment did not have a statistically significant effect on the change in species richness [LRT, $\chi^2(2) = 4.61$, $p = 0.100$; Fig. 4a], but did have a statistically significant effect on the change in Shannon diversity [LRT, $\chi^2(2) = 7.20$, $p = 0.027$; Fig. 4b], over the three-year experiment. Control and *H. amphibius* exclosure plots experienced similar declines in Shannon diversity [$t(8.50) = -0.58$, $p = 0.579$]. Total exclosure plots differed from Control plots in that they experienced a slight increase in Shannon diversity [$t(3.70) = 2.83$, $p = 0.052$]. In all exclosure treatments, we observed a statistically significant negative correlation between the pre-treatment value and the change in diversity for both species richness and Shannon diversity (Fig. S4). The ratio of grass to forb abundance increased over the course of the experiment to a similar extent in all experimental treatments (Fig. S5).

## Plant morphology

Experimental treatment had a statistically significant effect on log-transformed stem height [LRT, $\chi^2(2) = 12.41$, $p = 0.002$; Fig. 5a], log-transformed leaf: stem ratio [LRT, $\chi^2(2) = 17.87$, $p < 0.001$; Fig. 5b], and log-transformed mean internode distance [LRT, $\chi^2(2) = 11.26$, $p = 0.004$; Fig. 5c] of the dominant grass species, *C. plectostachyus*. On average, *C. plectostachyus* stems from *H. amphibius* exclosure plots differed significantly from those of Control plots in all three morphological measures; they were taller [$t(3.92) = 2.95$,
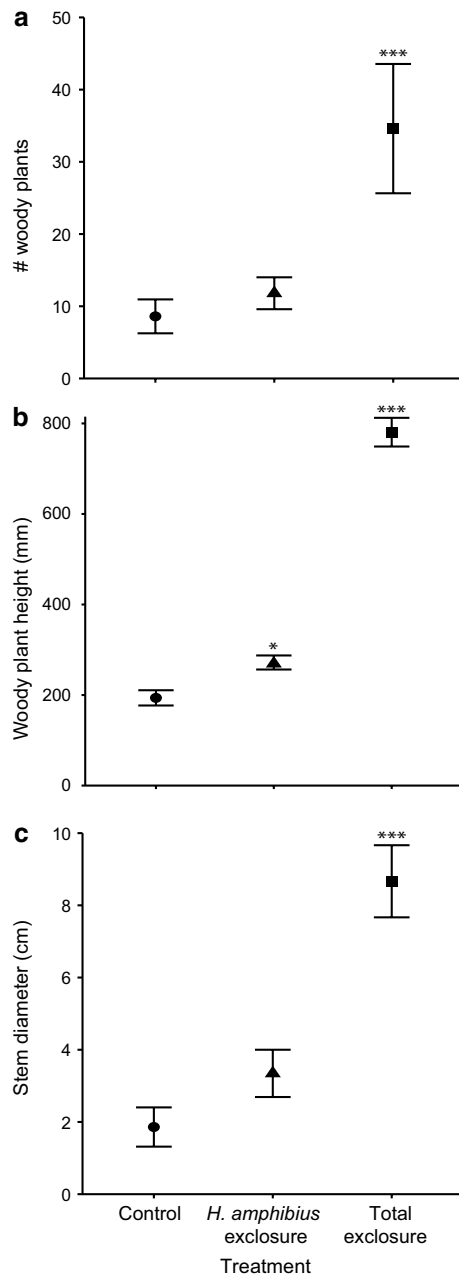
plots ($W = 4538$, $p = 0.198$), and was on average four times larger in Total exclosure plots ($W = 2368$, $p < 0.001$; Fig. 3c). Of the nine woody plant taxa observed in experimental plots, *Solanum incanum* and *Phyllanthus* spp. were the most common (Fig. S3).

**Fig. 3** The effect of experimental treatment on woody plant communities: **a** number of woody plants, **b** height of woody plants, and **c** diameter at soil level of woody plant stems. In plot **a** the points and error bars, respectively, represent means and standard errors calculated across plots. In plots **b** and **c** the points and error bars, respectively, represent means and standard errors calculated across all sampled woody plants. Experimental treatments are as shown in Fig. 1. Asterisks above points indicate statistical significance of differences between specific treatment and Control: *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$p < 0.001$. Statistical analysis of woody plant height was conducted on log-transformed data (Fig. S2)

$p = 0.043$], had smaller leaf: stem ratios [$t(5.47) = - 2.51$, $p = 0.050$], and had larger mean internode distances [$t(4.17) = 3.01$, $p = 0.037$]. Stems from Total exclosure
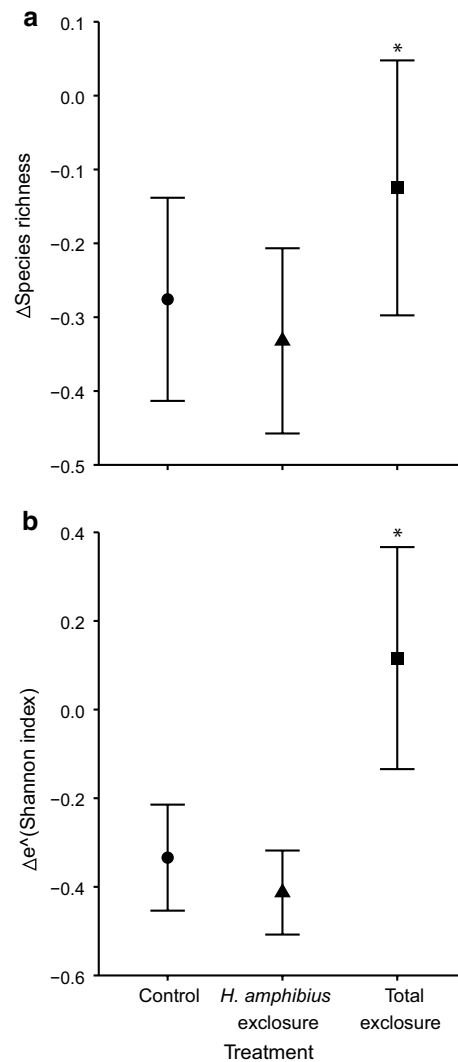


**Fig. 4** Effect of experimental treatment on the standardized change in plant **a** species richness and **b** exponential of Shannon Index. Points and error bars, respectively, represent means and standard errors calculated across plots. Experimental treatments are as shown in Fig. 1. Asterisks above points indicate statistical significance of differences between specific treatment and Control: *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$p < 0.001$. Raw species diversity values are shown in Fig. S4

plots showed even more exaggerated differences and were on average four times taller [$t(4.01) = 5.38$, $p = 0.006$], had more than 50% lower leaf: stem ratios [$t(4.07) = - 6.70$, $p = 0.002$], and their mean internode distances were over twice as large [$t(4.02) = 5.86$, $p = 0.004$] as those of Control plots.

## Soil chemistry

Five soil parameters were significantly affected by experimental treatment, and five differed significantly between grazing lawns and adjacent shrub forests in our landscape

**Fig. 5** The effects of experimental treatment on the morphology of the dominant grass *Cynodon plectostachyus*: **a** stem height, **b** leaf: stem ratio, **c** mean internode distance, **d** example stems from different experimental treatments. Points and error bars, respectively, represent means and standard errors calculated across all sampled stems. Experimental treatments are as shown in Fig. 1. Asterisks above points indicate statistical significance of differences between specific treatment and control: *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$p < 0.001$. Statistical analyses were conducted on log-transformed data (Fig. S6)
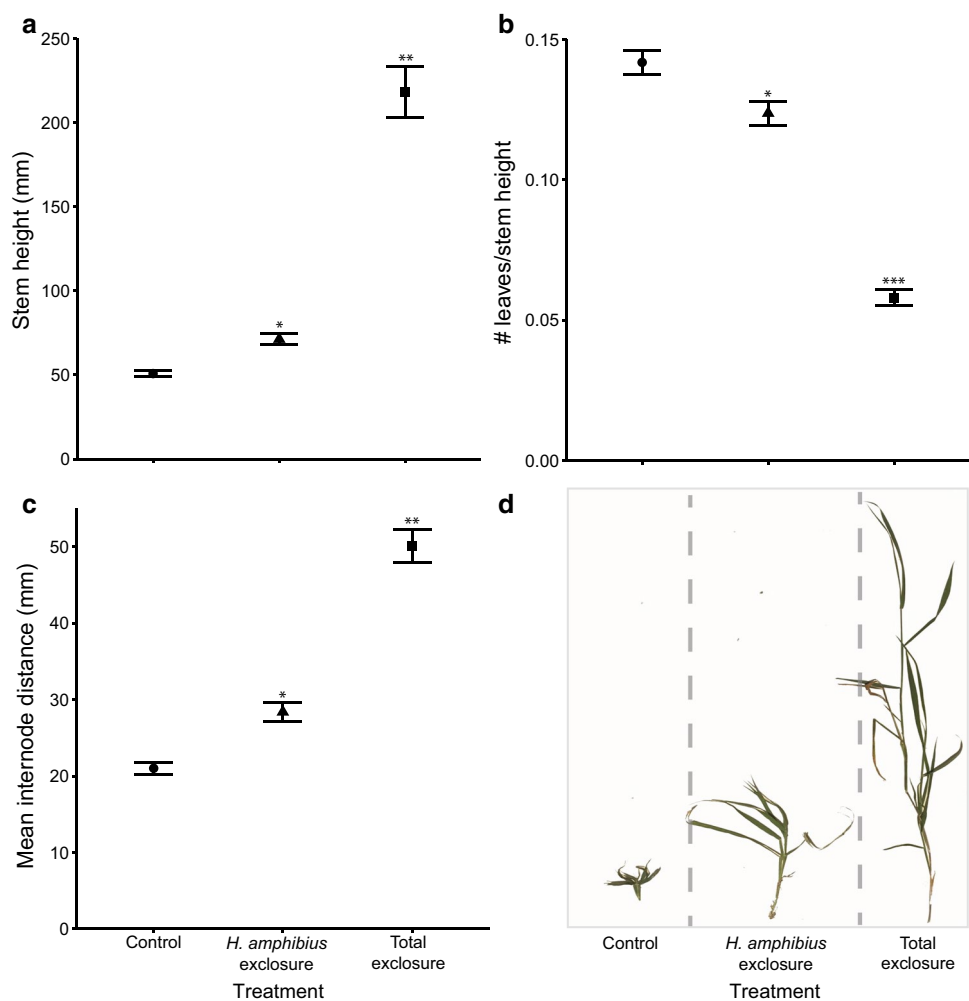


sampling; contributing to a total of six unique parameters that showed a statistically significant difference in either or both comparisons (Table 2; raw data in Table S3, S4). Importantly, the values of four of these six soil parameters (CEC, Ca, Mg, Mn) were lower in *H. amphibius* exclosure plots than Control plots, and were also significantly lower in shrub forests than grazing lawns (Fig. S7–S12). By contrast, the concentration of Al tended to be slightly lower (non-significant) in *H. amphibius* exclosure plots than Control plots but showed no difference between shrub forests and grazing lawns, and the concentration of K showed no difference between *H. amphibius* exclosure plots and Control plots but was significantly lower in shrub forests than grazing lawns. The soils of Total exclosure plots showed a strong resemblance to those of *H. amphibius* exclosure plots, but showed a smaller difference from Control plots in CEC and larger differences in Mg, Mn and Al (Fig. S7–S12). The soils of Total exclosures were more similar to those of shrub forests than were the soils of *H. amphibius* exclosures (Table S3, S4).

## Discussion

We observed significant changes in vegetation structure, plant community composition, and soil chemistry within *H. amphibius* exclosures relative to Control plots. These results provide useful insight into how *H. amphibius* removal is likely to shape terrestrial ecosystems. Comparisons of attributes of vegetation and soil communities inside *H. amphibius* exclosures relative to Total exclosure plots that removed all medium and large herbivores helped set these *H. amphibius* removal effects in context, with the conclusion emerging that the removal of all herbivores had much more pronounced impacts on vegetation and soils than the removal solely of *H. amphibius*.

**Table 2** Effects of experimental treatment (Control/*Hippopotamus amphibius* exclosure/Total exclosure) and habitat type (grazing lawn/adjacent shrub forest) on soil chemistry

| Soil parameter | Experimental treatment | | | Habitat type | | | Directional alignment? |
|---|---|---|---|---|---|---|---|
| | df | $\chi^2$ | p value | df | $\chi^2$ | p value | |
| CEC (meq/100 g) | 2 | 8.06 | 0.018* | 1 | 10.45 | 0.001** | Yes |
| Ca (mg/kg) | 2 | 10.48 | 0.005** | 1 | 8.70 | 0.003** | Yes |
| Mg (mg/kg) | 2 | 7.30 | 0.026* | 1 | 6.81 | 0.009** | Yes |
| Mn (mg/kg) | 2 | 7.30 | 0.026* | 1 | 4.81 | 0.028* | Yes |
| K (mg/kg) | 2 | 3.51 | 0.173 | 1 | 11.39 | 0.001*** | No |
| Al (mg/kg) | 2 | 8.07 | 0.018* | 1 | 0.41 | 0.522 | No |
| P (mg/kg) | 2 | 1.62 | 0.445 | 1 | 1.14 | 0.287 | – |
| $NO_3$ (ppm) | 2 | 2.23 | 0.328 | 1 | 0.93 | 0.335 | – |
| $NH_4$ (ppm) | 2 | 2.44 | 0.295 | 1 | 1.22 | 0.270 | – |
| B (mg/kg) | 2 | 1.88 | 0.391 | 1 | 1.33 | 0.248 | – |
| Cu (mg/kg) | 2 | 5.70 | 0.058 | 1 | 0.02 | 0.903 | – |
| Fe (mg/kg) | 2 | 1.38 | 0.503 | 1 | 0.09 | 0.764 | – |
| Na (mg/kg) | 2 | 2.80 | 0.247 | 1 | 1.54 | 0.214 | – |
| Zn (mg/kg) | 2 | 4.25 | 0.120 | 1 | 1.12 | 0.290 | – |
| pH | 2 | 1.13 | 0.567 | 1 | 1.18 | 0.277 | – |
| Organic matter (%) | 2 | 2.16 | 0.340 | 1 | 3.36 | 0.067 | – |

For each soil parameter that differed significantly between experimental treatments or habitat types it is indicated whether the directionality of differences between the *H. amphibius* exclosure plots and the unfenced Control plots match differences between grazing lawns (where *H. amphibius* was putatively common) and shrub forest (where *H. amphibius* was less common)

*$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$p < 0.001$

## Effect of *H. amphibius* removal on vegetation structure and species composition

Comparisons of vegetation data from Control and *H. amphibius* exclosure plots provide support for our hypothesis that *H. amphibius* removal influences the morphology of dominant grasses such that the ratio of leaf to stem tissue increases. Specifically, our results reveal that in the presence of *H. amphibius*, plant communities are shorter in stature, leafier, and contain less woody plant biomass.

The most pronounced difference we observed between Control and *H. amphibius* exclosure plots was in respect to the height of vegetation, which was, on average, approximately 50% lower in Control plots to which *H. amphibius* had access than *H. amphibius* exclosures. This observation parallels those of other exclosure studies that experimentally excluded all medium and large mammals but assumed the observed patterns were caused primarily by the exclusion of *H. amphibius* (Lock 1972; Verweij et al. 2006).

We also detected notable differences in the growth form of the dominant grass species, *C. plectostachyus,* between Control and *H. amphibius* exclosure plots. Individual *C. plectostachyus* in Control plots that were exposed to *H. amphibius* grazing were, on average, shorter and had higher leaf to stem ratios than *C. plectostachyus* inside *H. amphibius* exclosure plots (Fig. 5). Similar kinds of morphological shifts were apparent in other grasses common in the

experiment that were not measured during this study. These kinds of shifts in morphology have been reported in grazing lawns maintained by wildebeest (McNaughton 1984) and black-tailed prairie dogs (Painter et al. 1993), and also in areas of high-intensity grazing by livestock (Georgiadis and McNaughton 1988; Zhao et al. 2009).

In this study, neither plant species richness nor diversity differed between Control and *H. amphibius* exclosure plots, suggesting that presence of *H. amphibius* does not significantly affect either of these aspects of the plant communities—at least over the three-year time span of this study. These findings do not lend support to our hypothesis that *H. amphibius* presence increases plant diversity by preventing taller growing species from shading out the lower growing ones. This is an interesting finding given that this hypothesis is frequently proposed, and often empirically supported in other systems (McNaughton 1983; Belsky 1992; Karki et al. 2000). We suggest that the destructive nature of *H. amphibius* grazing [i.e., consumption of up to 40–50 kg (wet mass) of vegetation per night (Lewison and Carter 2004), tough horny lips that can grip vegetation very close to soil level, and frequent uprooting of the vegetation they feed upon (Lock 1972)] constitutes an intense form of disturbance that may not promote increases in plant diversity.

Our analysis of grass to forb abundance ratios revealed that, over the course of the experiment, the average proportion of grasses increased in all treatments. Increases

in grasses were in a large part driven by increases in the dominant grass *C. plectostachyus*. The relative abundance of *C. plectostachyus* compared to other grasses, increased in all three treatments, with the most pronounced increases noted in Control and *H. amphibius* exclosure treatments (Table S5). There were, however, no significant differences in grass to forb ratios detected between the treatments. These results suggest again that, at least over this time horizon, the presence of *H. amphibius* does not shape this important gross attribute of plant functional composition.

The smaller number and size of woody plants in Control plots than *H. amphibius* exclosure plots suggests that *H. amphibius* plays an influential role in preventing encroachment of near-river grasslands by woody plants. While *H. amphibius* are believed to feed predominantly on grasses, they are also known to consume other types of vegetation (Cerling et al. 2008), which may include woody plants. It is, therefore, plausible that the observed differences in woody plants may result from direct consumption. Trampling by *H. amphibius* provides an alternate or complimentary mechanism for causing these effects. A similar role has been attributed to other megaherbivores, and is often correlated with the creation of suitable habitat for other species (Pringle 2008; Hess et al. 2014; de Boer et al. 2015). Illuminating forces such as this, that may control woody encroachment, are of great interest because of the extensive effects that such shifts have on community and ecosystem ecology (Eldridge et al. 2011).

Viewed together, these shifts in both plant community structure and morphology following removal of *H. amphibius* are likely to result in lower quality forage (but more total forage) for many herbivores, thus suggesting that the presence of *H. amphibius* may facilitate certain other herbivores (Stachowicz 2001). This elevated quality results from the higher nutritional value of leaf tissue relative to stem tissue, and the increased density of vegetation which allows herbivores to obtain more nutrients and achieve higher caloric intake per processed bite (McNaughton 1984; Verweij et al. 2006; Hempson et al. 2015). This result is concordant with observations from West Africa (Verweij et al. 2006), suggesting that *H. amphibius* presence may have similar facilitative effects on vegetation structure across a broad geographic area. Facilitation of this sort may be especially important for females with increased energetic requirements due to parental care (Hempson et al. 2015), and during periods when high primary productivity overwhelms the ability of smaller herbivores (e.g., impala) to maintain grazing lawns (Waldram et al. 2008; Cromsigt and te Beest 2014). In addition, by reducing the height of vegetation and woody plant abundance, *H. amphibius* presence may also create areas of increased visibility and consequently reduced predation risk (Kanga et al. 2013). In support of these theories relating to habitat improvement, dominant male kob are known to defend territories on the grazing lawns of *H. amphibius* (Verweij et al. 2006). However, it should be noted that *H. amphibius* presence may decrease the quality of forage for herbivore species that are mechanically unable to forage efficiently on such low-growing vegetation, such as cape buffalo and waterbuck (Eltringham 1974).

The plant community shifts observed in *H. amphibius* exclosures suggest that *H. amphibius* and other large herbivores may also shape broader scale landscape and ecosystem processes. For example, fire is a natural part of the ecology of East African grassland systems and fire dynamics are clearly shaped by plant community dynamics. Research on fire ecology conducted in the same region as these exclosure experiments has indicated that fire influences a diverse range of ecological attributes including bird diversity (Gregory et al. 2010), mammalian grazing preferences (Sensenig et al. 2010), and even mutualism dynamics (Sensenig et al. 2017). By reducing canopy height, and the size and abundance of woody plants, *H. amphibius* presence may suppress fire spread and consequently impact a variety of ecosystem processes. Other experiments in this landscape have noted similar kinds of connections between increased grazing by wildlife, decreased herbaceous fuel loads, changes in burn temperatures, and shifts in ecological responses to fire (Kimuyu et al. 2014).

When reviewing the impacts of *H. amphibius* removal on vegetation communities, it is important to note that *H. amphibius* removal elicited far smaller responses for almost all measured vegetation attributes than did the removal of all medium and large herbivores via the Total exclosures (Figs. 2, 3, 4, 5, S1, S2, S3, S6). For example, grass canopy height was nine times greater in Total exclosures than open Control plots, but only twice as high in *H. amphibius* exclosure plots relative to Control plots. The much more pronounced responses observed within the Total exclosures reminds that these vegetative communities would be much more significantly affected by complete herbivore defaunation relative to the selective loss of *H. amphibius*. Observations of the sole impacts of *H. amphibius* on vegetation communities relative to the impacts of the broader suite of medium and large herbivores does, however, deserve further investigation in contexts where *H. amphibius* are more abundant. For example, the abundance of *H. amphibius* in watersheds elsewhere in East Africa can easily become one to two orders of magnitude greater than those recorded in our study system (Olivier and Laurie 1974).

## Effects of *H. amphibius* removal on soil chemistry

Measurements of soil chemistry made in the *H. amphibius* exclosure experiment revealed that the concentrations of four elements (Ca, Mg, Mn, Al), as well as CEC were higher in the soils where *H. amphibius* were permitted to graze.

However, unlike areas of intense cattle grazing (Young et al. 1995), *H. amphibius* grazing lawns do not appear to have higher concentrations of the major plant-limiting nutrients N and P relative to surrounding grasslands. This pattern is similar to those observed on white rhino grazing lawns of Hluhluwe-iMfolozi Park, which did not differ from surrounding bunch grass areas in soil N concentration (Stock et al. 2010; Cromsigt et al. 2017). The soil chemistry results, therefore, provide mixed support for our hypothesis that presence of *H. amphibius* does not increase soil nutrient concentrations. Such a result, however, may not be surprising given the relatively short time frame of our experiment. At least two possible mechanisms may explain the element concentrations that were observed to be elevated in the plots accessed by *H. amphibius*. First, the *H. amphibius* foraging in these plots may themselves have increased the concentrations; e.g. via urine additions (McNaughton 1985). Alternatively, other large herbivores that were present in higher abundance in the Control plots than the *H amphibius* plots (Table 1) may have increased element concentrations via their own excretion (Young et al. 1995; Stock et al. 2010). The fact that vegetation is cropped extremely short in the treatments *H. amphibius* access, appears to negate the possibility that these increases in element concentrations are derived from the buildup of additional plant litter. Other direct impacts of *H. amphibius* on soil properties, such as soil compaction, soil salinity and soil moisture, deserve further investigation.

Interestingly, patterns of difference for four of these soil parameters that differed between Control and *H. amphibius* exclosure plots matched patterns of difference observed between soils sampled in grazing lawns and the surrounding acacia shrub forests (Table 2; Fig. S7–S12). Combined with our vegetation data, that demonstrate *H. amphibius* removal appears to produce the early stages of a conversion from grassland to shrub land, this conforms with our theory that reductions in grazing following removal of *H. amphibius* may lead to shrub encroachment and soil chemistry conditions that are more similar to shrub forests. We note that soil chemistry changes following *H. amphibius* exclusion may also be partly the result of the reduced abundances of other herbivores (Table 1, S2). We further highlight that the greater similarity between shrub forest and Total exclosure soils than between shrub forest and *H. amphibius* exclosure soils suggests that an important role is played by other herbivores (Table S3, S4).

## Mechanisms driving change in *H. amphibius* exclosures

Changes observed within the *H. amphibius* exclosures were very likely strongly driven by the successful experimental removal of *H. amphibius*. In these experiments, we did not investigate the specific mechanisms by which *H. amphibius*

removal shaped observed shifts in soil and plant communities (e.g., reductions in consumption, trampling, soil compaction, and urination by *H. amphibius*). As alluded to above, recorded changes in vegetation and soil attributes may, however, also have been influenced by observed shifts in herbivore abundance that occurred in association with *H. amphibius* removal. We note that our camera and dung sampling within the *H. amphibius* exclosures revealed significant reductions for a subset of other large herbivores (Table 1, S2). These reductions in the abundance of select non-*H. amphibius* large herbivores could have resulted from two non-mutually exclusive mechanisms. First, as previously mentioned, removal of *H. amphibius* may have created sub-optimal foraging conditions (e.g., reduced nutritional value of vegetation with a lower leaf: stem ratio; Verweij et al. 2006) for certain other medium and large herbivores thereby dissuading them from using the *H. amphibius* exclosures. Such shifts would represent ecologically realistic and important consequences that might follow the loss of *H. amphibius* in a natural landscape. Some of the observed differences in non-*H. amphibius* herbivore abundance between *H. amphibius* exclosure plots and Contol plots are at least consistent with the logic of the facilitation mechanism. For example, the dung survey results conducted early in 2012, revealed no differences in herbivore abundance—an observation that might be predicted to arise given that the exclosure plots had only been in place for 6 months and few shifts in plant communities may yet have taken hold. The last round of dung surveys conducted towards the end of the experiment, however, revealed significantly reduced abundances of large herbivores and scrub hare in *H. amphibius* exclosure plots. Differences in the nutritional and morphological properties of vegetation inside *H. amphibius* exclosures might have contributed to deterring these herbivore groups.

The second alternate hypothesis is that the design of the *H. amphibius* exclosures physically or behaviorally deterred certain non-*H. amphibius* herbivores from entering and interacting with these plots. Camera trap and dung survey data provides indication that medium and large herbviores were physically capable of entering plots (e.g., species richness of non-*H. amphibius* herbivores was highly similar between Control and *H. amphibius* exclosure plots; Table 1, S1, S2). Additionally, reviews of camera trap images where non-*H. amphibius* herbivores entered *H. amphibius* exclosure plots revealed that these animals were able to access the plots by walking unimpeded between the posts (e.g., no evidence of saltation or other more challenging entry modes required) that barred entry to the much wider and shorter statured *H. amphibius* (Fig. S13). There also did not appear to be evidence of one-sided size-selective filtering by the *H. amphibius* exclosure whereby the experimental design was biased against only larger herbivores. As above, dung

sampling results between *H. amphibius* exclosures and Control plots at the end of experiment (2016) revealed no differences between these two treatments for the largest herbivore *L. Africana* (elephant), which appeared capable of walking through the *H. amphibius* exclosures, but we did detect significantly lower abundances of the smallest detectable mammal *L. saxatilis* (scrub hare) inside the *H. amphibius* exclosures, relative to the Controls. Even taking this evidence into consideration, we cannot and do not rule out the possibility that the *H. amphibius* exclosure posed some behavioral filter to entry for other non-*H. amphibius* herbivores that was not readily detectable using these methods and which may have influenced our results.

## Conclusion

The diverse responses observed in these experimental manipulations are useful in contextualizing the impact of both historic and contemporary *H. amphibius* loss. Representatives of the lineage Hippopotamidae once were found across Africa, into northern Europe and Asia, on Mediterranean islands, and in Madagascar (Boisserie et al. 2011). During the Pleistocene, the hippopotamuses became confined to Africa, and during this last century they have been further restricted to select watersheds in sub-Saharan Africa. In addition to these range contractions, extant populations of *H. amphibius* have been drastically reduced in abundance—a pattern that is predicted to continue as human populations and infrastructure increase in sub-Saharan Africa and associated development around water resources intensifies. Current projections suggest that populations of *H. amphibius* may decrease by 30% in the next three decades (Lewison et al. 2008).

This study suggests that these local extinctions and sustained reductions in the abundance of *H. amphibius* may have altered plant and soil communities in ways that are largely underappreciated. Our results suggest that loss of *H. amphibius* is likely to precipitate: changes in the morphology of certain plant species, alterations in the structure of plant communities (e.g., changes in grassland canopy height), shifts in soil nutrient composition, early signs of woody encroachment, and changes in habitat use by other herbivores. It is possible that these diverse local-scale effects of *H. amphibius* removal will scale up to affect even larger processes such as landscape-level habitat heterogeneity (Kanga et al. 2013; e.g., via loss of near-river open grassland habitats), with potential ramifications for ecosystem structure and functioning.

Importantly, these results only provide insight into the acute ecological shifts that are likely to occur in the years immediately following *H. amphibius* removal. Future work will be required to determine how the absence of *H.* *amphibius* affects plant, soil, and wildlife communities over longer time horizons (i.e., decades). Additional study will also be needed to identify with greater precision the mechanisms by which *H. amphibius* exclusion triggers some of the ecological changes that we document and to better ascertain if and how changes in other non-*H. amphibius* herbivore communities contributed to the results we observed in these experiments. The observations that we report here add new information to the body of knowledge that can and should be utilized by ecologists seeking to better understand the ecological consequences of *H. amphibius* and ecosystem managers endeavoring to highlight the significance of the sustained loss of these unique megaherbivores.

**Author contribution statement** DJM, JSB, JMG, MO, WDN, TED, MEP, and JN conceived and designed the experiments. DJM and LFH conducted fieldwork. DJM and SIG analyzed the data. DJM and SIG wrote the manuscript; all other authors edited the manuscript.

## Compliance with ethical standards

## References

Augustine DJ, McNaughton SJ (2006) Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. Ecosystems 9:1242–1256

Bakker ES, Gill JL, Johnson CN et al (2016) Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. Proc Natl Acad Sci 113:847–855. https://doi.org/10.1073/pnas.1502545112

Barnosky AD, Koch PL, Feranec RS et al (2004) Assessing the causes of late pleistocene extinctions on the continents. Science 306:70–75. https://doi.org/10.1126/science.1101476

Barnosky AD, Lindsey EL, Villavicencio NA et al (2016) Variable impact of late-quaternary megafaunal extinction in causing ecological state shifts in North and South America. Proc Natl Acad Sci 113:856–861. https://doi.org/10.1073/pnas.1505295112

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Belsky AJ (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. J Veg Sci 3:187–200. https://doi.org/10.2307/3235679

Boisserie J-R, Fisher RE, Lihoreau F, Weston EM (2011) Evolving between land and water: key questions on the emergence and history of the Hippopotamidae (Hippopotamoidea, Cetancodonta, Cetartiodactyla). Biol Rev 86:601–625. https://doi.org/10.1111/j.1469-185X.2010.00162.x

Caylor KK, Gitonga J, Martins DJ (2017) Mpala research centre meteorological and hydrological dataset [Datafile]. Mpala Research Centre, Laikipia

Cerling TE, Harris JM, Hart JA et al (2008) Stable isotope ecology of the common hippopotamus. J Zool 276:204–212. https://doi.org/10.1111/j.1469-7998.2008.00450.x

Chao A, Chiu C-H, Jost L (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annu Rev Ecol Evol Syst 45:297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Core Team R (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Cromsigt JPGM, te Beest M (2014) Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. J Ecol 102:566–575. https://doi.org/10.1111/1365-2745.12218

Cromsigt JPGM, Veldhuis MP, Stock WD et al (2017) The functional ecology of grazing lawns: how grazers, termites, people, and fire shape HiP's savanna grassland mosaic. In: Cromsigt JPGM, Archibald S, Owen-Smith N (eds) Conserving Africa's megadiversity in the Anthropocene: the Hluhluwe-iMfolozi Park story. Cambridge University Press, Cambridge, UK, pp 135–160

Dahnke W, Johnson GV (1990) Testing soils for available nitrogen. In: Westerman RL (ed) Soil testing and plant analysis. Soil Science Society of America Inc, Madison, pp 128–139

de Boer WF, Van Oort JWA, Grover M, Peel MJS (2015) Elephant-mediated habitat modifications and changes in herbivore species assemblages in Sabi Sand, South Africa. Eur J Wildl Res 61:491–503. https://doi.org/10.1007/s10344-015-0919-3

Detling JK, Painter EL (1983) Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 57:65–71

Eldridge DJ, Bowker MA, Maestre FT et al (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis: synthesizing shrub encroachment effects. Ecol Lett 14:709–722. https://doi.org/10.1111/j.1461-0248.2011.01630.x

Eltringham SK (1974) Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus. J Appl Ecol 11:855. https://doi.org/10.2307/2401750

Eltringham SK (1999) The hippos: natural history and conservation. Princeton University Press, Princeton

Frank DA, Groffman PM, Evans RD, Tracy BF (2000) Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. Oecologia 123:116–121

Georgiadis NJ, McNaughton SJ (1988) Interactions between grazers and a cyanogenic grass, *Cynodon plectostachyus*. Oikos 51:343. https://doi.org/10.2307/3565316

Gill JL (2014) Ecological impacts of the late quaternary megaherbivore extinctions. New Phytol 201:1163–1169. https://doi.org/10.1111/nph.12576

Gosling CM (2014) Biotic determinants of heterogeneity in a South African savanna. University of Groningen, PhD

Gregory NC, Sensenig RL, Wilcove DS (2010) Effects of controlled fire and livestock grazing on bird communities in East African savannas. Conserv Biol 24:1606–1616. https://doi.org/10.1111/j.1523-1739.2010.01533.x

Hempson GP, Archibald S, Bond WJ et al (2015) Ecology of grazing lawns in Africa: African grazing lawns. Biol Rev 90:979–994. https://doi.org/10.1111/brv.12145

Hess AN, Hess RJ, Hess JLM et al (2014) American bison influences on lepidopteran and wild blue lupine distribution in an oak savanna landscape. J Insect Conserv 18:327–338. https://doi.org/10.1007/s10841-014-9640-x

Hobbs NT (1996) Modification of ecosystems by ungulates. J Wildl Manag 60:695. https://doi.org/10.2307/3802368

Johnson CN, Rule S, Haberle SG et al (2016) Geographic variation in the ecological effects of extinction of Australia's Pleistocene megafauna. Ecography 39:109–116. https://doi.org/10.1111/ecog.01612

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373. https://doi.org/10.2307/3545850

Kanga EM, Ogutu JO, Piepho H-P, Olff H (2013) Hippopotamus and livestock grazing: influences on riparian vegetation and facilitation of other herbivores in the Mara Region of Kenya. Landsc Ecol Eng 9:47–58. https://doi.org/10.1007/s11355-011-0175-y

Karki JB, Jhala YV, Khanna PP (2000) Grazing lawns in Terai Grasslands, Royal Bardia National Park, Nepal. Biotropica 32:423. https://doi.org/10.1646/0006-3606(2000)032%5b0423:GLITGR%5d2.0.CO;2

Kimuyu DM, Sensenig RL, Riginos C et al (2014) Native and domestic browsers and grazers reduce fuels, fire temperatures, and acacia ant mortality in an African savanna. Ecol Appl 24:741–749

Knapp AK, Blair John M, Briggs John M et al (1999) The keystone role of bison in North American tallgrass prairie Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. Bioscience 49:39–50

Lewison RL, Carter J (2004) Exploring behavior of an unusual megaherbivore: a spatially explicit foraging model of the hippopotamus. Ecol Model 171:127–138. https://doi.org/10.1016/S0304-3800(03)00305-3

Lewison R, Oliver W (IUCN SSC Hippo Specialist Subgroup) (2008) *Hippopotamus amphibius*. The IUCN red list of threatened species. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T10103A3163790.en. Accessed 6 Jan 2017

Lock JM (1972) The effects of hippopotamus grazing on grasslands. J Ecol 60:445. https://doi.org/10.2307/2258356

McCauley DJ, Dawson TE, Power ME, et al (2015) Carbon stable isotopes suggest that hippopotamus-vectored nutrients subsidize aquatic consumers in an East African river. Ecosphere 6:art52. https://doi.org/10.1890/es14-00514.1

McCauley DJ, Hardesty-Moore M, Halpern BS, Young HS (2016) A mammoth undertaking: harnessing insight from functional ecology to shape de-extinction priority setting. Funct Ecol. https://doi.org/10.1111/1365-2435.12728

McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92–94

McNaughton SJ (1983) Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol Monogr 53:291–320. https://doi.org/10.2307/1942533

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. Am Nat 124:863–886

McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. Ecol Monogr 55:259–294. https://doi.org/10.2307/1942578

Mehlich A (1984) Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun Soil Sci Plant Anal 15:1409–1416. https://doi.org/10.1080/00103628409367568

Olivier RCD, Laurie WA (1974) Habitat utilization by hippopotamus in the Mara River. Afr J Ecol 12:249–271

Owen-Smith NR (1988) Megaherbivores. Cambridge University Press, Cambridge

Painter EL, Detling JK, Steingraeber DA (1993) Plant morphology and grazing history. Vegetatio 106:37–62

Person BT, Herzog MP, Ruess RW et al (2003) Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–592

Pringle RM (2008) Elephants as agents of habitat creation for small vertebrates at the patch scale. Ecology 89:26–33

Ripple WJ, Newsome TM, Wolf C et al (2015) Collapse of the world's largest herbivores. Sci Adv 1:e1400103–e1400103. https://doi.org/10.1126/sciadv.1400103

Ross D, Ketterings Q (1995) Recommended soil tests for determining exchange capacity. In: Sims JT, Wolf A (eds) Recommended soil testing procedures for the northeastern United States. Northeastern Regional Bulletin #493. Ag Experiment Station, University of Delaware, Newark, pp 62–69

Ruess RW, Seagle SW (1994) Landscape patterns in soil microbial processes in the Serengeti National Park, Tanzania. Ecology 75:892–904. https://doi.org/10.2307/1939414

Schulte E, Hopkins B (1996) Estimation of soil organic matter by weight loss-on ignition. In: Magdoff FR, Tabatabai MA, Hanlon EA Jr (eds) Soil organic matter: analysis and interpretation. (ed) Special publication No. 46. Soil Sci. Soc. Am., Madison, WI, pp 21–32

Sensenig RL, Demment MW, Laca EA (2010) Allometric scaling predicts preferences for burned patches in a guild of East African grazers. Ecology 91:2898–2907

Sensenig RL, Kimuyu DK, Ruiz Guajardo JC et al (2017) Fire disturbance disrupts an acacia ant–plant mutualism in favor of a subordinate ant species. Ecology 98:1455–1464

Singer FJ, Schoenecker KA (2003) Do ungulates accelerate or decelerate nitrogen cycling? For Ecol Manag 181:189–204. https://doi.org/10.1016/S0378-1127(03)00133-6

Smith FA, Doughty CE, Malhi Y et al (2016a) Megafauna in the Earth system. Ecography 39:99–108. https://doi.org/10.1111/ecog.02156

Smith FA, Hammond JI, Balk MA et al (2016b) Exploring the influence of ancient and historic megaherbivore extirpations on the global methane budget. Proc Natl Acad Sci 113:874–879. https://doi.org/10.1073/pnas.1502547112

Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities. Bioscience 51:235–246. https://doi.org/10.1641/0006-3568(2001)051%5b0235:MFATSO%5d2.0.CO;2

Stock WD, Bond WJ, van de Vijver CADM (2010) Herbivore and nutrient control of lawn and bunch grass distributions in a Southern African savanna. Plant Ecol 206:15–27

Subalusky AL, Dutton CL, Rosi-Marshall EJ, Post DM (2015) The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. Freshw Biol 60:512–525. https://doi.org/10.1111/fwb.12474

Verweij RJT, Verrelst J, Loth PE et al (2006) Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. Oikos 114:108–116

Waldram MS, Bond WJ, Stock WD (2008) Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. Ecosystems 11:101–112. https://doi.org/10.1007/s10021-007-9109-9

Young TP, Patridge N, Macrae A (1995) Long-term glades in Acacia bushland and their edge effects in Laikipia, Kenya. Ecol Appl 5:97–108. https://doi.org/10.2307/1942055

Young HS, McCauley DJ, Helgen KM et al (2013) Effects of mammalian herbivore declines on plant communities: observations and experiments in an African savanna. J Ecol 101:1030–1041. https://doi.org/10.1111/1365-2745.12096

Zhao W, Chen S-P, Han X-G, Lin G-H (2009) Effects of long-term grazing on the morphological and functional traits of Leymus chinensis in the semiarid grassland of Inner Mongolia, China. Ecol Res 24:99–108. https://doi.org/10.1007/s11284-008-0486-0