RESEARCH ARTICLE

# Experimental evidence that effects of megaherbivores on mesoherbivore space use are influenced by species' traits

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## Abstract

1. The extinction of 80% of megaherbivore (>1,000 kg) species towards the end of the Pleistocene altered vegetation structure, fire dynamics and nutrient cycling world-wide. Ecologists have proposed (re)introducing megaherbivores or their ecological analogues to restore lost ecosystem functions and reinforce extant but declining megaherbivore populations. However, the effects of megaherbivores on smaller herbivores are poorly understood.

2. We used long-term exclusion experiments and multispecies hierarchical models fitted to dung counts to test (a) the effect of megaherbivores (elephant and giraffe) on the occurrence (dung presence) and use intensity (dung pile density) of mesoherbivores (2–1,000 kg), and (b) the extent to which the responses of each mesoherbivore species was predictable based on their traits (diet and shoulder height) and phylogenetic relatedness.

3. Megaherbivores increased the predicted occurrence and use intensity of zebras but reduced the occurrence and use intensity of several other mesoherbivore species. The negative effect of megaherbivores on mesoherbivore occurrence was stronger for shorter species, regardless of diet or relatedness.

4. Megaherbivores substantially reduced the expected total use intensity (i.e. cumulative dung density of all species) of mesoherbivores, but only minimally reduced

the expected species richness (i.e. cumulative predicted occurrence probabilities of all species) of mesoherbivores (by <1 species).

5. Simulated extirpation of megaherbivores altered use intensity by mesoherbivores, which should be considered during (re)introductions of megaherbivores or their ecological proxies. Species' traits (in this case shoulder height) may be more reliable predictors of mesoherbivores' responses to megaherbivores than phylogenetic relatedness, and may be useful for predicting responses of data-limited species.

## 1 | INTRODUCTION

Populations of megaherbivores (i.e. herbivores >1,000 kg) have declined steeply as a consequence of the expansion of humans across the planet. Hunting by Neolithic humans contributed to extinctions of about 80% of the ~45 megaherbivore species present during the Pleistocene (Sandom et al., 2014; Smith et al., 2018). Over the last century, extant megaherbivores have undergone geographic range contractions, in many cases resulting in either actual or functional local extinctions (Ripple et al., 2015). Of the nine extant megaherbivore species, three are critically endangered, one is endangered, four are vulnerable and one is near threatened, and all are restricted to sub-Saharan Africa and southern Asia (Ripple et al., 2015).

The reduction or disappearance of megaherbivores and other large mammals is thought to have had a substantial impact on ecosystem structure and function, affecting vegetation structure (Gill et al., 2009), seed dispersal (Campos-Arceiz & Blake, 2011), carbon fluxes (Doughty, Wolf, et al., 2016), methane budgets (Smith et al., 2010), nutrient cycling (Doughty, Roman, et al., 2016), fire regimes (Waldram et al., 2008) and soil biota (Andriuzzi & Wall, 2018). Most studies of megaherbivore effects have focused on vegetation responses (Kerley et al., 2008). For example, elephants and giraffes reduce tree densities (Bond & Loffell, 2001; Guldemond & Van Aarde, 2008) and elephants also alter the relative abundances of grasses and forbs (Coverdale et al., 2016; Odadi et al., 2009; Veblen et al., 2016). However, the effects of megaherbivores on other fauna, such as mesoherbivores (2–1,000 kg), are poorly understood (le Roux et al., 2018).

Because mesoherbivores also shape their environments (Ford et al., 2014, 2015; Veblen et al., 2016), their interactions with megaherbivores should influence the degree to which megaherbivore defaunation affects ecosystem structure and function. There is some evidence that the responses of mesoherbivores to megaherbivores is influenced by species' traits such as diet (Fritz et al., 2002) and body size (Valeix et al., 2011). Phylogenetic relatedness may also predict whether megaherbivores compete with or facilitate mesoherbivores (Kartzinel et al., 2015). However, most evidence of megaherbivore–mesoherbivore interactions comes from short-term observational studies, which may not capture the net effects of megaherbivores that can be revealed through long-term experimental manipulations (Fritz, 2017).

Where megaherbivores and mesoherbivores still coexist, experimental manipulations enable tests of the effects of megaherbivore loss (Bakker et al., 2016; Bakker & Svenning, 2018). Conversely, long-term exclosure experiments can also elucidate the potential consequences of megaherbivore reintroductions. In central Kenya, a network of long-term exclosures provide a unique opportunity to study the potential consequences of such reintroductions and evaluate the net effects of megaherbivores on mesoherbivores over decadal time-scales. However, previous analyses of data from these exclosures have yielded mixed results, with both positive and negative impacts of megaherbivores on use intensity (measured as dung pile density) by wild mesoherbivores (Goheen et al., 2013, 2018; Kimuyu et al., 2017).

To better understand the effect of megaherbivores on the mesoherbivore community, we combined two 12-year datasets from two separate long-term experimental manipulations of extant megaherbivores (elephants and giraffes) that span an aridity gradient in central Kenya. We incorporated new information on animal diets (Kartzinel et al., 2019; Kartzinel & Pringle, 2020) and leveraged recent developments in multispecies statistical modelling (Tikhonov et al., 2020) to address the following questions: How do megaherbivores affect occurrence and use intensity of mesoherbivores and to what extent are these effects predictable based on the traits and phylogenetic relatedness of the mesoherbivores? Our results provide new insights into megaherbivore–mesoherbivore interactions and allow us to infer the potential ecological effects of megaherbivore reintroduction.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We conducted work at Mpala Research Centre (0°17′N, 36°52′E, 1,800 m a.s.l.) in Laikipia, Kenya, and collected data from two

herbivore exclusion experiments—the Kenya Long-term Exclosure Experiment (KLEE; Riginos et al., 2012; Young et al., 2018) and the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment (Goheen et al., 2013; Kartzinel et al., 2014). KLEE (established in 1995) consists of 4-ha plots on heavy-clay vertisols, while UHURU (established in 2008) consists of 1-ha plots on adjacent sandy luvisols (Figure 1; Figure S1). The clay soils are dominated (~95%) by *Acacia (Vachellia) drepanolobium*, while the sandy soils are dominated by *A. (Senegalia) mellifera*, *A. (Vachellia) etbaica* and *A. (Senegalia) brevispica* (mean tree densities are reported in Table S1). Some mesoherbivore species are commonly recorded on both clay and sandy soils (e.g. zebra *Equus* spp., eland *Tragelaphus oryx* and buffalo *Syncerus caffer*), while others are recorded predominantly (hares *Lepus* spp., impala *Aepyceros melampus* and warthog *Phacochoerus africanus* on sandy soils) or almost exclusively (e.g. hartebeest *Alcelaphus buselaphus*, oryx *Oryx beisa*, Grant's gazelle *Nanger granti*, duiker *Sylvicapra grimmia* and steenbok *Raphicerus campestris* on clay soils; dik-dik *Madoqua guentheri* and waterbuck *Kobus ellipsiprymnus* on sandy soils) on one soil type (Goheen et al., 2013; Kimuyu et al., 2017). UHURU consists of three sites spanning a 20-km rainfall gradient, with less rainfall in the north and more in the south. KLEE is ~2.5 km west of UHURU's southern site and has similar rainfall. Rainfall is weakly trimodal with a pronounced dry season spanning between December and March. Annual rainfall averaged 613 mm/year (range: 421–1,099 mm/year, inter-annual coefficient of variation: 27%) at KLEE between 2001 and 2019, and 601, 576 and 519 mm/year (ranges: 369–910, 235–785 and 200–749 mm/year, inter-annual coefficient of variation: 26, 30 and 29%) at UHURU's southern, central and northern sites, respectively, between 2009 and 2019 (Figure 1). For further details of these experiments and their environmental contexts, see Goheen et al. (2018), Pringle et al. (2016), and Young et al. (2018).

Here, we focus on two treatments common to KLEE and UHURU: (a) plots excluding wild megaherbivores (elephant and giraffe) and (b)

plots accessible to all wild herbivores. These two treatments are replicated once each in 12 blocks (three in KLEE and nine in UHURU), for a total of 24 plots. The 12 blocks are clustered in four locations or 'sites', with three blocks per site (KLEE: one site and UHURU: three sites; Figure 1).

## 2.2 | Data collection

Dung count surveys provide a robust metric of occurrence and relative use intensity within species (Kimuyu et al., 2017; Riginos & Grace, 2008)—the latter metric incorporates information on the number of animals and the duration of use, but not separately. We could reliably distinguish the dung of eight of the 12 mesoherbivore species included in this study, as confirmed by molecular verification of field identifications. Dung was not distinguished for four pairs of species: two zebra species (plains zebra *Equus quagga* and Grevy's zebra *E. grevyi*) two hare species (*Lepus capensis* and *L. saxatilis*; Kartzinel et al., 2019), cattle/buffalo (*Bos indicus* and *Syncerus caffer*) and duiker/steenbok (*Sylvicapra grimmia* and *Raphicerus campestris*). A camera trapping study in KLEE (Wells, Kimuyu, et al., 2021) indicated that the number of independent detections (images separated by at least 1 hr) per trap night for plains zebra is 81 times that of Grevy's zebra for the treatments analysed in this study. The number of independent detections per trap night for duiker and buffalo were, on average, over three times that of steenbok and cattle respectively (Wells, Kimuyu, et al., 2021). For species pairs whose dung were not distinguishable, these differences in camera trap detections provide an indication of the contributions of each species to the combined dung of both species.

No duiker/steenbok dung was recorded at UHURU, but buffalo/cattle and plains/Grevy's zebras were present in both experiments. Because Grevy's zebra are more common on sandy soils (Zero et al., 2013), the contribution of Grevy's zebra dung to
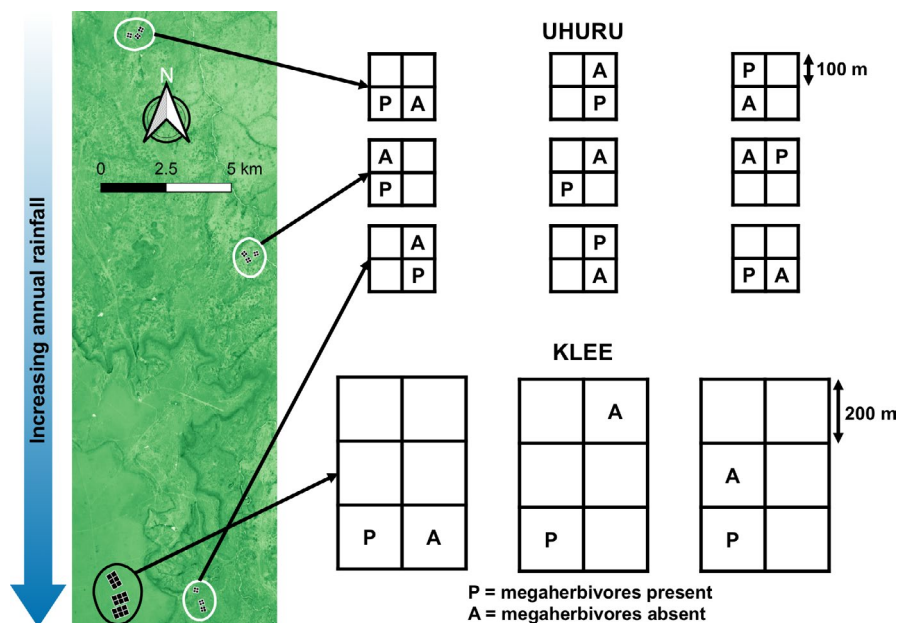


**FIGURE 1** Study area and experimental layout. Location of the Kenya Long-term Exclosure Experiment (KLEE; black circle) and Ungulate Herbivory Under Rainfall Uncertainty (UHURU; white circles) experiment plots (24 plots within 12 blocks). Map shows 2015–2020 annual mean normalized difference vegetation index (NDVI) from Sentinel-2 images (darker green indicates greater primary productivity). Megaherbivores (>1,000 kg) = elephants and giraffes

dung recorded as plains/Grevy's zebra may be higher in UHURU compared to KLEE, although plains zebras still predominate. The contribution of cattle dung to dung recorded as buffalo/cattle at UHURU is unknown but is also likely to be dominated by buffalo as observed via camera trapping in KLEE. The proportion of dung from the two hare species, *L. capensis* versus *L. saxatilis*, was not possible to infer from camera trap data because these species are difficult to distinguish visually. In sum, based on the camera trap data, cattle and steenbok are likely to be contributing more to dung identified as 'buffalo' and 'duiker', respectively, relative to Grevy's zebra's contribution to dung identified as 'zebra' (i.e. plains and Grevy's zebras collectively).

Within KLEE, dung surveys were conducted along six 4 × 100 m permanent transects twice per year (March–May and September–November). Within UHURU, dung surveys were conducted along three 5 × 60 m permanent transects quarterly from 2008 to 2015 and every other month from 2016 to 2020. We counted fresh and old dung, crushing it to prevent recounting in subsequent surveys. Dung decay rates can bias estimates of habitat use but are not affected by treatments in KLEE (Riginos, 2015) or UHURU (Goheen et al., 2013). Ratios of new to old dung may be expected to decline with longer time periods between surveys if old dung accumulates. However, for the mesoherbivore species with sufficient data (>20 observations; i.e. buffalo, dik-dik, hares, impala, warthog, zebras), there was no detectable relationship between the ratio of new to old dung and the time elapsed since the previous survey (with the marginal exception of impala, for which the relationship approached statistical significance; Table S2). This indicates that most recorded dung (both 'old' and 'new') is deposited within the 1–2 months prior to each survey. We therefore conclude that the differences in sampling frequency between KLEE and UHURU (and within UHURU) surveys did not bias total dung counts (old plus new dung). Moreover, Riginos (2015) found that imperfect detection of dung is minimal in these narrow (4- or 5-m) transects that are thoroughly surveyed. Further details of the dung survey methodology are described elsewhere for KLEE (Kimuyu et al., 2017) and UHURU (Goheen et al., 2013).
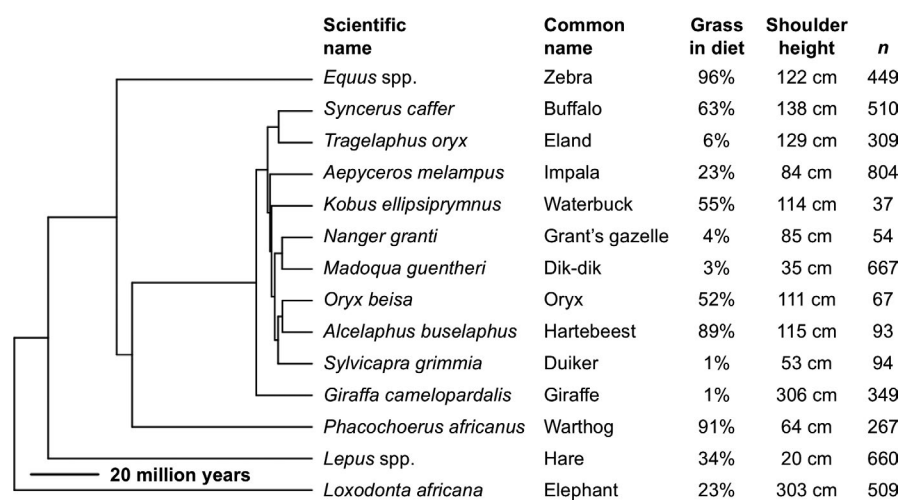
## 2.3 | Data analysis

We analysed the data by fitting a joint species distribution model (Warton et al., 2015) using the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen et al., 2017). By statistically borrowing information from other species with similar traits or evolutionary histories (Abrego et al., 2017), HMSC allows inclusion of rare species with insufficient data for single-species analyses (Ovaskainen et al., 2017). The integration of traits (diet and shoulder height) and phylogeny into the analyses facilitates extrapolating results to other systems with different but related or functionally similar species.

To ensure that dung data were comparable between experiments, we summed species-specific dung counts (old and new) within plots, and then calculated dung density (piles 900 m$^{-2}$) using the area surveyed (KLEE: 2,352 m$^2$/plot and UHURU: 900 m$^2$/plot). We analysed data from a total of 81 surveys (KLEE: 24 surveys and UHURU: 57 surveys) spanning 12 years (2009–2020). We treated unique surveys of each plot as a 'sampling occasion', yielding 1,170 sampling occasions (KLEE: 144 sampling occasions and UHURU: 1,026 sampling occasions). We excluded mesoherbivore species whose dung was recorded in <10 sampling occasions, leaving 12 species (Figure 2).

Due to the zero-inflated nature of the data, we chose a hurdle approach comprising one model for occurrence probability (hereafter, 'occurrence models') and another for the intensity of use conditional on presence (hereafter, 'use intensity models'). We define 'occurrence probability' as the proportion of sampling occasions with at least one dung pile recorded, and we define 'use intensity' as the density of dung piles where at least one dung pile was recorded (i.e. conditional on occurrence). We calculated predicted species richness for each posterior sample by summing the expected species-specific occurrence probabilities of all 12 species from the occurrence model. We calculated predicted total use intensity for each posterior sample by summing the expected species-specific use intensities conditional on occurrence from the use intensity model. We calculated community-weighted mean trait values (for diet and shoulder height) for each posterior sample by multiplying



**FIGURE 2** Traits (diet and shoulder height), phylogeny and sample sizes of the species studied. Trait values (from Kartzinel et al., 2019; Kartzinel & Pringle, 2020) are averaged across members of species groups. *n* = number of unique surveys of each treatment plot in which a species' dung was recorded, out of the 1,170 unique plot-survey combinations

| Scientific name | Common name | Grass in diet | Shoulder height | *n* |
|---|---|---|---|---|
| *Equus* spp. | Zebra | 96% | 122 cm | 449 |
| *Syncerus caffer* | Buffalo | 63% | 138 cm | 510 |
| *Tragelaphus oryx* | Eland | 6% | 129 cm | 309 |
| *Aepyceros melampus* | Impala | 23% | 84 cm | 804 |
| *Kobus ellipsiprymnus* | Waterbuck | 55% | 114 cm | 37 |
| *Nanger granti* | Grant's gazelle | 4% | 85 cm | 54 |
| *Madoqua guentheri* | Dik-dik | 3% | 35 cm | 667 |
| *Oryx beisa* | Oryx | 52% | 111 cm | 67 |
| *Alcelaphus buselaphus* | Hartebeest | 89% | 115 cm | 93 |
| *Sylvicapra grimmia* | Duiker | 1% | 53 cm | 94 |
| *Giraffa camelopardalis* | Giraffe | 1% | 306 cm | 349 |
| *Phacochoerus africanus* | Warthog | 91% | 64 cm | 267 |
| *Lepus* spp. | Hare | 34% | 20 cm | 660 |
| *Loxodonta africana* | Elephant | 23% | 303 cm | 509 |

20 million years

species-specific trait values by the proportional contribution of that species to predicted richness or total use intensity in the occurrence and use intensity models, respectively, then summing the resulting values across all species.

The hurdle approach also allowed us to assess differences in the effect of megaherbivores on mesoherbivore presence versus use intensity. For the occurrence model, we fitted a probit regression model to the dung density data, truncating values >1 dung pile 900 m$^{-2}$ to 1 to indicate presence. For the use intensity model, we applied a log-normally over-dispersed Poisson regression to dung density. Because the model is conditional on species being present, all absence data (zeros) are declared as missing data (NAs). This two-part model overcomes zero inflation issues while assessing potential contrasting effects of megaherbivores on mesoherbivore occurrence and use intensity (Mullahy, 1986). Statistically supported megaherbivore effects on mesoherbivore use intensity but not occurrence probability can occur if megaherbivores alter use intensity on sampling occasions in which a mesoherbivore species is present, while occurrence probability across all sampling occasions remains constant.

To test the effect of megaherbivores, we coded 'megaherbivores (present/absent)' as the fixed effect. Use intensities of the two megaherbivore species, elephants and giraffes, were also determined via the same dung surveys as the mesoherbivores. However, we focused on the effects of megaherbivore accessibility per se because we were interested in their overall effects over the long-term rather than short-term fluctuations in their use intensities. There was no difference in elephant use intensity in megaherbivore-accessible plots between the KLEE and UHURU experiments (ANOVA, $F_{1,4} = 3.53$, $p = 0.135$), but giraffe use intensity in KLEE was two times that of UHURU (ANOVA, $F_{1,4} = 42.2$, $p = 0.002$).

Because the study plots for both KLEE and UHURU are small relative to the home ranges of mesoherbivores, individuals can move among plots. To account for potential pseudoreplication and unmeasured environmental variation at the level of blocks and plots (e.g. soil qualities, plant species) and individual sampling occasions (e.g. weather), we coded a nested random-effect structure comprising 'sampling occasion within plot, within block, within time' (time = months since January 2009; i.e. the first year of dung survey dataset analysed). We used temporally structured latent variables with a negative-exponential function to account for any temporal autocorrelation resulting from the repeated measures design (Ovaskainen et al., 2016).

To examine the influence of traits and phylogeny on species' responses to megaherbivores, we examined the effects of diet (proportional grass consumption recorded at our study site; Kartzinel et al., 2019), shoulder height (from Kingdon et al., 2013) and phylogenetic distance according to a dated phylogenetic tree (Upham et al., 2019) on mesoherbivore responses to megaherbivores. The effects of traits and phylogeny are measured by different parameters. To assess the influence of traits, we evaluated the proportion of among-species variation in species' responses to megaherbivores explained by traits (Abrego et al., 2017). The

parameter measuring phylogenetic signal takes values between 0 (no influence of phylogenetic relatedness on species' responses to megaherbivores) and 1 (variation in species' responses to megaherbivores is fully structured by phylogeny, with more closely related species responding more similar to megaherbivores than expected by random). For those species pairs for which dung could not be attributed to a single species, we averaged species' traits and used phylogenetic data for the most common species. Further details of the model structure and the statistical framework used are presented in Appendix S1.

All statistical analyses were performed in R version 3.6.2 (R Core Team, 2019). We fitted the HMSC model using the Hmsc package version 3.0 (Tikhonov et al., 2020), assuming the default prior distributions (Ovaskainen & Abrego, 2020). We sampled the posterior distribution using four Markov chain Monte Carlo (MCMC) chains, each run for 300,000 iterations. We discarded the first 50,000 as burn-in and thinned by 1,000 to yield 250 samples per chain and 1,000 posterior samples in total. We assessed MCMC convergence of the HMSC models by visually inspecting the posterior traces and ensuring that the potential scale reduction factor values for all regression parameters were <1.01 (Gelman & Rubin, 1992), both for the occurrence and use intensity models. We visually confirmed normality and homoscedasticity of residuals.

We examined the explanatory power of the probit models through species-specific coefficients of discrimination, Tjur's $R^2$ (Tjur, 2009) and area-under-curve (AUC; Fawcett, 2006). Tjur's $R^2$ measures the difference in average predicted occurrence probability between sampling occasions where species were present versus absent. AUC measures the probability that the difference in predicted occurrence probabilities between pairs of randomly selected sampling occasions where species were present versus absent exceeds 0. We used coefficients of determination ($R^2$) to evaluate the explanatory power of the use intensity model. To quantify the drivers of occurrence and use intensity by the mesoherbivore assemblage (excluding megaherbivores), we partitioned the explained variation among the fixed and random effects (measured by Tjur's $R^2$ and $R^2$ in the occurrence and use intensity models respectively).

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 a predictor variable is positive, the posterior support is the proportion of posterior samples >0, which can be interpreted as the probability of the effect being positive. We also evaluated the posterior statistical support that the species-level (occurrence probability and use intensity) and assemblage-level (expected species richness and total use intensity) predictions for one level of a categorical variable (megaherbivore accessible/inaccessible) was larger or smaller than another level. For example, the posterior support that predicted species richness is lower in megaherbivore-accessible plots than megaherbivore-excluding plots is the proportion of posterior samples for which the predicted species richness is lower in megaherbivore-accessible plots than megaherbivore-excluding

plots. 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 (2018), 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).

## 3 | RESULTS

### 3.1 | Megaherbivores reduce total mesoherbivore use intensity, but only minimally reduce expected mesoherbivore richness

Model convergence and fit were satisfactory for both occurrence and use intensity models (Appendix S1). On average, megaherbivore accessibility explained 4% (range: 0% [eland] to 19% [warthog]) and 13% (range: 1% [hare] to 42% [waterbuck]) of the variation in occurrence probability and use intensity of mesoherbivores respectively (Figure 3). The remaining variation was explained by the latent variables that we used to account for unmeasured spatial and temporal effects while evaluating the effects of megaherbivores (Figure S2). Of the 12 species, occurrence probabilities of four species (dik-dik, impala, warthog and duiker) and use intensities of five species (eland, Grant's gazelle, duiker, warthog and waterbuck) were lower in megaherbivore-accessible plots. In contrast, zebra occurrence and use intensity were higher in megaherbivore-accessible plots. We found weaker statistical support for an effect of megaherbivores on the remaining mesoherbivore species (occurrence probabilities of seven species, all <86% posterior support; and use intensities of six species, all <88% posterior support; Figure 4).

For mesoherbivores collectively, the predicted total use intensity in a given sampling occasion was 12% lower (equivalent to 6 dung piles 900 m$^{-2}$) in megaherbivore-accessible plots (98% posterior support; Figure 5). Similarly, expected species richness of mesoherbivores in a given sampling occasion was 7% lower (equivalent to <1 species) in megaherbivore-accessible plots (91% posterior support).

### 3.2 | Traits, but not phylogeny, predicted mesoherbivore responses to megaherbivores

Diet and shoulder height jointly explained 31% and 12%, respectively, of the among-species variation in mesoherbivores' responses (in terms of occurrence probability and use intensity) to megaherbivores. We found weak statistical support for an influence of grass consumption on species' responses to megaherbivores (51% and 76% posterior support for occurrence probability and use intensity respectively; Figure 6c,d). The statistical support for this effect was stronger when warthogs (an apparent outlier) were excluded from the models (73% and 89% posterior support for occurrence probability and use intensity respectively). When all 12 mesoherbivore species were included in the models, megaherbivore-accessible plots tended to be dominated to a greater extent by grazers, evidenced by 4% (89% posterior probability) and 8% (91% posterior probability) higher community-weighted mean proportional grass consumption in the occurrence and use intensity models respectively (Figure S3).

The occurrence of shorter species was negatively impacted by megaherbivores to a greater extent than taller species (93% posterior probability; Figure 6a), but we did not detect this effect in the use intensity model (35% posterior probability; Figure 6b). Taller species tended to dominate in megaherbivore-accessible plots, evidenced by 5% (99% posterior probability) higher community-weighted mean shoulder height in the occurrence model, but not in the use intensity model (<1% difference, 49% posterior probability; Figure S4).

We found limited evidence that more closely related species responded more similar to megaherbivores. After accounting for species' trait effects, the phylogenetic signal parameter averaged 0.45 (CI: 0–0.94) and 0.57 (CI: 0–0.97) for the occurrence and use intensity models respectively.

## 4 | DISCUSSION

We quantified the effect of megaherbivore exclusion on the occurrence (dung presence) and use intensity (dung pile density) of mesoherbivores in long-term exclosure experiments in Kenya. The



**FIGURE 3** Proportion of variance explained by megaherbivore accessibility (dashed lines show cross-species means) for the occurrence (a) and use intensity (b) models. We fitted a joint species distribution model using the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen et al., 2017), detailed in Appendix S1
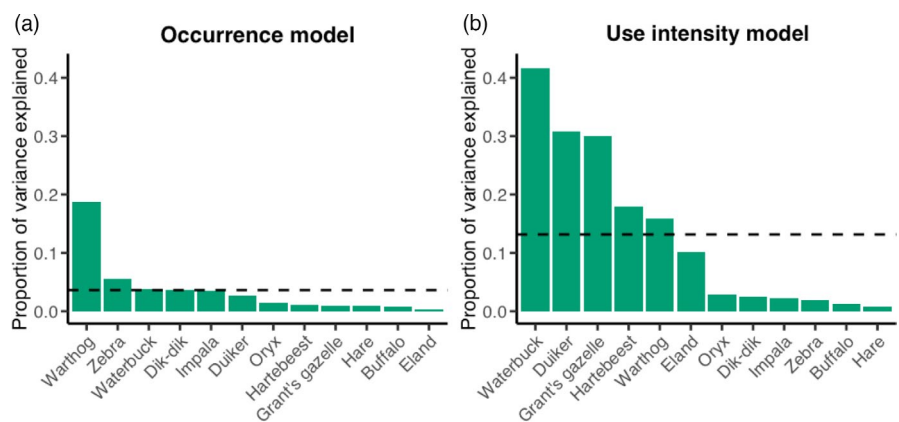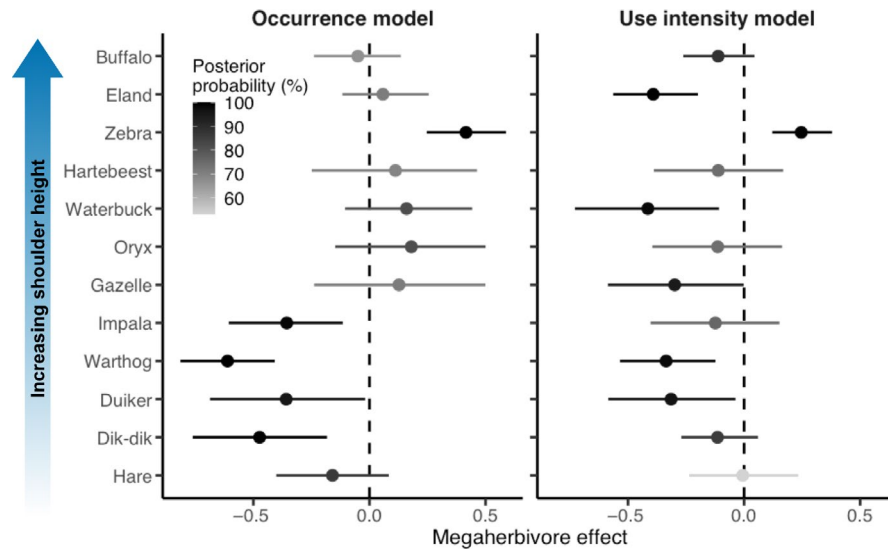
**FIGURE 4** Species-level responses of mesoherbivores to megaherbivores. Effects of megaherbivores on species occurrence probability and use intensity that is conditional on presence (means ± 89% credible intervals). Positive and negative megaherbivore effect values indicate higher and lower mesoherbivore occurrence or use intensity in megaherbivore-accessible plots respectively. Credible interval bars not overlapping with the dotted line indicate that the mean megaherbivore effect was less than or greater than zero with 89% probability. Posterior probability is the proportion of posterior samples for which the megaherbivore effect is either positive or negative. For example, if the megaherbivore effect is positive, the posterior probability is the proportion of posterior samples exceeding zero, which can be interpreted as the probability of the effect being positive
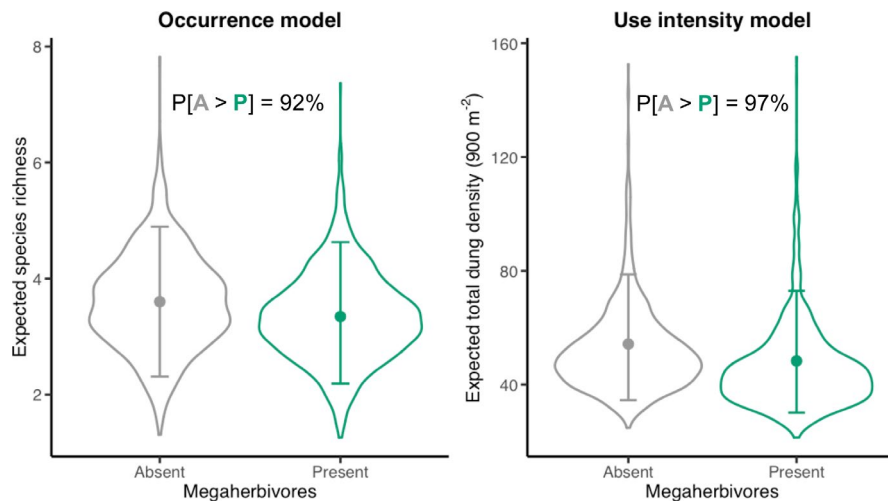


**FIGURE 5** Assemblage-level responses to megaherbivores. Responses of expected species richness (a) and total use intensity (b) to the presence (P) and absence (A) of megaherbivores ('Mega') from occurrence and use intensity conditional on presence models respectively (means ± 89% credible intervals). 'P[A > P]' = posterior probability that the predicted value (expected richness or total use intensity) where megaherbivores are absent (A) exceeds the prediction where megaherbivores are present (P). Note that the effect sizes (difference in means between treatments) are small even though the posterior probabilities that a difference exists is high

occurrence probability and use intensity of several mesoherbivore species were lower in megaherbivore-accessible plots, while zebras responded positively to megaherbivores. The negative effect of megaherbivores on mesoherbivore occurrence was stronger for shorter species, regardless of diet or phylogenetic relatedness.

For all mesoherbivores collectively, megaherbivore exclusion increased estimated total use intensity (total dung pile density of all mesoherbivore species), but insufficiently to increase expected

richness (summed mesoherbivore species occurrence probabilities) by more than one species. Although several studies on indirect ecological effects have focused on trophic cascades initiated by predators (e.g. Alston et al., 2019; Atkins et al., 2019; Donadio & Buskirk, 2016; Ripple & Beschta, 2004), our results substantiate the importance of indirect effects triggered by megaherbivores and mediated by changes in vegetation structure and composition (Coverdale et al., 2016; Kimuyu et al., 2017; Valeix et al., 2011).

**FIGURE 6** The influence of traits on species' responses to megaherbivores (means ± 89% credible intervals). The traits investigated were shoulder height (a, b) and proportional grass consumption (c, d) from occurrence (a, c) and use intensity conditional on presence (b, d) models. Positive and negative megaherbivore effect values indicate higher and lower mesoherbivore occurrence or use intensity in megaherbivore-accessible plots respectively. 'P[T > 0]' = posterior probability that the effect (i.e. the slope parameter) of a trait on the responses of mesoherbivores to megaherbivores exceeds 0
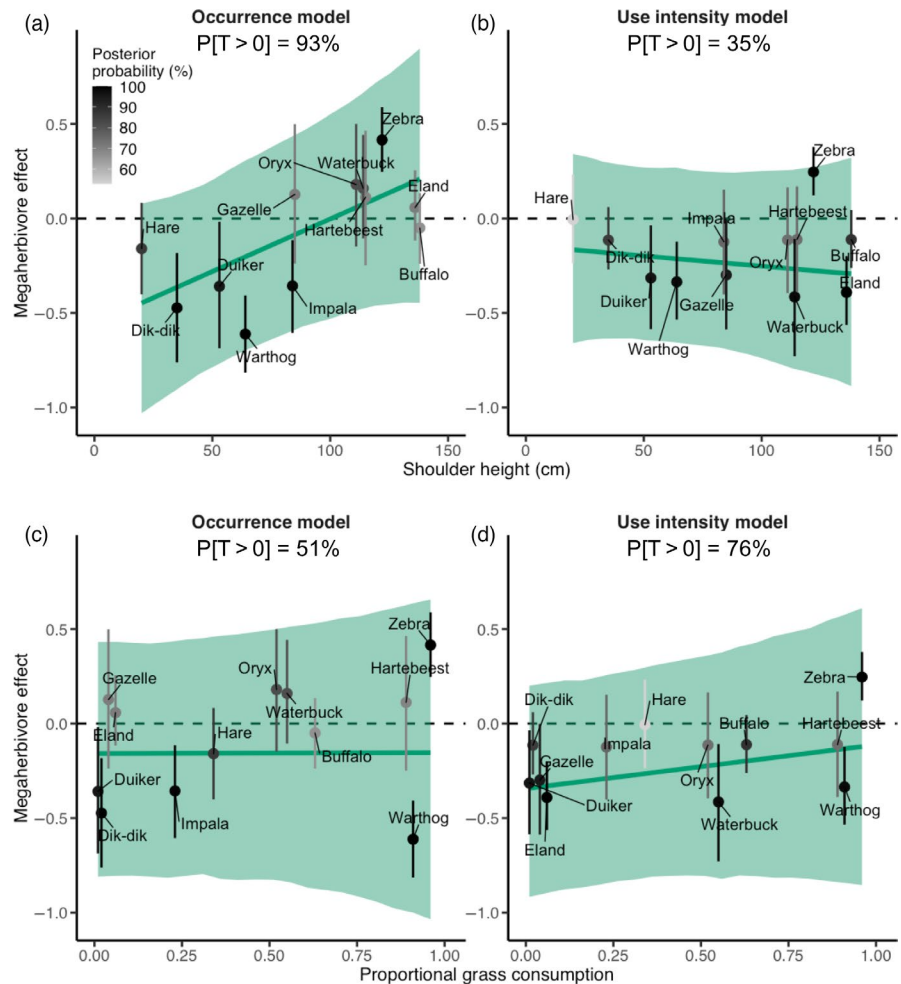


## 4.1 | How megaherbivores affect mesoherbivores is predicted by shoulder height

The effect of megaherbivores on mesoherbivores could be governed by foraging opportunities, predation risk or both, such that each mesoherbivore species negotiates unique trade-offs (Hopcraft et al., 2012; Riginos & Grace, 2008). By thinning overstorey vegetation, megaherbivores can create more open habitats, which can alter resource selection by mesoherbivores that evade predators by freezing and hiding (Atkins et al., 2019; Ford & Goheen, 2015; le Roux et al., 2018; Valeix et al., 2011). Reliance on such cryptic predator avoidance behaviours likely underlies responses of duiker and dik-dik in our study (Figures 4 and 6). Elephants can also reduce the availability of forbs (Coverdale et al., 2016; Kimuyu et al., 2017), which comprise a substantial proportion of the diets of mesoherbivore species with lower proportional grass consumption (Figure S5; Kartzinel et al., 2019). This effect may explain the responses of impala, eland, Grant's gazelle, duiker and dik-dik (Figures 4 and 6). The absence of a statistically supported effect of megaherbivores on buffalo, which could compete with elephants for forbs, may reflect our inability to distinguish between buffalo and cattle dung.

Previous research suggests that megaherbivores facilitate browsing mesoherbivores by increasing the availability of foliage regenerating from damaged woody vegetation in 'browsing lawns', at least over shorter time-scales (Fornara & du Toit, 2007; Makhabu et al., 2006; Rutina et al., 2005). In our study, any evidence of this facilitative effect may have been overridden by the aforementioned costs of reduced forage or perceived predation risk (Fritz et al., 2002; Valeix et al., 2011), both of which may be exacerbated by the recent increase in elephant abundance in this region of Kenya (Ogutu et al., 2016).

Zebras were the only species that responded positively to megaherbivores, consistent with previous research in this system (Goheen et al., 2013; Kimuyu et al., 2017). This may in part be because megaherbivores increase visibility by reducing stalking cover for large carnivores such as lions *Panthera leo* (Ng'weno et al., 2019; Riginos & Grace, 2008). Additionally, megaherbivores could increase zebra occurrence and use intensity by enhancing grass cover (zebras in this system eat ≥95% grass, more than any other species; Kartzinel & Pringle, 2020).

Mesoherbivore occurrence responses to megaherbivores varied as a function of mesoherbivore shoulder height. The occurrence probabilities of shorter species were more negatively impacted by megaherbivores (Figure 6a), mirroring the preference by smaller vertebrates for areas with higher tree densities (Atkins et al., 2019; Otieno et al., 2019; Underwood, 1982; Wells, Kimuyu, et al., 2021).

This provides further evidence of an indirect effect of elephants on smaller bodied vertebrates via tree density reduction and increased predation risk (Valeix et al., 2011). Taller mesoherbivores are also heavier and tend to form larger herds (Figure S6; Crego et al., 2020), both of which mitigate predation risk (Creel & Winnie, 2005). However, given mesoherbivore species occurrence, we found that mesoherbivore shoulder height did not predict megaherbivore effects on mesoherbivore use intensity.

Unlike shoulder height, grass consumption—a key component of diet—was not correlated with megaherbivore effects on mesoherbivore occurrence probabilities (Figure 6c,d). Thus, the suppression of woody plants and forbs and facilitation of grasses by megaherbivores do not necessarily consistently favour grazing mesoherbivores, contrary to a previous study in this system (Kimuyu et al., 2017). This may in part be because we analysed a larger mesoherbivore assemblage. In particular, the inclusion of warthog (a grazer that was suppressed by megaherbivores) may have obscured the patterns documented by Kimuyu et al. (2017). This may have been because of the effect of megaherbivores on unmeasured key resources for warthogs such as rhizomes and burrows (Kingdon et al., 2013) outweighs any megaherbivore-induced increases in grass cover or reductions in predation risk.

Phylogenetic relatedness did not explain the response of mesoherbivores to megaherbivores. The strong posterior support for trait effects (specifically, shoulder height) and comparatively weak phylogenetic signal suggests that morphological traits can be more important predictors of species' responses to megaherbivores than relatedness. Our results could be extrapolated to species not considered in this study based on similarity in shoulder height (Figure 6) and to some extent diet (Figure S4), but phylogeny may be a less useful predictor of species' responses to megaherbivores. However, the small number of species analysed yields low statistical power for detecting phylogenetic effects.

The megaherbivore effect was detected for several species (e.g. eland, gazelle and waterbuck) in the use intensity model, but not the occurrence model, likely because the former model is sensitive to variation in the magnitude and duration of use that the latter is not.

## 4.2 | Implications for rewilding

The concept of reintroducing large mammals has gained popularity in recent years. It has been proposed that reintroducing megaherbivores in areas from which they have been extirpated could restore key ecosystem functions (Bakker & Svenning, 2018; Guyton et al., 2020), mitigate climate change (Sandom et al., 2020; Zimov et al., 2012) and create refugia for species threatened in their current geographic ranges (Ali et al., 2019; Svenning et al., 2016). For extinct species, it has been proposed that extant ecological equivalents could be introduced to fulfil similar ecological functions (Donlan, 2005; Seddon et al., 2014; Svenning et al., 2016). Yet, as the replacement of wild ungulates by livestock in Africa showcases, putative ecological analogues are not necessarily functionally suitable

(Goheen et al., 2018; Hempson et al., 2017). The relationships documented here provide further evidence that predicting the effects of reintroductions will be challenging. We note, however, that seemingly 'negative' effects of megaherbivore reintroductions, such as reduced tree cover or suppression of mesoherbivores, may simply reflect the re-establishment of historical ecological conditions (Alston et al., 2019; Kuiper & Parker, 2014; Young et al., 2021).

Our findings suggest that the responses of mesoherbivores to the reintroduction of predominantly browsing megaherbivores may be influenced more by the mesoherbivores' shoulder heights than by their diets. Interactions between megaherbivores and mesoherbivores will influence the overall impact of the herbivore community on vegetation. For instance, reintroducing elephants may reduce overall mesoherbivore use intensity, which in turn may promote fires by raising herbaceous fuel loads (Hempson et al., 2017). Moreover, height-based responses of mesoherbivores to megaherbivores suggest that some mesoherbivores are responding to a 'landscape of fear' that shifts both spatially and seasonally (Gaynor et al., 2019; Laundré et al., 2001; Riginos, 2015). Therefore, predation pressure may be an important predictor of how mesoherbivores respond to megaherbivores. Megaherbivore reintroduction efforts might consider how species' traits shape biotic interactions to better predict the ecological effects of species reintroductions.

It is important to note that environmental factors such as rainfall and soil strongly influence mesoherbivore habitat use (Fritz et al., 2002; Goheen et al., 2013), as indicated by random effects that accounted for most of the variation in mesoherbivore occurrence and use intensity (Figure S2). These environmental factors also determine the extent to which our results can be extrapolated elsewhere. For instance, some mesoherbivores in our study were present on both clay-rich and sandy soils (zebra, eland, buffalo) while others were solely (hartebeest, oryx, Grant's gazelle, duiker on clay-rich soils and dik-dik and waterbuck on sandy soils) or predominantly (impala, hare and warthog on sandy soils) recorded on one soil type. Similarly, the magnitude of reductions in tree density by megaherbivores varies soil and vegetation types (Goheen & Palmer, 2010; Table S1), while the magnitude of herbivore-induced indirect effects depends on primary productivity (Daskin & Pringle, 2016). In less productive ecosystems, megaherbivore–mesoherbivore interactions can switch from facilitation to competition as megaherbivores tend to monopolize resources and dominate total herbivore biomass (Fritz et al., 2002). Megaherbivore reintroduction efforts could consider how environmental factors might mediate megaherbivore–mesoherbivore interactions.

Although the results show that megaherbivores influence (and generally supress) space use by mesoherbivores, the nature of these effects likely depends on the species of megaherbivore. In our study, megaherbivores consisted of elephants and giraffes, both of which reduce tree densities. However, the effects of mega-grazers such as white rhinoceroses *Ceratotherium simum* and hippopotamus *Hippopotamus amphibious* are likely to differ from that of predominantly browsing elephants and giraffes (e.g. through the creation and maintenance of grazing lawns; Cromsigt & te Beest, 2014; Kanga

et al., 2013). Long-term experiments that manipulate other mega-herbivore species will be necessary to more fully anticipate potential effects of reintroducing lost megafauna.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

H.B.M.W. and R.D.C. conceived the study and led the writing of the manuscript; S.K., A.A.H., L.M.K., J.M.A., C.G.R., S.W., J.R.G., T.R.K., D.M.K. and H.B.M.W. conducted the fieldwork and prepared the datasets; T.P.Y., T.M.P., J.R.G. and R.M.P. designed and established the exclosures; H.B.M.W., R.D.C. and Ø.H.O. analysed the data. All authors made significant contributions to the drafts and approved it for publication.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.9ghx3ffhp (Wells, Crego, et al., 2021).

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## SUPPORTING INFORMATION

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