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RESEARCH ARTICLE

Wild herbivores enhance resistance to invasion by exotic cacti in an African savanna

Harry B. M. Wells[1,2,3] | Ramiro D. Crego[1,4] | Jesse M. Alston[5,6] | S. Kimani Ndung'u[7] | Leo M. Khasoha[7,8] | Courtney G. Reed[7,9,10] | Abdikadir A. Hassan[7] | Samson Kurukura[7] | Jackson Ekadeli[7] | Mathew Namoni[7] | Peter S. Stewart[11] | Duncan M. Kimuyu[7,12] | Amelia A. Wolf[13] | Truman P. Young[7,14] | Tyler R. Kartzinel[7,9,10] | Todd M. Palmer[7,15] | Jacob R. Goheen[7,8] | Robert M. Pringle[16]

[1]Lolldaiga Hills Research Programme, Nanyuki, Kenya; [2]Sustainability Research Institute, School of Earth and Environment, University of Leeds, Leeds, UK; [3]Space for Giants, Nanyuki, Kenya; [4]National Zoo and Smithsonian Conservation Biology Institute, Conservation Ecology Center, Front Royal, Virginia, USA; [5]School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona, USA; [6]Center for Advanced Systems Understanding (CASUS), Görlitz, Germany; [7]Mpala Research Centre, Nanyuki, Kenya; [8]Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA; [9]Institute at Brown for Environment and Society, Brown University, Providence, Rhode Island, USA; [10]Department of Ecology, Evolution, and Organismal Biology, Brown University, Providence, Rhode Island, USA; [11]Department of Biosciences, Durham University, Durham, UK; [12]Department of Natural Resources, Karatina University, Karatina, Kenya; [13]Department of Integrative Biology, University of Texas, Austin, Texas, USA; [14]Department of Plant Sciences and Ecology Graduate Group, University of California, Davis, California, USA; [15]Department of Biology, University of Florida, Gainesville, Florida, USA and [16]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

Correspondence
Harry B. M. Wells
Email: harrybmwells@gmail.com

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Abstract

1. Whether wild herbivores confer biotic resistance to invasion by exotic plants remains a key question in ecology. There is evidence that wild herbivores can impede invasion by exotic plants, but it is unclear whether and how this generalises across ecosystems with varying wild herbivore diversity and functional groups of plants, particularly over long-term (decadal) time frames.
2. Using data from three long-term (13- to 26-year) exclosure experiments in central Kenya, we tested the effects of wild herbivores on the density of exotic invasive cacti, *Opuntia stricta* and *O. ficus-indica* (collectively, *Opuntia*), which are among the worst invasive species globally. We also examined relationships between wild herbivore richness and elephant occurrence probability with the probability of *O. stricta* presence at the landscape level (6150 km^2).
3. *Opuntia* densities were 74% to 99% lower in almost all plots accessible to wild herbivores compared to exclosure plots. *Opuntia* densities also increased more rapidly across time in plots excluding wild herbivores. These effects were largely driven by megaherbivores (≥1000 kg), particularly elephants.
4. At the landscape level, modelled *Opuntia stricta* occurrence probability was negatively correlated with estimated species richness of wild herbivores and

Harry B. M. Wells and Ramiro D. Crego contributed equally.

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elephant occurrence probability. On average, *O. stricta* occurrence probability fell from ~0.56 to ~0.45 as wild herbivore richness increased from 6 to 10 species and fell from ~0.57 to ~0.40 as elephant occurrence probability increased from ~0.41 to ~0.84. These multi-scale results suggest that any facilitative effects of *Opuntia* by wild herbivores (e.g. seed/vegetative dispersal) are overridden by suppression (e.g. consumption, uprooting, trampling).

5. *Synthesis*. Our experimental and observational findings that wild herbivores confer resistance to invasion by exotic cacti add to evidence that conserving and restoring native herbivore assemblages (particularly megaherbivores) can increase community resistance to plant invasions.

KEYWORDS
biotic resistance, elephants, invasion ecology, long-term exclosure experiments, megaherbivores, multi-trophic interactions, *Opuntia stricta*, prickly pear

1 | INTRODUCTION

Globally, invasive species are increasing in number, impacting ecosystems and human livelihoods (Pyšek et al., 2020). Because this problem is so pervasive, the characteristics of communities that resist invasion by exotic species is a major topic of research interest in basic and applied ecology (Gallien & Carboni, 2017; Zefferman et al., 2015). The enemy release hypothesis, which posits that the lack of natural enemies allows species to expand into new ecosystems, is often assumed to underlie competitive dominance by invasive species (Elton, 1958; Schulz et al., 2019). In some cases, however, interactions with resident species can reduce the severity of exotic invasions, termed 'biotic resistance' (Levine et al., 2004; Maron & Vilà, 2001). Community ecology theory also suggests that more taxonomically, phylogenetically and functionally diverse communities should be more resistant to invasions (Beaury et al., 2020; Funk et al., 2008; Funk & Wolf, 2016; Shea & Cheson, 2002). Despite empirical support for all of these ideas, the factors that shape variation in invasion severity are difficult to pinpoint. Specifically, geographic and taxonomic biases in the literature, scale effects and contradictions between experimental and observation studies leave a number of important questions unresolved.

Large mammalian herbivores play important roles in structuring plant communities (Bakker et al., 2016; Mortensen et al., 2018) and may confer biotic resistance to plant invasions in some situations (Maron & Vilà, 2001). Meta-analyses suggest that wild herbivores generally tend to suppress exotic plants and that herbivory is as important for controlling invasive plants as interspecific competition by native plants (Levine et al., 2004; Parker et al., 2006). In parts of Africa and Asia where diverse communities of large herbivores persist, including megaherbivores (≥1000 kg; Ripple et al., 2015), herbivory may have especially powerful effects on plant invasion dynamics. For example, a recent study from Gorongosa National Park, Mozambique, demonstrated that reestablishing wild herbivores increased resistance to invasion by the pantropical invasive shrub *Mimosa pigra* (Guyton et al., 2020).

However, it is unclear whether biotic resistance conferred by wild large herbivores is a widespread and general phenomenon across a wide range of ecological contexts (Maron & Vilà, 2001). In part, this is because global assessments are limited by a shortage of studies outside of North America, Europe, and Australasia (Lowry et al., 2013; Parker et al., 2006; Pyšek et al., 2012; Seabloom et al., 2015). In addition, wild and domestic ungulates can exert both negative (e.g. via consumption and trampling) and positive (e.g. dispersal, suppression of competitors) effects on exotic plant populations (e.g. Chuong et al., 2016; Vavra et al., 2007), making the net effect of these interactions difficult to predict. In some cases, invasive plants can repel native herbivores, reducing the likelihood of effective top-down control (Rozen-Rechels et al., 2017).

Tropical African savannas are thought to be among the most resistant ecosystems to biological invasions (Foxcroft et al., 2010). Nonetheless, many exotic plant species are well established across large parts of the continent, with significant ecological and economic consequences. For instance, the prickly pears *Opuntia stricta* and *O. ficus-indica* (hereafter collectively, *Opuntia*), the two most widespread invasive cacti globally (Novoa et al., 2015), are now among the top invasive plants in Africa (Foxcroft et al., 2010). *O. stricta* is considered one of the world's 100 worst invasive species (Lowe et al., 2004), impacting biodiversity (Oduor et al., 2010; Tesfay & Kreyling, 2021), livestock production and the rural communities dependent on these resources (Shackleton et al., 2017, 2019). Many of the ecosystems invaded by *O. stricta* support large-herbivore communities (Foxcroft et al., 2010; Foxcroft & Rejmánek, 2007; Strum et al., 2015), which may play significant roles in the cactus' invasion and population dynamics. Elephants *Loxodonta africana* and baboons *Papio* spp. are assumed to be major seed dispersers of *O. stricta* in southern and eastern African savannas (Foxcroft et al., 2004; Strum et al., 2015; Appendix S2), but the full extent of their roles in *O. stricta* invasions is unknown (Foxcroft & Rejmánek, 2007). Extant vectors of *Opuntia* seeds in their native ranges are diverse, including birds, reptiles, small mammals (i.e. rodents and lagomorphs), large mammals (e.g. bovids, cervids, and suids), canids and ants (Janzen, 1986;

Padrón et al., 2011). Many of these animals also consume cactus cladodes, which provide an important source of moisture and nutrients during dry periods (Chavez-Ramirez et al., 1997; Theimer & Bateman, 1992) and could lead to vegetative dispersal if animals drag, spit or regurgitate propagules. The net effect of facilitative (via dispersal) and suppressive (via consumption, uprooting, etc.) influences of animals on *Opuntia* populations remains a key management question, making *Opuntia* an important case study to investigate the degree of biotic resistance that diverse wild herbivore communities may provide.

To experimentally test whether wild herbivores confer resistance to *Opuntia* invasion, we used data from three different long-term (13- to 26-year) herbivore-exclusion experiments in a semi-arid savanna ecosystem in central Kenya, along with large-scale observational data from the surrounding landscape. Specifically, we addressed two questions: (i) How does the loss of different subsets of wild herbivore species affect the dynamics of the *Opuntia* invasion? (ii) Are the effects of wild herbivores on *Opuntia* observed in experimental plots also apparent at the landscape level? We evaluated two alternative hypotheses:

1. Wild herbivores have a net positive effect on the *Opuntia* invasion at both local and landscape levels because facilitation (e.g. seed/vegetative dispersal; Foxcroft et al., 2004; Strum et al., 2015) outweighs suppression (e.g. herbivory).
2. Wild herbivores have a net negative effect on the *Opuntia* invasion at both local and landscape levels because any positive effects (e.g. of dispersal) are outweighed by suppression via physical disturbance (e.g. uprooting, consumption, trampling).

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted our research in Laikipia, central Kenya. Laikipia County (8700 km^2) comprises a diverse mosaic of land uses, with more than two-thirds of the area dedicated to livestock production and/or wildlife conservation. *O. stricta* is the primary invasive cactus in Kenya and is particularly abundant in Laikipia (Witt et al., 2020), where it was first introduced by British colonists for use as living fences in Doldol village (*c.* 30 km east of our main study site) in the 1950s together with at least three other related species (*O. monacantha*, *O. ficus-indica*, and *Austrocylindropuntia subulata* [syn. *Opuntia exaltata*]; Strum et al., 2015). It has been proposed that sedentarization of pastoralists and associated increases in land degradation triggered expansion of the invasion around the early 2000s (Strum et al., 2015). With the goal of controlling the invasion, cochineal insects *Dactylopius opuntiae* were released as a biocontrol agent in 2014 (Witt et al., 2020). In Laikipia, local pastoralists perceive *O. stricta* as the greatest threat to livestock production and regard wild herbivores, primarily olive baboons *Papio anubis* and elephants, to be the main dispersers of the cactus (Shackleton et al., 2017).

2.2 | Experimental design

We collected data from three long-term herbivore-exclusion experiments at Mpala Research Centre in central Laikipia (0°17′N, 37°52′E, 1600-m elevation): Ungulate Herbivory Under Rainfall Uncertainty [UHURU, established in 2008 and consisting of 1-ha (100 × 100 m) plots; Alston et al., 2022; Goheen et al., 2013; Kartzinel et al., 2014], the Kenya Long-term Exclosure Experiment [KLEE, established in 1995 and consisting of 4-ha (200 × 200 m) plots; Riginos et al., 2012; Young et al., 2018], and the Glade Legacies And Defaunation Experiment [GLADE; established in 1999 and consisting of 0.49-ha (70 × 70 m) plots; Sankaran & Augustine, 2004]. UHURU and GLADE are both located on sandy luvisols dominated by *Acacia* (*Senegalia*) *brevispica*, *A.* (*S.*) *mellifera*, and *A.* (*Vachellia*) *etbaica*, whereas KLEE is located on adjacent heavy-clay vertisols dominated (*c.* 95%) by *A.* (*V.*) *drepanolobium*. To minimise the potentially confounding influence of rainfall (which increases from north to south across the study site) and propagule pressure (propagule supply and therefore cactus density are likely to decline with distance to the origin of the invasion; Foxcroft et al., 2004; Strum et al., 2015), we focused on the eight (of 12) GLADE plots and the 12 (of 36) UHURU plots proximate to the KLEE plots (Figure 1). Rainfall at Mpala Research Centre is weakly trimodal with a pronounced dry season from December–March. Between 2009 and 2021, annual rainfall averaged 579 mm $year^{-1}$ (range: 369–839 mm $year^{-1}$, inter-annual coefficient of variation: 24%) at the focal UHURU plots, 622 mm $year^{-1}$ (range: 420–1009 mm $year^{-1}$, inter-annual coefficient of variation: 30%) at KLEE, and 629 mm $year^{-1}$ (range: 324–1016 mm $year^{-1}$, inter-annual coefficient of variation: 30%) at a rain gauge close to GLADE.

We analysed *Opuntia* survey data for all treatments of the focal UHURU and GLADE plots. The focal UHURU plots consist of three replicates of four treatments (12 plots in total): (1) total exclusion of all large mammalian herbivores (LMH; from ≥1000-kg megaherbivores, elephant and giraffe, to 5-kg dik-dik *Madoqua guentheri*), (2) exclusion of both mesoherbivores (*c.* 10 to 1000 kg; i.e. larger than dik-dik) and megaherbivores (elephants and giraffes), (3) exclusion of megaherbivores only and (4) unfenced plots accessible to all herbivores. The GLADE exclosures are similar to the first of these UHURU treatments because they exclude all large mammalian herbivores. These GLADE exclosures are replicated four times (two of which contain treeless glades created by abandoned livestock corrals; Sankaran & Augustine, 2004) and are each paired with adjacent unfenced plots (eight plots in total). We note that in two (of four) GLADE exclosure-control pairs, the exclosure fences were removed in 2017 (5 years prior to sampling), which might diminish the effect of wild LMH exclusion; however, we included these plots according to their originally assigned treatments, which (a) is conservative with respect to our hypotheses that herbivores have strong effects (whether positive or negative) on *Opuntia* and (b) enables us to at least preliminarily evaluate whether herbivore 'reintroduction' rapidly homogenises *Opuntia* densities after nearly two decades of exclusion (cf. Coverdale et al., 2021). The KLEE plots consist of three replicates of three

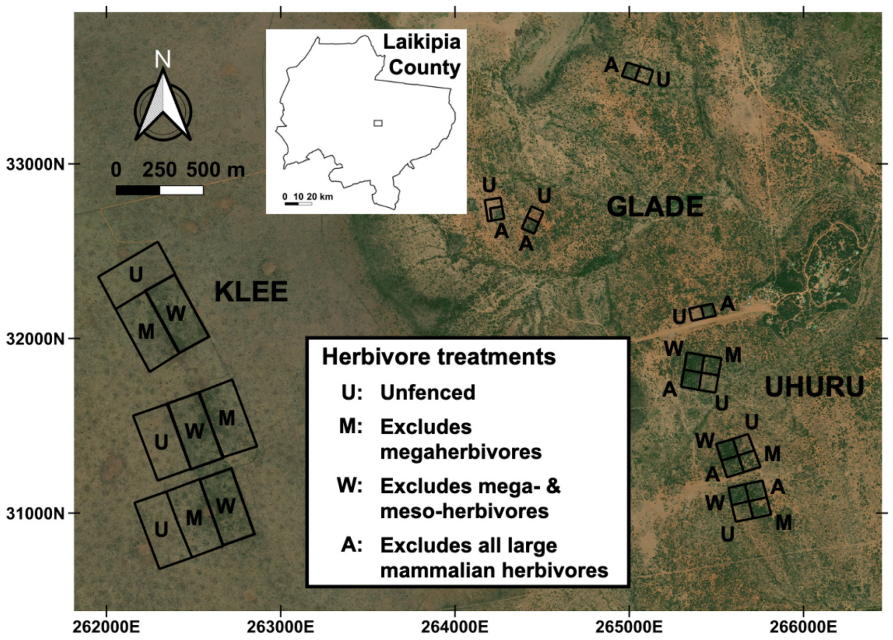

FIGURE 1 Map of study site illustrating the three exclosure experiments: UHURU (Ungulate Herbivory Under Rainfall Uncertainty), KLEE (Kenya Long-term Exclosure Experiment), and GLADE (Glade Legacies and Defaunation Experiment). Inset locates the exclosures (rectangle) within Laikipia County.

wild herbivore treatments, which are each crossed with livestock manipulation (one accessible to cattle and the other excluding cattle, for a total of 12 plots): (1) exclusion of meso- and mega-herbivores, (2) exclusion of only megaherbivores and (3) unfenced plots accessible to all herbivores (Figure 1). In KLEE, cattle had no detectable effect on the combined volumetric density of the two *Opuntia* (median difference in volume = 0.4 cm^3 ha^{-1}, 89% credible intervals [CRI] = [−5.4, 6.4]; see next paragraph on how volumetric density was measured). Accordingly, and due to the low *Opuntia* densities (six of the 12 4-ha plots had fewer than five plants), we summed *Opuntia* density in the three wild herbivore treatments, irrespective of cattle presence/absence, effectively resulting in six 8-ha plots. This resulted in a total of 29 plots (19 exclosures and 10 unfenced controls) across the three experiments (Figure 1). For further details of these experiments and their environmental contexts, see Goheen et al. (2013, 2018), Alston et al. (2022), Sankaran and Augustine (2004), and Young et al. (2018).

2.3 | Data collection

To estimate cactus density (as volume per unit area), we conducted surveys of *Opuntia* in January 2021 (UHURU), January 2022 (KLEE), and March 2022 (GLADE). To estimate cactus volume, we measured the height and canopy dimensions (widest axis and its perpendicular) of each *Opuntia* plant. We calculated cylindrical volume for each plant as: $\pi \times$ height $\times$ (width/2) $\times$ (depth/2), summing across all plants within each plot to estimate total *Opuntia* volume. To ensure comparability between the three experiments, we calculated the volumetric density (hereafter, simply 'density') of *Opuntia* by dividing the total plot-level cactus volume by the surveyed area in each plot (the central 0.36 ha for UHURU; 8 ha for KLEE; the central 0.25 ha for GLADE) to quantify *Opuntia* density in m^3 ha^{-1}.

Additionally, at UHURU (but not KLEE or GLADE), we counted all Opuntia plants taller than 1 m within the central 0.36 ha (60 × 60 m) of each 1-ha plot as part of annual vegetation surveys between 2009, when there were zero plants >1 m tall in any of the treatments, and 2021 (excluding 2010, 2011 and 2015; Alston et al., 2022). Permission to conduct fieldwork was granted by Kenya's National Commission of Science, Technology and Innovation (permit number: NACOSTI/P/19/70975/31058).

2.4 | Data analysis

To test the effect of wild herbivore exclusion on *Opuntia* densities (log-transformed for normality) in 2021/2022, we fit an ANOVA (for UHURU and KLEE) and a Gaussian t-test with unequal variances (for GLADE). Given the limited number of experiments and replicates (plots) and the differences in experimental duration and soil type, we fit separate models for each of the three experiments.

To evaluate the effect of megaherbivore exclusion on the number of *Opuntia* plants across the years surveyed in UHURU (2009–2021), we fit a negative binomial analysis of covariance (ANCOVA) model. Negative binomial models are robust to overdispersion, which is common in count data (Hui, 2016). Using a log link allowed us to model the nonlinear growth of the number of *Opuntia* plants as the invasion progressed between 2009 and 2021. We model the interaction between herbivore treatment and survey year.

For all models, we sampled the posterior distribution using three Markov Chain Monte Carlo (MCMC) chains, each run for 30,000 iterations. We discarded the first 10,000 iterations as burn in and thinned by 20 to yield 1000 samples per chain and 3000 posterior samples in total. We assessed the performance and convergence of the MCMC chains by visually inspecting the posterior traces, inspecting effective sample sizes, and ensuring that the potential scale

reduction factor values for all regression parameters were <1.1 (Gelman & Rubin, 1992). We visually confirmed normality and homoscedasticity of Pearson residuals, and ensured that the posterior predictive distribution fit the data well by checking that the Bayesian p-value was close to 0.5 (Gelman et al., 2013).

We evaluated the posterior statistical support (i.e. the proportion of posterior samples for which the focal effect occurs) for the effect of a predictor variable being either positive or negative. For example, if the effect of megaherbivores on *Opuntia* density is positive, the posterior support is the proportion of posterior samples >0, which can be interpreted as the probability of the effect of megaherbivores on *Opuntia* density being positive. Posterior support, therefore, indicates the probability that a focal effect occurs, while credible intervals provide an indication of the uncertainty surrounding the estimated mean value. As proposed by McElreath (2020) we use 89% credible intervals, which represent the intervals within which the mean value lies with 89% probability. The 89% credible intervals are more stable than the equally arbitrary 95% level (Kruschke, 2015).

All statistical analyses were performed in R version 4.1.2 (R Core Team, 2021) and all models fit using NIMBLE package version 0.12.2 (de Valpine et al., 2017).

2.5 | Landscape-level analysis

To explore the relationship between wild herbivores and *O. stricta* at the landscape level, we used estimates of *O. stricta* occurrence probability (from data in Wells et al., 2021) and of elephant occurrence and large herbivore species richness (from data in Crego et al., 2020) at a resolution of 5×5 km across 6150 km^2 of savanna rangeland (*c.* 70% of Laikipia County).

We generated predictive maps of *O. stricta* occurrence at 30×30 m (900 m^2) resolution by associating satellite imagery (all eight bands of Landsat 8 tier 1 surface reflectance scenes) with *O. stricta* presence/absence data from 654 random 1000-m^2 sampling locations using a machine-learning algorithm, extreme gradient boosting (Wells et al., 2021). Then, to facilitate comparison with the wild herbivore data, we averaged the occurrence probability of *O. stricta* over the same 5×5 km cells as the elephant occupancy and large herbivore species richness datasets.

Species richness of an assemblage of 15 common herbivore species was estimated at 5×5 km grid cells using 8 years of data from aerial surveys (February–March of 2001, 2004, 2006, 2008, 2010, 2012, 2015 and 2016) and multi-species occupancy models (Crego et al., 2020). The 15 species included buffalo *Syncerus caffer*, elephant *Loxodonta africana*, oryx *Oryx beisa*, common warthog *Phacochoerus africanus*, waterbuck *Kobus ellipsiprymnus*, eland *Tragelaphus oryx*, gerenuk *Litocranius walleri*, Grant's gazelle *Nanger granti*, Grevy's zebra *Equus grevyi*, hartebeest *Alcelaphus buselaphus*, impala *Aepyceros melampus*, ostrich *Struthio camelus*, plains zebra *Equus quagga*, giraffe *Giraffa camelopardalis*, and Thomson's gazelle *Eudorcas thomsonii*. Annual species-specific occupancy probabilities were estimated as functions of distance to permanent water, vegetation productivity (Normalised Difference Vegetation Index) and livestock abundance. Species richness for each year was calculated by summing the number of estimated herbivore species occurring in each cell. For more details on data collection and model specifications, see Crego et al. (2020).

To account for the potential effect of distance to the origin of the invasion, we extracted herbivore species richness and *O. stricta* occurrence probability within an 80-km radius around the origin of the invasion (Doldol village; Strum et al., 2015), beyond which predicted *O. stricta* occurrence probability declines (Appendix S1: Figure S1). We also excluded upland forest habitat, restricting the analysis to savanna habitats to improve comparability with the experimental plots. This resulted in 246 5×5 km cells. We averaged estimated herbivore species richness and elephant occurrence probability across the 8 years to account for effects of interannual variability. Finally, we explored relationships using Spearman's rank correlation coefficients (ρ).

3 | RESULTS

We recorded a total of 1827 *Opuntia* plants (1813 *O. stricta* and 14 *O. ficus-indica*) across all 29 experimental plots (total surveyed area of 78.3 ha) in 2021/2022. Sandy luvisols (UHURU and GLADE) had on average >1000 times higher *Opuntia* volumetric densities than clay-rich vertisols (KLEE). In UHURU, *Opuntia* densities increased super-linearly from 0 in 2009 to 47 plants ha^{-1} in 2021 (for volumes of individual cacti and a comparison of volume- and count-based cactus densities see Appendix S1: Figures S2 and S3).

3.1 | Wild herbivores suppress invasive cacti

Consistent with our second hypothesis, we found that exclusion of wild herbivores generally resulted in higher *Opuntia* densities and counts across all three experiments. Regarding megaherbivore effects, in the sandy luvisol soils (UHURU), our model showed a 95% posterior probability that plots excluding elephant and giraffe had higher *Opuntia* density than unfenced plots (megaherbivore-excluded, median = 21.2×10^6 cm^3 ha^{-1}, 89% CRI = [8.4×10^6, 55.6×10^6]; unfenced, median = 5.8×10^6 cm^3 ha^{-1}, 89% CRI = [2.2×10^6, 14.3×10^6]; Figure 2). Likewise, in the clay-rich vertisol soils (KLEE), our model showed an 87% posterior probability that plots excluding megaherbivores had higher *Opuntia* densities than unfenced plots (megaherbivore-excluded, median = 24,506 cm^3 ha^{-1}, 89% CRI = [146, 4.2×10^6]; unfenced, median = 197 cm^3 ha^{-1}, 89% CRI = [1.2, 34,150]; Figure 2).

Exclusion of all large mammalian herbivores (i.e. all species ≥5 kg) in UHURU produced similar results to the exclusion of megaherbivores (elephant and giraffe) alone. Our model showed 99% and 92% posterior probabilities that plots excluding all LMH had higher *Opuntia* density than unfenced plots for both UHURU (LMH-excluded,

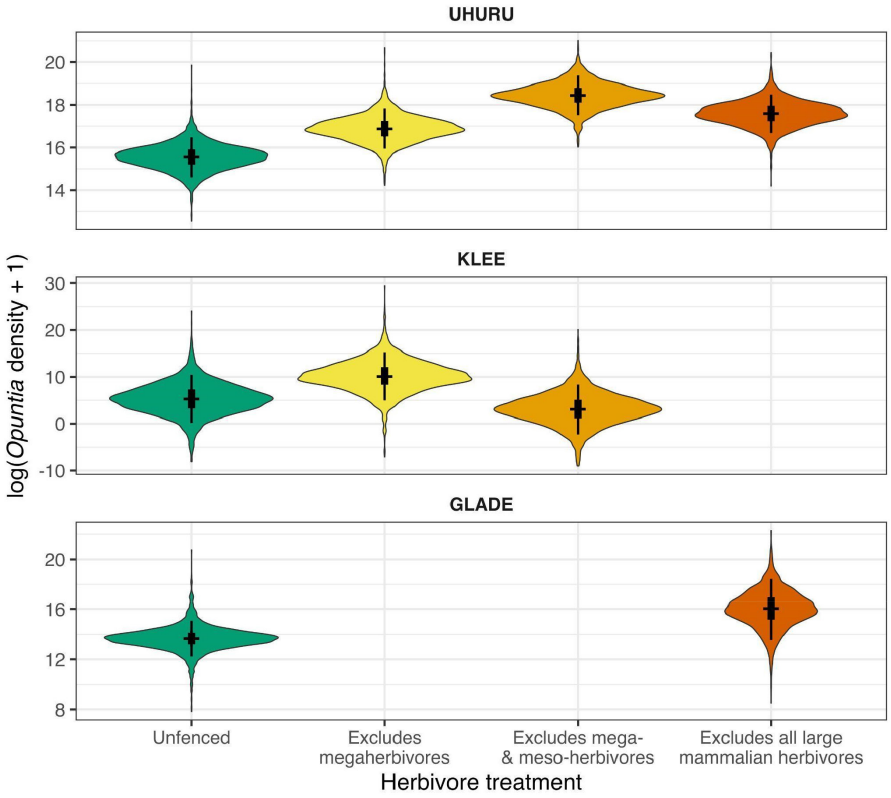

FIGURE 2 Response of *Opuntia* volumetric density ($cm^3\ ha^{-1}$) to wild herbivore exclusion. Distribution of the 3000 posterior samples illustrated by violin plots and boxplots. In the boxplots, the horizontal line indicates the median, while the filled box and error bars represent the 50% and 89% credible intervals, respectively. UHURU ($n = 12$; 12 years since establishment) and GLADE ($n = 8$; 22 years since establishment) overlie sandy luvisols, while KLEE ($n = 9$; 26 years since establishment) is located on clay-rich vertisols. Sampling conducted *c*. 70 years after *Opuntia* cacti were introduced in the landscape.

median = 43.4×10^6 $cm^3\ ha^{-1}$, 89% CRI = [17.4×10^6, 106.4×10^6]; unfenced, median = 5.8×10^6 $cm^3\ ha^{-1}$, 89% CRI = [2.2×10^6, 14.3×10^6]; Figure 2) and GLADE plots, respectively (LMH-excluded, median = 9.4×10^6 $cm^3\ ha^{-1}$, 89% CRI = [0.9×10^6, 105.1×10^6]; unfenced, median = 0.9×10^6 $cm^3\ ha^{-1}$, 89% CRI = [0.2×10^6, 3.7×10^6]; Figure 2).

Similarly, for UHURU, our model showed a nearly 100% posterior probability that plots accessible to all wild herbivores had lower *Opuntia* density than plots excluding both mesoherbivores and megaherbivores (mesoherbivore-excluded, median = 102.1×10^6 $cm^3\ ha^{-1}$, 89% CRI = [40.3×10^6, 260.5×10^6]; unfenced, median = 5.8×10^6 $cm^3\ ha^{-1}$, 89% CRI = [2.2×10^6, 14.3×10^6]; Figure 2). This effect was slightly greater than that of excluding megaherbivores alone, indicating a marginal additional effect of medium-sized ungulates. However, results from KLEE showed only 30% posterior probability that plots accessible to mesoherbivores had lower *Opuntia* density than plots excluding mesoherbivores (mesoherbivore-excluded, median = 22.1 $cm^3\ ha^{-1}$, 89% CRI = [0.1, 4364]; unfenced, median = 197 $cm^3\ ha^{-1}$, 89% CRI = [1.2, 34,150]; Figure 2).

In UHURU, the increase in the number of *Opuntia* plants per plot through time was more rapid in all three treatments that excluded wild herbivores than the treatment accessible to all wild herbivores (Figure 3). Although no cacti were recorded in any of the treatments in 2009, by 2021 the megaherbivore-exclusion treatment had a median of 13.0 more individual plants per plot (89% CRI = [7.2, 22.1]) in the fitted model than the unfenced treatment, a 383% difference. These patterns were somewhat stronger for the treatment that excluded both mesoherbivores and megaherbivores, in which the

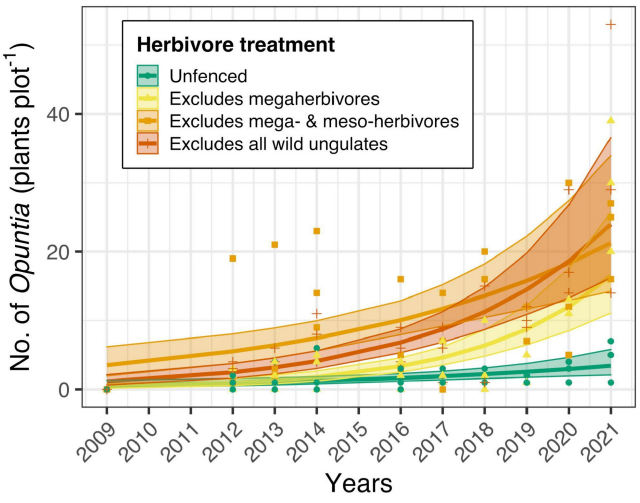

FIGURE 3 Temporal dynamics of *Opuntia* density (>1 m tall) in UHURU's herbivore treatments (medians ±89% credible intervals). Note that the zero values can include multiple overlapping data points.

fitted model had a median of 17.8 more plants per plot by 2021 (89% CRI = [10.3, 29.3]) compared to the treatment accessible to all wild herbivores (526% difference). Further excluding the smallest wild ungulates (i.e. dik-dik) had a similar effect to excluding both mesoherbivores and megaherbivore, with a median of 20.5 more plants per plot by 2021 (89% CRI = [12.4, 33.8]) compared to the treatment accessible to all wild herbivores (606% difference).

Consistent with these experimental results (and our second hypothesis), we found a negative correlation ($\rho = -0.30$, $p < 0.001$)

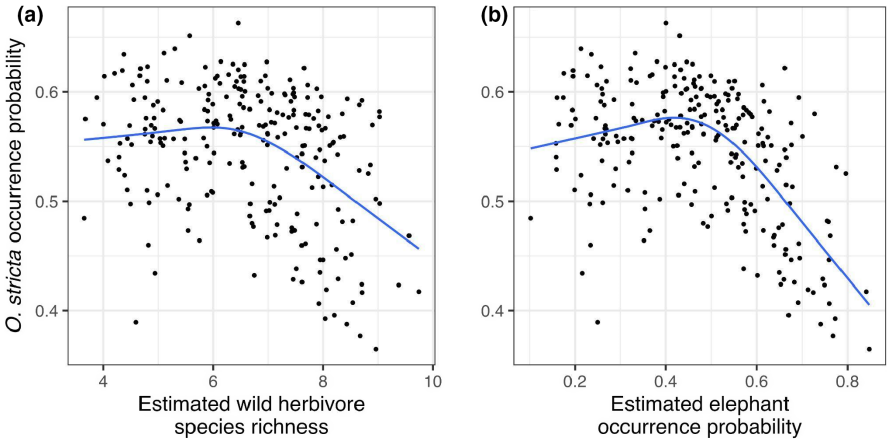

FIGURE 4 Correlation between predicted *Opuntia stricta* occurrence probability (from Wells et al., 2021) and (a) wild herbivore species richness and (b) elephant occurrence probability (from Crego et al., 2020) across a 6150 km^2 landscape at 5 × 5 km spatial resolution. Blue line shows a generalised additive model trend.

between modelled *O. stricta* occurrence probability and estimated wild herbivore species richness at the landscape scale, across a 6150 km^2 area (Figure 4a). The correlation between modelled occurrence probabilities of *O. stricta* and occupancy probabilities of elephants alone was even stronger ($\rho = -0.41$, $p < 0.001$; Figure 4b).

4 | DISCUSSION

Both experimental and landscape-scale observational data indicate that native herbivores enhance the resistance of East African savannas to *Opuntia* invasion. When megaherbivores were excluded, *Opuntia* densities were many times higher than in neighbouring plots that remained accessible to megaherbivores, and occurrence probabilities of *O. stricta* and elephants were anticorrelated in the surrounding savannas. Smaller native ungulates (*c.* 5 to 1000 kg) exerted small additive effects in reducing *Opuntia* densities, and species richness of wild herbivore communities was correlated with reduced *Opuntia* occurrence at the landscape scale. These results indicate that large mammalian herbivores confer biotic resistance to invasive plants and suggest that reintroducing wild herbivores or restoring their populations may have substantial benefits for invasive plant management. Herbivore-mediated biotic resistance is predicted to occur when (1) specialist herbivores consume a large proportion of an exotic plant (Maron & Vilà, 2001); (2) generalist native herbivores preferentially consume an exotic plant (Levine et al., 2004) and/or (3) an exotic plant is evolutionarily naïve and not well defended against generalist native herbivores (Parker et al., 2006). Our results may be influenced by the third process, although *Opuntia* do share a co-evolutionary history with large mammal communities that included Proboscideans (Janzen, 1986).

Wild herbivores' suppression of *Opuntia* might be direct and/or indirect. Direct suppression of the cacti could occur via consumption or physical disturbance. Anecdotally, we have observed elephants, bushbuck *Tragelaphus scriptus*, and hippopotamus *Hippopotamus amphibius* eating *Opuntia* cladodes in Laikipia (Figure 5; Appendix S3), but the frequency and intensity of these interactions is unclear. Extensive analysis of large-herbivore diets at Mpala Research Centre using faecal DNA metabarcoding (Kartzinel et al., 2015, 2019; Kartzinel & Pringle, 2020) did not detect *O. stricta* and detected *O. ficus-indica* only at very low levels in the diets of several species (elephant, hippopotamus, buffalo, dik-dik, and bush hyrax *Heterohyrax brucei*). However, this discrepancy likely reflects a negative bias arising from mismatches with the PCR primers used in those studies rather than a lack of herbivory (Stapleton et al., 2022; Weinstein et al., 2021). Further research is therefore needed to quantify the frequency and impacts of direct consumption and trampling of *Opuntia* by large herbivores in Laikipia. Notably, even low levels of damage to relatively sparse and slow-growing species may effectively suppress growth and dispersal. In other dryland ecosystems with higher cactus densities, a related species, *O. lindheimeri*, can comprise 55% of the diet of white-tailed deer *Odocoileus virginianus* (Everitt & Gonzalez, 1979) and 74% of the diet of collared peccaries *Dicotyles tajacu* (Everitt et al., 1981). In semi-arid Ethiopian rangelands, *O. stricta* and *O. ficus-indica* were among the top five most frequently consumed plants by elephants (Biru & Bekele, 2012). Herbivory of cacti by native herbivores in African savannas may, therefore, be sufficient to suppress *Opuntia* densities.

Wild herbivores may also indirectly suppress *Opuntia* by altering competitive/facilitative interactions between native and exotic plants (Maron & Vilà, 2001). For example, megaherbivores may suppress cacti indirectly by reducing the densities of trees (Guldemond & Van Aarde, 2008) that could otherwise have facilitated *Opuntia* invasion. Trees can reduce herbivory via concealment (Louthan et al., 2014), associational refugia (Coverdale et al., 2016), and creating favourable microclimates. Such associational effects are well documented for columnar cacti elsewhere in the world (Rojas-Aréchiga & Vázquez-Yanes, 2000). Trees can also attract seed dispersers, such as baboons and birds (Foxcroft & Rejmánek, 2007). The improved edaphic conditions beneath trees can also enhance germination, a process from which *O. stricta* appears to benefit (Novoa et al., 2021). Whether changes in native plant diversity, biomass, and/or nursing mediate the observed suppression of *Opuntia* by herbivores requires further investigation. For example, neighbour-removal experiments conducted inside and outside of exclosures could be used to disentangle the direct and indirect effects of herbivores (Coverdale et al., 2019; Louthan et al., 2014).

FIGURE 5 Camera trap images of *Opuntia stricta* being uprooted and consumed by elephants *c*. 5 km from the experimental exclosures, dated 12–14 March 2021. Cladodes of uprooted cacti can root, but our findings suggest that this vegetative reproduction does not compensate for the stress of damage/uprooting. Images obtained from an unpublished dataset collected by Peter S. Stewart, Peter Leidura, and Ibrahim Adan as part of a project funded by the NERC Iapetus2 Doctoral Training Program and the Durham Invasion Science Laboratory.

Our results suggest that, overall, negative effects of the herbivore assemblage on *Opuntia* outweigh positive effects, whether direct (e.g. long-range seed dispersal or short-range vegetative dispersal; Foxcroft & Rejmánek, 2007; Strum et al., 2015) or indirect (e.g. suppression of seed-predating rodents; Dudenhoeffer & Hodge, 2018). The net negative effects are evinced by the time series of *Opuntia* densities, which provided insights into the number of cacti taller than 1 m that established and survived in each herbivore treatment over time, and on volumetric *Opuntia* density, which provided an integrative snapshot of establishment and growth by cacti of all sizes after years of herbivore exclusion. Furthermore, the landscape-level patterns aligned with the experimental results, as seen from the association of higher herbivore richness and higher elephant occupancy probability with lower *O. stricta* occurrence probability. These correlative results suggest that our experimental findings are scalable and offer a broader picture of how herbivores in general and elephants in particular influence cactus distribution in the surrounding savannas. This correspondence between experimental and landscape-scale patterns is noteworthy given that studies of biotic resistance at different scales often produce contrasting results (Beaury et al., 2020).

While all but one of the herbivore-exclusion treatments led to higher *Opuntia* densities, the removal of megaherbivores accounted for the majority of this effect (Figure 2–3). It is likely that elephants dominate the megaherbivore effect because giraffes do not appear to consume or destroy the cacti based on their foraging behaviour (Kartzinel et al., 2019; O'Connor, 2015). The predominant effect of megaherbivores also suggests that wild herbivore communities are unlikely to resist invasions as effectively if megaherbivores are absent. Topographical features that deter megaherbivore activity, such as steep terrain, could therefore act as refugia for the cacti, as is the case for native woody flora (Freeman et al., 2022; Kimuyu et al., 2021). Alternatively, it is also possible that the megaherbivore exclusion effect is influenced by domestic camels, which are known to consume *Opuntia* (pers. obs.). This could occur if camels regularly enter the unfenced plots but not the megaherbivore-exclusion treatments, however, there is little evidence for this (Appendix S1: Table S1).

Although megaherbivores appeared to dominate the effect of excluding wild herbivores, further removal of mesoherbivores (including a number of browsing bovid species) did result in slightly higher *Opuntia* density (except KLEE). This suggests that the mesoherbivore community also contributes to invasion resistance in the absence of megaherbivores. Similar lack of functional redundancy has been documented among mammalian browser size classes in regulating encroachment by native woody plants at our study site (Coverdale et al., 2021; Pringle et al., 2014). For example, model-based inferences by Pringle et al. (2014) predicted that megaherbivores are always net suppressors of the encroaching shrub *Solanum campylacanthum* despite potential dispersal benefits, whereas the net effect of mesoherbivores was predicted to depend on the magnitude of the dispersal benefit. The absence of an additional effect

of mesoherbivore exclusion on *Opuntia* density in KLEE may be because cacti have not colonised the mesoherbivore-exclusion treatment in two of three replicate blocks (they are near-absent from the surrounding habitat matrix of KLEE). In the block where the cactus has established, the treatment excluding mesoherbivores had higher densities than the unfenced plot.

4.1 | Implications for invasion ecology

Studies on herbivore-induced biotic resistance to invasive plants are dominated by invasive herbaceous or woody plants and rarely include succulents such as cacti (Guyton et al., 2020; Levine et al., 2004; Parker et al., 2006), several of which are among the most damaging invasive plant species in the world (Novoa et al., 2015). The control of *Opuntia* by wild herbivores demonstrated by this study echoes a similar effect reported for encroachment by a native climbing succulent (*Cynanchum viminale*; Coverdale et al., 2021), but whether this is a generalisable pattern for other native and nonnative succulents requires further investigation.

In central Kenya, it has been suggested that *Opuntia* have expanded as a consequence of overgrazing by livestock, which creates microsites suitable for establishment (Strum et al., 2015). However, our findings suggest the hypothesis that indirect facilitation of *Opuntia* by livestock may be mediated more by the suppression of wild herbivores that tends to accompany livestock production (Crego et al., 2020; Wells, Crego, Ekadeli, et al., 2022) than by the reduction of competition with native understory plants. It may be that cactus establishment is hampered by competition with understory vegetation in herbivore exclosures during the early stages of invasion (as observed in a related species, *O. fragilis*; Burger & Louda, 1994), but that this effect is later overshadowed by herbivore-induced suppression (Levine et al., 2004). Unfortunately, we lack data during the relevant window for UHURU (2010–2011) and, by 2012, most (10/12) plots had at least one cactus >1 m tall.

One unanswered question is why the *Opuntia* invasion at Mpala Research Centre has (marginally) increased through time even in plots accessible to all herbivores, which suggests a limit to the efficacy of biotic resistance as noted elsewhere (e.g. Maron & Vilà, 2001). Elephant densities have been largely stable in the area throughout the study period (Ogutu et al., 2016), and anthropogenic drivers such as pastoralist sedentarization are not present at Mpala. Evaluating trends over longer time-scales will be necessary to tease apart the influence of potential contributing factors such as climate and atmospheric CO_2 enrichment (Drennan & Nobel, 2000).

By synthesising long-term experimental and landscape-scale observational data, our study provides unique insights into the role of wild herbivores in conferring resistance to invasion by exotic cacti. At the local level, *Opuntia* densities are higher in areas where large mammalian herbivores are experimentally excluded. Our findings at the scale of experimental plots are mirrored at the landscape level, where *O. stricta* occurrence probability is lower in areas where large herbivore species richness and elephant occurrence probability are higher. Our findings add to previous work on herbivore-mediated biotic resistance (Foxcroft et al., 2010; Guyton et al., 2020; Levine et al., 2004; Parker et al., 2006) highlighting that intact wild herbivore communities (particularly megaherbivores) can play an important role in enhancing resistance to exotic plant invasions. The strategy of enhancing ecological integrity by restoring native herbivores assemblages may be an effective means to control exotic species invasions and complement other approaches, such as mechanical removal and introducing nonnative biocontrol agents, which can be costly, ineffective, and/or involve significant ecological risks (Schulz et al., 2019).

AUTHOR CONTRIBUTIONS

Harry B. M. Wells and Ramiro D. Crego conceived the study, led the writing of the manuscript and analysed the data. Harry B. M. Wells, S. Kimani Ndung'u, Abdikadir A. Hassan, Mathew Namoni, Jackson Ekadeli, Leo M. Khasoha, Courtney G. Reed and Jesse M. Alston conducted the fieldwork and prepared the datasets. Truman P. Young, Jacob R. Goheen and Robert M. Pringle designed and established the exclosures. Peter S. Stewart provided camera trap images. All authors made significant contributions to the drafts and approved it for publication.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.sbcc2fr9q (Wells, Crego, Alston, et al., 2022).

ORCID

Harry B. M. Wells https://orcid.org/0000-0001-5463-9297
Ramiro D. Crego https://orcid.org/0000-0001-8583-5936
Jesse M. Alston https://orcid.org/0000-0001-5309-7625
Peter S. Stewart https://orcid.org/0000-0001-6338-6279
Truman P. Young https://orcid.org/0000-0002-7326-3894
Tyler R. Kartzinel https://orcid.org/0000-0002-8488-0580
Robert M. Pringle https://orcid.org/0000-0001-7487-5393

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