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Vegetation Ecology

Megaherbivores suppress precipitation-driven plant irruptions in a tropical savanna

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Abstract

Irruptions in plant and animal populations are not uncommon, but the factors underlying irruptions are rarely explored quantitatively. In addition, it has been suggested that these irruptions may be reduced by predators or herbivores, but there is a paucity of controlled experimental evidence. Using data from the Kenya Long-term Exclosure Experiment (KLEE), we show that populations of perennial *Hibiscus* spp. (primarily *Hibiscus flavifolius*) show multiple short-term irruptions a year after rainy periods, increasing in abundance in some cases by more than an order of magnitude before declining in ensuing months and years. We demonstrate that these irruptions are largely limited to experimental plots from which large mammalian herbivores have been excluded, particularly megaherbivores (elephants, mostly). This represents a rare controlled, replicated experimental demonstration of top-down regulation of irruptions. African elephants and giraffes are often at greater risk of local extirpation than other large mammals, and their absence appears to destabilize this African savanna ecosystem.

KEYWORDS
elephants, giraffes, *Hibiscus*, Kenya, KLEE, Laikipia, stability

INTRODUCTION

Top-down effects have increasingly been identified as drivers of population, community, and ecosystem effects. Among chordates, this includes the keystone roles played by wolves (Gable et al., 2023; Ripple & Beschta, 2004), elephants (Dublin et al., 1990; Laws, 1970), giraffes (Parker & Bernard, 2005; Pellew, 1983), and sharks (Ferretti et al., 2010; Myers et al., 2007). These top-down effects have implications for conservation when they are driven by threatened taxa (Sinclair, 2003; Young et al., 2021) or anthropogenic introductions (Gordon et al., 2023; Parker & Bernard, 2005).

Episodic recruitment and sudden increases in population size are common in the natural world in both plants and animals, but the underlying drivers of their increases and subsequent declines are still poorly understood. The term "irruption," which is most often applied to animals and microorganisms, can simply indicate a sudden increase (Caughley, 1970; Leopold, 1943; Prugh et al., 2009) but can also be applied more specifically in situations where this increase is temporary (Brun et al., 2022; Chávez et al., 2019; Leopold, 1943; Miller et al., 2010).

In plants, episodic recruitment is not uncommon in arid and semi-arid ecosystems, where soil moisture conditions that are favorable to recruitment may only occur in rare (wetter) years, creating single-aged stands (Austin & Williams, 1988; Chávez et al., 2019; Holmgren et al., 2006; Young & Lindsay, 1988). The specific cues for episodic recruitment events are often reported in relatively general terms (i.e., "wet years"), and more detailed analyses of climatic drivers are uncommon (but see Austin & Williams, 1988; Pitt & Heady, 1978)—perhaps because long-term studies capable of documenting multiple irruption events over many years are rare (Reinke et al., 2019).

In plants, ephemeral rainfall-driven irruptions of annual plants in desert ecosystems (e.g., "super blooms") have been documented in a variety of terrestrial ecosystems (Chávez et al., 2019; Puritty et al., 2019; Wiegand et al., 2004). In aquatic systems, algal irruptions can occur (Deibel & Daly, 2007; Miller et al., 2010). Among perennial plants, shorter-duration recruitment events (ephemeral irruptions) and their underlying climatic triggers are less frequently documented (but see Austin & Williams, 1988). Episodic recruitment of perennial plant species does occur, but these events tend to produce longer-lasting effects and often have been characterized as non-ephemeral (long-term) threshold events (e.g., "Windows of Opportunity"), sometimes underlying regime shifts (Balke et al., 2014; Bond, 2008; Holmgren et al., 2006, 2013). In invertebrates, irruptions of locusts and conifer beetles have been, respectively, linked to rainfall (Zhang et al., 2019) and winter-temperature events (Jaime et al., 2024).

One source of regulation of irruptions is top-down suppression. In vertebrate animals, predator regulation of irruptions has been documented or suggested in both terrestrial and aquatic ecosystems (Myers et al., 2007; Prugh et al., 2009; Ramirez et al., 2024; Smith & Peterson, 2021; Wilmers et al., 2006), although with considerable variation in such regulation (Wilmers et al., 2020). Regulation of mammalian irruptions has been sometimes linked to climatic factors (Wilmers et al., 2020). Conversely, it has been proposed that top-down forces (carnivores or pathogens) are drivers of some irruptive predator–prey cycles (Newey et al., 2007, but see Barraquand et al., 2017). However, controlled replicated demonstrations are rare. In the field of biological control, top-down regulation of invertebrate pest population irruptions has been shown experimentally (Carson & Root, 2000; Murdoch et al., 2005), but such experiments are rare and exhibit variable results (Mills, 2018). In particular, herbivore suppression of plant irruptions has not been experimentally documented, perhaps because when such suppressive herbivory is present, no irruptions occur.

Here, we use a long-term exclosure experiment that uniquely allowed us to (1) document multiple ephemeral irruptions of sporadically abundant perennial semi-woody *Hibiscus* spp.; (2) explore the rainfall drivers of its episodic recruitment; and (3) experimentally demonstrate that large mammalian herbivores, in particular megaherbivores (>1000 kg), effectively suppress these irruptions.

STUDY SITE AND METHODS

This research was carried out from 2007 to 2024 in the Kenya Long-term Exclosure Experiment (KLEE), located on the property of the Mpala Research Centre (0°17′ N, 36°52′ E; 1800 m above sea level) in Laikipia, Kenya. Annual rainfall at the site is highly variable interannually and, during the study period, averaged 597 ± 196 mm/year (mean ± SD; range 330–1009 mm/year; Figure 1c). The intra-annual rainfall pattern is weakly trimodal, peaking in March–May. The study site is a semi-arid savanna ecosystem underlain with "black cotton" vertisol soils and dominated by the tree *Acacia [Vachellia] drepanolobium* Harms ex Sjöstedt and five grass species: *Pennisetum mezianum* Leeke, *Pennisetum stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf., and *Brachiaria lachnantha* (Hochst.) Stapf. (Young et al., 1997). Approximately 100 other species of plants occur at lower numbers in the plots, including several *Hibiscus* species (tab. S1 in Porensky et al., 2013). *Hibiscus* spp. are a sporadically abundant perennial semi-woody taxa in this ecosystem. Mpala is managed for both livestock production (at low to moderate densites) and wildlife conservation and supports a diverse variety of herbivores.

The KLEE experiment was established in 1995 and uses semi-permeable barriers to create six 200 × 200 m herbivore exclosure treatments replicated in three blocks, for a total of 18 plots. Treatments and abbreviations are as follows: O, all large (>25 kg) herbivores excluded; W,

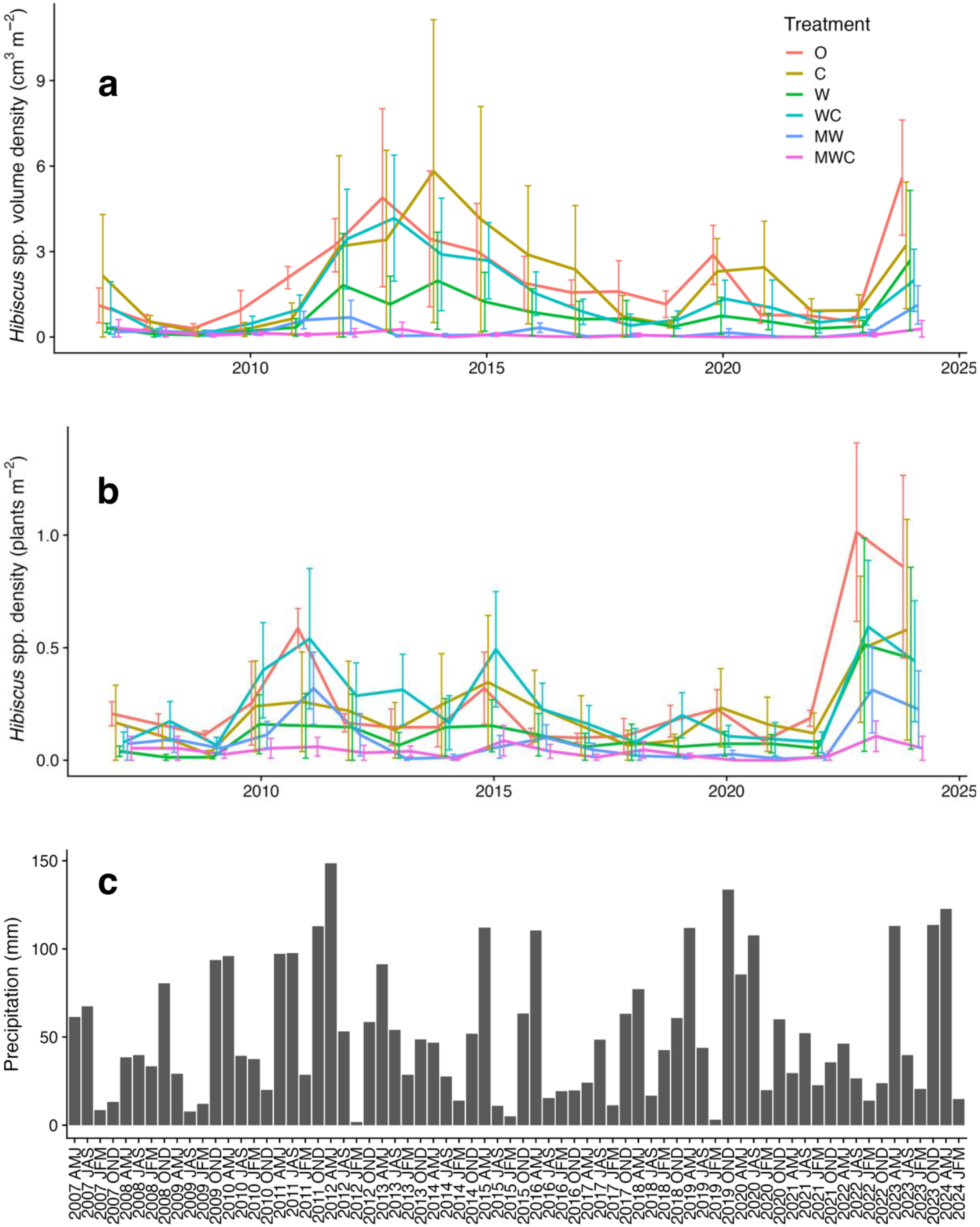

FIGURE 1 Legend on next page.

wild mesoherbivores present (25–1000 kg); C, cattle present (*Bos indicus* L.); WC, cattle and wild mesoherbivores present; MW, megaherbivores and wild mesoherbivores present; and MWC, all herbivores present (Young et al., 1997). In this ecosystem, the megaherbivores are elephants (*Loxodonta africana* Blumenbach) and giraffes (*Giraffa camelopardalis* L.). The mesoherbivores are represented by plains zebras (*Equus quagga* Boddaert), Grevy's zebras (*Equus grevyi* Oustelet), elands (*Tragelaphus oryx* Pallas), Grant's gazelles (*Nanger [Gazella] granti* Brooke), cape buffaloes (*Syncerus caffer* Sparrman), oryx (*Oryx beisa* Rüppell), and hartebeests (*Alcelaphus buselaphus* Pallas). Non-excluded mammalian herbivores (<25 kg) include steinbucks (*Raphicerus campestris* Thunberg), bush duikers (*Sylvicapra grimmia* L.), hares (*Lepus* spp.), and several rodent species.

Surveys of *Hibiscus* spp. were carried out in June of each year from 2007 to 2024 (approximately 2–3 months after peak rainfall). The two species represented in this data set, *Hibiscus flavifolius* Ulbr. and *Hibiscus aponeurus* Sprague and Hutch, are subject to occasional conspicuous irruptions, becoming temporarily dominant among the non-grass plant species. These two *Hibiscus* species are distinguishable only in flower and are lumped here. Both are single- to few-stemmed, semi-woody perennial herbs that can attain heights of 2–3 m. Based on the proportions of these two species observed flowering in the area, the great majority (>85%) of sampled plants were *H. flavifolius* (Ruiz-Guajardo et al., 2018). In each of the 18 KLEE plots, we counted the number and measured the heights of all these *Hibiscus* spp. plants in 50 1 × 1 m quadrats, located every 20 m along 10 parallel transects. As a proxy for plant biomass density, we estimated *Hibiscus* spp. cylindrical volume density (in cubic centimeters per square meter; volume density hereafter) by summing the volumes of all plants in each experimental plot before dividing by the sampled area. Cylindrical volumes of each plant were calculated as: $\pi \times \text{height} \times (\text{root collar diameter}/2)^2$. Because we did not measure root collar diameters of all *Hibiscus* spp. plants throughout the study period, we estimated these values based on the allometric relationship between root collar diameter and height. This relationship was estimated from all observed *Hibiscus* spp. plants in a 50 × 50 m subplot within each of the 18 treatment plots during a survey conducted in 2020, pooling across all treatments ($n = 497$ plants; linear regression, $F_{1,495} = 911.7$, $R^2_{\text{adj}} = 0.65$, $p < 0.001$; Appendix S1: Figure S1). This volume density estimate both complements and has advantages over numerical (count-based) density, which does not account for the large range in plant heights (1–330 cm), particularly if the height distributions vary by treatment and/or year. We report both volume density and numerical density.

Statistics

All statistical analyses were performed in R version 4.3.2 (R Core Team, 2023). To identify the months of rainfall that had the strongest influence on *Hibiscus* spp. density, we used the Bayesian functional linear regression with sparse step functions (BLiSS) framework (Grollemund et al., 2019), implemented through the *bliss* R package (Grollemund et al., 2019). BLiSS is a parsimonious method of identifying periods of time that most influence a scalar outcome (Grollemund et al., 2019). Because rainfall in the previous year may have lagged effects, particularly on perennial shrubs such as *Hibiscus* spp., we included monthly rainfall for 1–17 months prior to vegetation sampling (i.e., May of the sampling year to January of the year prior to sampling). We scaled and centered monthly precipitation and square-root transformed the *Hibiscus* spp. density prior to analysis. We set the number of intervals in the coefficient functions from the prior (hyperparameter *K*) equal to 2. We selected a low value of *K* to maintain parsimony and reduce overfitting (based on low Bayesian information criterion). Sensitivity analysis showed that the months identified as being most influential were not strongly influenced by values of *K* (Appendix S1: Figure S2). We sampled the posterior distribution using three Markov chain Monte Carlo (MCMC) chains. We ran each chain for 1200 iterations, discarding the first 200 as burn-in to yield 1000 samples per chain and 3000 posterior samples in total. We assessed MCMC chain convergence by visually inspecting trace plots and ensuring that the potential scale reduction factors for all parameters were <1.1 (Gelman & Rubin, 1992).

Here, we define irruptiveness as interannual variability (SD of annual density: σ). To evaluate the effect of

FIGURE 1 Times series of rainfall and *Hibiscus* spp. density in different herbivore treatments in the Kenya Long-term Exclosure Experiment (KLEE). In general, (a) volume density is driven by larger plants, while (b) count-based density is driven by smaller plants (mean ± SE; for detailed count distributions, see Appendix S1: Figure S3). O, all large (>25 kg) herbivores excluded; W, wild mesoherbivores present; C, cattle present; WC, cattle and wild mesoherbivores present; MW, megaherbivores (giraffes, elephants) and wild mesoherbivores present; MWC, all herbivores present. For visual clarity, (c) monthly rainfall is averaged over 3-month periods (AMJ, April/May/June; JAS, July/August/September; JFM, January/February/March; OND, October/November/December).

megaherbivores on *Hibiscus* spp. density and irruptiveness, we fit Gaussian linear mixed-effects models, square-root transforming to normalize. For irruptiveness (a metric that aggregates over time), we coded megaherbivore exclusion as the fixed effect and a random effect of the block. For *Hibiscus* spp. density (not aggregated over time), we coded megaherbivore exclusion, cumulative precipitation of the months that best predict *Hibiscus* density as identified by the BLiSS analysis (June–August of the previous year), and their interaction as the fixed effects and coded a nested random effect of the replicate block within year for density to account for temporal autocorrelation of repeated measurements across time. We included the interaction term because the effect of megaherbivores on *Hibiscus* spp. density may be mediated by precipitation, for example, by altering megaherbivore habitat use or the resistance/resilience of *Hibiscus* plants to herbivory. We fit all mixed-effects models using the *glmmTMB* package (Brooks et al., 2017).

RESULTS

Measured by both volume density (Figure 1a) and numeric density (Figure 1b), *Hibiscus* spp. exhibited three irruptions during the 18-year study period, as well as the apparent ending of a possible fourth irruption (at the beginning of the study; Figure 1a). The first (peaking in 2013–2014) and third (peaking in 2024) irruptions were of greater amplitude and duration than the second (peaking in 2020–2021). The densities of *Hibiscus* spp. in plots accessible to megaherbivores (MW and MWC) were significantly lower (−44%, 0.32 vs. 0.57 $\text{cm}^3\ \text{m}^{-2}$, $Z = -3.80$, $\text{df} = 317$, $p < 0.001$) and significantly less irruptive (lower interannual SD; −73%, 0.6 vs. 2.3, $Z = -2.77$, $\text{df} = 14$, $p = 0.006$; Figure 2) than in other herbivore treatments (O, C, W, and WC).

The Bayesian approach to identifying the month(s) of rainfall that best explain the temporal dynamics of *Hibiscus* spp. density (particularly in O and WC plots) identified June–August of the previous year (10–-12 months prior to sampling), followed by April (2 months prior to sampling) of the year of the surveys as the best predictors of these irruptions (note the high posterior probabilities in Figure 3). In particular, for treatments that excluded elephants (O, C, W, and WC), the month of precipitation that had the greatest statistical support for influencing *Hibiscus* spp. density was July of the previous year (i.e., 11 months prior to sampling), the strongest statistical support being for O and WC (posterior probabilities >0.5). However, in the two treatments accessible to elephants (MW and MWC), February of the sampling year (i.e., 4 months prior to sampling) and March of the previous year (i.e., 15 months prior to sampling) had the greatest statistical support for influencing *Hibiscus* spp. density, but neither was strongly supported statistically in these far less irruptive populations (posterior probabilities <0.5). Thus, *Hibiscus* spp. density in megaherbivore exclusion plots was generally lower, less variable, and less sensitive to precipitation compared with treatments accessible to elephants.

Cumulative June–August precipitation of the previous year did have a weak positive bottom-up effect on *Hibiscus* spp. density, which increased by 0.1 $\text{cm}^3\ \text{m}^{-2}$ for every 100 mm of rainfall ($Z = 1.89$, $\text{df} = 137$, $p = 0.059$). However, this was much weaker than the top-down effect of megaherbivores (−44%, 0.32 vs. 0.57 $\text{cm}^3\ \text{m}^{-2}$, $Z = -3.80$, $\text{df} = 317$, $p < 0.001$), which did not significantly interact with the effect of cumulative June–August precipitation of the previous year ($Z = -1.62$, $\text{df} = 137$, $p = 0.10$).

DISCUSSION

Rainfall triggers hibiscus irruptions

It is not surprising that increased precipitation increases the recruitment of some plant species in this semi-arid ecosystem (see also Porensky et al., 2013). In many other ecosystems in which sudden increases of certain plant species occur, rainfall has been proposed as the driving factor in the timing of the increase (Austin & Williams, 1988; Balke et al., 2014; Bond, 2008; Chávez et al., 2019; Deibel & Daly, 2007; Holmgren et al., 2013; Miller et al., 2010; Puritty et al., 2019; Wiegand et al., 2004). Greater-than-normal rainfall may trigger germination, allow establishment through critical initial seedling stages, and/or release a bud-bank or sapling bank. We do not have information allowing us to distinguish among these mechanisms for our *Hibiscus* spp.

Why the lag?

Although these irruptions apparently began in wet years, they did not peak until many months later, resulting in a statistical lag ("lag effects" or "legacy effects"); in this case, a lag of approximately one year (Figure 1b). For a similar but shorter term delay (in an Australian grassland), see Austin and Williams (1988). One possible mechanism for the delay in this study is that in wet years, many *Hibiscus* spp. seedlings are successfully recruited but do not achieve appreciable size (or contribute much to volume density) until the following year. This is supported by Figure 1b, which shows that the absolute density of *Hibiscus* spp. individuals (independent of size) does indeed peak at the beginning of an irruption (seedlings appearing in the high rainfall year). Vaughn and

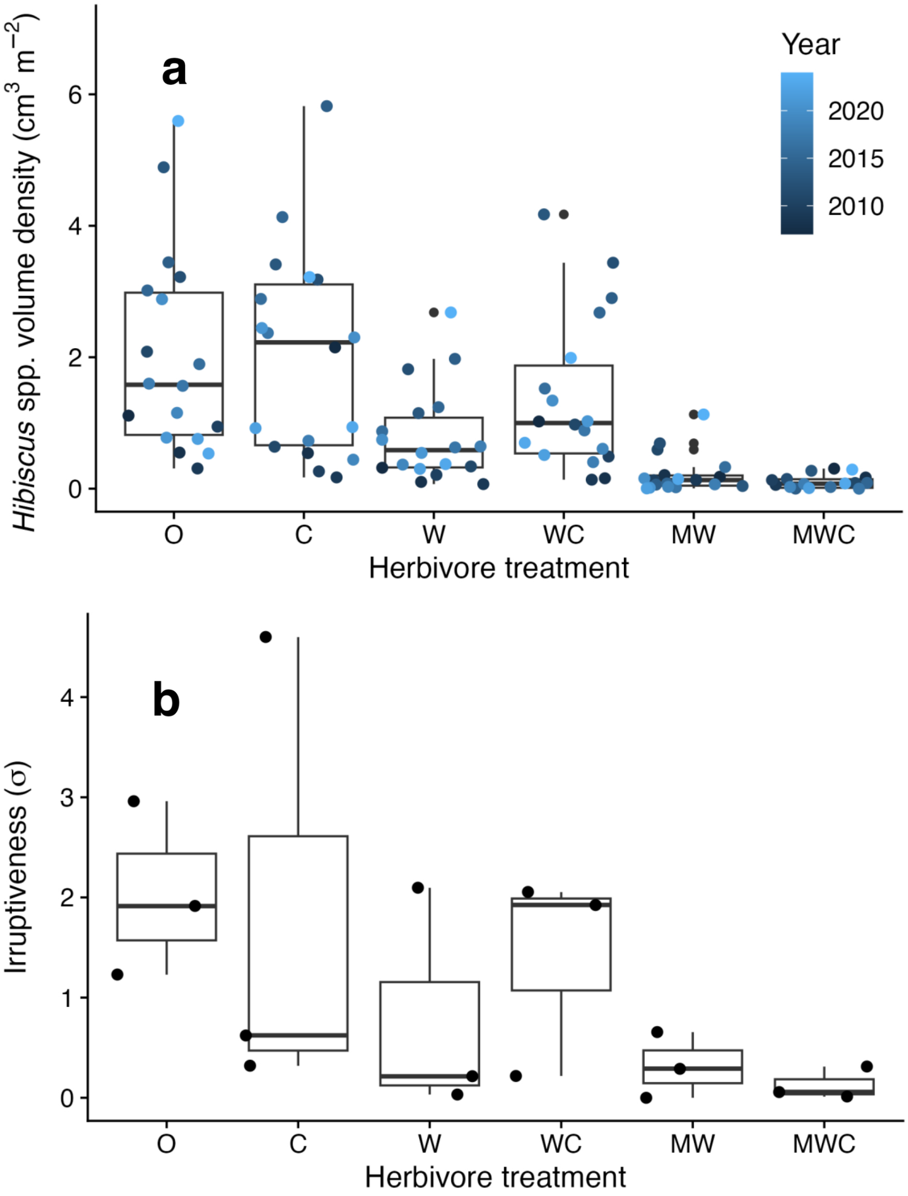

FIGURE 2 (a) Megaherbivores reduced *Hibiscus* spp. density, and (b) megaherbivores reduced the irruptiveness (interannual SD, σ) of *Hibiscus* spp. density. O, all large (>25 kg) herbivores excluded; W, wild mesoherbivores present; C, cattle present; WC, cattle and wild mesoherbivores present; MW, megaherbivores (giraffes and elephants) and wild mesoherbivores present; MWC, all herbivores present. Volume-based densities of *Hibiscus* spp. in plots accessible to megaherbivores (MW and MWC) were significantly lower ($Z = -9.82$, df = 319, $p < 0.001$) and significantly less irruptive (lower interannual SD [σ]; $Z = -2.77$, df = 14, $p = 0.009$) than in other herbivore treatments (O, C, W, and WC). Boxplots show the median (line), 25% and 75% quantiles (upper and lower hinges), and 1.5× the interquartile range (whiskers).

Young (2015) similarly reported that although recruitment of grasses occurred in the year of seeding (in a California prairie restoration setting), substantial overall abundance (cover) did not increase appreciably until the following years, when individuals made large gains in size.

What drives declines?

Even in herbivore treatments where there are substantial irruptions, *Hibiscus* spp. density eventually declines to very low levels (Figure 1b). We suggest three possible explanations, which are not mutually exclusive. (1) The non-megaherbivores (mesoherbivores, cattle, and the non-excluded smaller herbivores <25 kg) do not represent a high enough browsing pressure to completely prevent the irruptions but are sufficient to eventually consume (and/or trample) the established adults over the coming months and years. (2) Three to four years may represent the age of natural senescence of *Hibiscus* spp. individuals in single-aged stands (cf. Young & Lindsay, 1988). (3) We are observing some version of successional

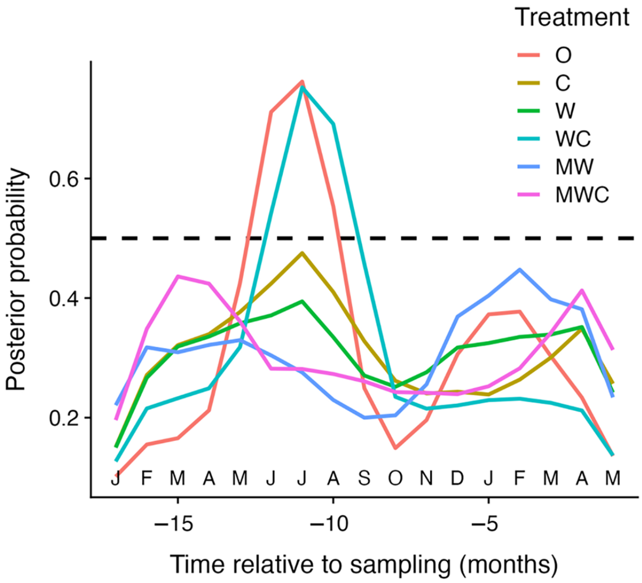

FIGURE 3 Lagged effects of rainfall on *Hibiscus* spp. density varied among herbivore treatments. Posterior probability exceeding 0.5 (dashed line) indicates strong statistical support.

turnover, where other perennial plant species, also triggered by the increased precipitation, but more slowly, eventually outcompete the *Hibiscus* spp.

Megaherbivores suppress irruptions, and *Hibiscus* generally

This study represents a rare controlled, replicated experiment on the role of top-down forces in regulating population dynamics, in particular irruptions. The model of Scheffer et al. (2008) suggests that top-down control can limit resource-driven pulses in plant population growth but only below some threshold of resource pulse. This is consistent with the pattern for the other herbivores in the assemblage (mesoherbivores and cattle) which may suppress *Hibiscus* except in high rainfall years but not for the megaherbivores, which managed to suppress *Hibiscus* irruptions even in these very favorable years.

Both elephants and giraffes have been identified as agents of ecological change (i.e., instability) through their ability to convert wooded communities to more open landscapes (Caughley, 1976; Dublin et al., 1990; Laws, 1970; Parker & Bernard, 2005; Pellew, 1983; Sinclair, 2003) and even eliminate certain plant species from communities (Young et al., 2022). In this study, however, megaherbivores represent a strong stabilizing force in community dynamics, at least with regard to *Hibiscus* irruptions.

Our experimental treatments do not distinguish between the effects of elephants and the effects of giraffes. However, giraffes rarely feed at heights lower than 1 m (Young & Isbell, 1991), and the *Hibiscus* spp. in our study are mostly less than 1 m tall (66%), especially in megaherbivore plots (99%; Appendix S1: Figure S3), so it is likely that elephants account for most of this suppression, most likely through direct herbivory.

Since all plots accessible to megaherbivores (MW and MWC) are also accessible to meso-wildlife, there is a possibility that wildlife species facilitated by megaherbivores may contribute to the suppression of *Hibiscus*. However, the presence of megaherbivores did not affect plot use by most other wildlife, although they did facilitate use by zebras (strict grazers), perhaps through their suppression of cattle foraging (Kimuyu et al., 2017) and decreased use by elands (mixed feeders) (Kimuyu et al., 2017; Wells et al., 2021). Therefore, the effects of megaherbivores on *Hibiscus* reported here are likely due to elephants themselves.

The impacts of (threatened) megaherbivores

We as yet have little information about the broader impacts of variation in *Hibiscus* abundance in this system, but *Hibiscus* spp. may provide ecosystem services, including providing pollination and food resources, which are likely to be reduced by large mammalian herbivores (see also Wilkerson et al., 2013). For example, at least 35 taxa of insects from five orders have been observed visiting the flowers of *H. flavifolius* and *H. aponeurus* (tab. S1 in Ruiz-Guajardo et al., 2018). In addition, fire intensity and severity in this system are strongly related to the abundance of fine woody fuels (Kimuyu et al., 2014), to which these *Hibiscus* spp. are likely to contribute when abundant.

This study adds to the rich literature documenting the important roles of individual species (Bond, 1993; Sinclair, 2003), in this case elephants. African elephants are currently under threat (Gobush et al., 2022; Muller et al., 2018), and their loss or even reduction may have multiple (often but not always negative) effects on ecosystem function and biodiversity (Bond, 1993; Young et al., 2021). The ability of megaherbivores to stabilize this African savanna ecosystem in the face of precipitation-driven plant irruptions provides yet another example of their impacts and the consequences associated with their loss.

AUTHOR CONTRIBUTIONS

Harry B. M. Wells: Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (lead); project administration (supporting);

validation (lead); visualization (lead); writing—original draft (lead). **Duncan M. Kimuyu:** conceptualization (supporting); investigation (equal); methodology (equal); project administration (lead); data curation (lead). **Kari E. Veblen:** Conceptualization (supporting); project administration (supporting); writing—original draft (supporting). **Truman P. Young:** Conceptualization (equal); project administration (lead); formal analysis (supporting); investigation (supporting); methodology (supporting); writing—original draft (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Wells et al., 2025) are available in Dryad: https://doi.org/10.5061/dryad.tb2rbp0bh.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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