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Elephant Fences Result in Limited Impacts on Movement of Non-Target Species

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ABSTRACT

Mega-herbivore or elephant fences aim to prevent target animals (here: African savanna elephant *Loxodonta africana*, giraffe *Giraffa giraffa*) from crossing while allowing others, often with the intention to protect an area against elephants—for conservation, economic or research purposes. However, little is known about mega-herbivore fence effectiveness and impact on non-target species, for example impact on meso-herbivore movement, or fence avoidance. We hypothesised that mega-herbivore fences are effective in excluding mega-herbivores, whereas other species remain unaffected. We tested this hypothesis by comparing mammalian species abundance in (i) full exclosures, (ii) mega-herbivore exclosures and (iii) open plots. These plots were part of the Lapalala Elephant Landscape Experiment (LELE) project in Lapalala Wilderness, South Africa. Systematic dung pile recording and animal track counts—supported with video footage from camera traps—were used to quantify species-specific animal abundance using generalised linear mixed-effect models. The dung piles showed no difference in the abundance of non-target species between mega-herbivore exclosures and open plots, while target species were successfully excluded. Interestingly, we found fewer tracks of large non-target herbivores, such as plains zebra (*Equus quagga*) and greater kudu (*Tragelaphus strepsiceros*) crossing mega-herbivore fences compared to open plots, indicating that some individuals avoided crossing the mega-herbivore fence lines. We suggest that this avoidance is due to a combination of species-specific vigilance and deterrence of large specimens. Further research is needed to determine whether this avoidance persists over time, and if the absence of large non-target animals affects ecosystem functioning. Mega-herbivore fences are an effective means to prevent the movement of target species. However, some individuals of non-target species also avoid crossing these fences, likely large animals due to the minimum height of the fence. We recommend monitoring the movement of species once elephant fences are erected, and to increase minimum fence height if non-target species are affected.

1 | Introduction

The African savanna elephant (*Loxodonta africana*) affects savanna ecosystem dynamics, potentially targeting palatable species (Elzinga et al. 2025; Gadd 2002; Owen-Smith and Chafota 2012; Young et al. 2021), or even altering entire landscapes (Gordon et al. 2023; Guldemond et al. 2017; Kalwij et al. 2010; Skarpe et al. 2004; Tambling et al. 2013).

Consequently, ecosystem managers and the public regularly express the need to protect savanna landscapes from undesired elephant impacts while allowing free passage for other species (Coller and Siebert 2020; Davies and Asner 2019; Riginos et al. 2012). For this reason, semi-permeable fence constructions have been developed consisting of an electrified barrier set at a certain height (Scholes and Mennell 2008; Wigley-Coetsee et al. 2022). These fences are designed to exclude mega-herbivores such as elephants and giraffes (*Giraffa giraffa*), while allowing non-target species to cross without being affected (Goheen et al. 2013; Slotow 2012; Young et al. 1998). However, since no further studies have systematically tested the side effects of mega-herbivore fences on non-target species, little remains known about how the movement of non-target species is affected (Goheen et al. 2018; McInturff et al. 2020).

Mega-herbivore fences can severely affect large animal movement in savanna ecosystems (Scholes and Mennell 2008; Slotow 2012). For example, a fence can affect the seasonal movement pattern of African elephants (Loarie et al. 2009), while increased displacement near fences results in an edge effect (Vanak et al. 2010). Additionally, if non-target species are tall enough to come into contact with the electric wire, fence avoidance may occur, especially shortly after its construction (Hoare 1992; McKillop and Sibly 1988). Predators have also been observed using fences to corner prey species (Van Dijk et al. 2017; Van Dyk and Slotow 2003). As a result, prey species may eventually avoid fences to reduce predation risk (Dupuis-Desormeaux et al. 2016). Other fence effects are more indirect, arising only after a long period. For example, increased tree and shrub density due to the absence of elephants in elephant exclosures can result in a higher predator hunting success rate (Dupuis-Desormeaux et al. 2016), or increased numbers of zebras in open plots as elephants may increase grass cover (Wells et al. 2021). The immediate impact of mega-herbivore fences on non-target species is, therefore, best observed shortly after fence construction.

To properly test the impact of mega-herbivore fences on non-target species movement, the study area needs to have a mammal diversity representative of the ecosystem—including a natural predator/prey ratio—with relatively low anthropogenic disturbance. Ideally, such an area is also large enough for species to behave naturally, without prior experience with mega-herbivore fences. Lapalala Wilderness Nature Reserve, one of the largest private nature reserves in southern Africa, meets these criteria. The reserve harbours a variety of reintroduced mammal species, including a herd of elephants since 2017, and experiences relatively little wildlife tourism. To monitor the impact of elephant reintroduction on ecosystem dynamics, a research project involving mega-herbivore fences was initiated: the Lapalala Elephant Landscape Experiment (LELE) project. The LELE project consists of 48 1-ha plots of either regular fences, mega-herbivore fences or open plots. Thus, Lapalala Wilderness is an ideal area for testing the early impact of recently established elephant fences on non-target species.

Here, we hypothesised that the establishment of mega-herbivore fences effectively exclude mega-herbivores (elephant and giraffe), while the movement and habitat use of non-target species remains unaffected. To test this hypothesis, we used a combination of dung pile counts, animal track surveys and wildlife camera trapping to quantify species movement and record behaviour near fences. Since we were primarily interested in the immediate impact of mega-herbivore fences on non-target species, we conducted this study shortly after the construction of the experimental fences, before environmental conditions within or near the experiment plots had changed. This study also provides practitioners with insight into how species respond to newly erected mega-herbivore fences.

2 | Methods

2.1 | Study Area

Lapalala Wilderness Nature Reserve is a 53,000-ha private reserve within the Waterberg Biosphere, Limpopo, South Africa (Figure 1; 28°10–26′ E, 23°42–56′ S). The reserve has a subtropical climate with mean minimum and maximum temperatures ranging from 18.1°C to 31.5°C in January, from 2.3°C to 23.0°C in July, and a mean annual rainfall of 594.4 mm predominantly falling in the summer season (October–April; Popp and Kalwij 2023). Annual precipitation fluctuated strongly between 1990 and 2020, with levels ranging from 370 mm in 2005 to 1002 mm in 2006. The landscape comprises rocky hills and plains at an elevation of 1000–1200 m intersected by the perennial Palala and Kgogong (Bloklandsspruit) rivers. Its geology is characterised by nutrient-poor, sandy soils derived from Palaeoproterozoic siliciclastic rocks of the Kransberg Subgroup (Ben-Shahar 1987; Callaghan et al. 1991).

Lapalala Wilderness vegetation is classified as Waterberg Mountain Bushveld with over 60 woody species in the plots of the LELE project alone, including *Combretum* spp., *Dichrostachys cinerea* and *Terminalia sericea* (Mucina and Rutherford 2006; Popp and Kalwij 2023). Since September 2017, 26 African savanna elephants have been reintroduced. The reserve also hosts various large indigenous mammal species, such as giraffe, hyaenas (*Hyaena brunnea* and *Crocuta crocuta*), lion (*Panthera leo*), plains zebra (*Equus quagga*), rhinos (*Ceratotherium simum* and *Diceros bicornis*) and various other ruminants.

2.2 | Experimental Design

To investigate the long-term impact of elephants on the savanna dynamics of Lapalala Wilderness, fences for the LELE project were constructed between October 2020 and June 2021. The project followed a full-factorial design with eight landscape replicates (blocks) located across the reserve within the home range of the elephant population, and in similar habitats. Each block had three treatment levels: (i) full exclosure, (ii) mega-herbivore exclosure and (iii) open plots. Each treatment consisted of a 1-ha plot and was replicated twice per block in a randomised spatial configuration (Figure 2), resulting in 6-ha blocks with a total sample size of 48 plots as follows:

i. Full exclosure plots ($N = 16$) were designed to exclude all mammalian species crucial for wildlife management and conservation (from small bovids and antelopes to elephants and large carnivores). Fences consisted of horizontal wires

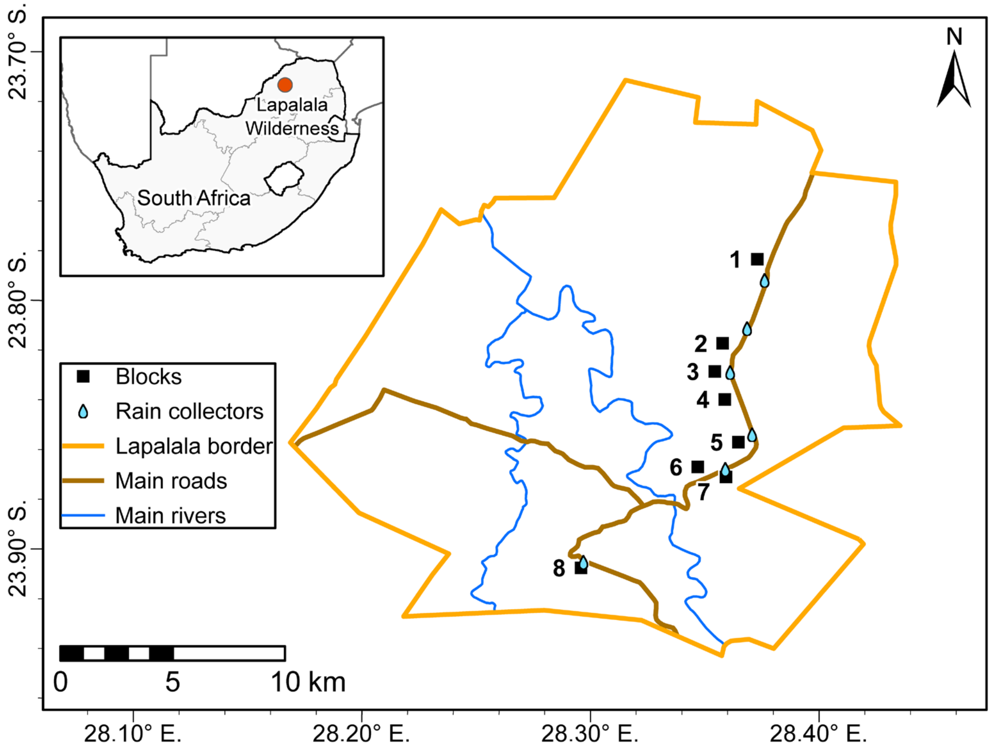

FIGURE 1 | Overview of Lapalala Wilderness Nature Reserve with the location of eight Lapalala Elephant Landscape Experiment blocks (depicted as black squares), the six rain collectors (blue droplets), main access roads (brown lines), and the perennial rivers (blue lines). The location of Lapalala Wilderness in Limpopo, South Africa, is marked with a red dot (inset). Projection: WGS 1984, UTM zone 35S.

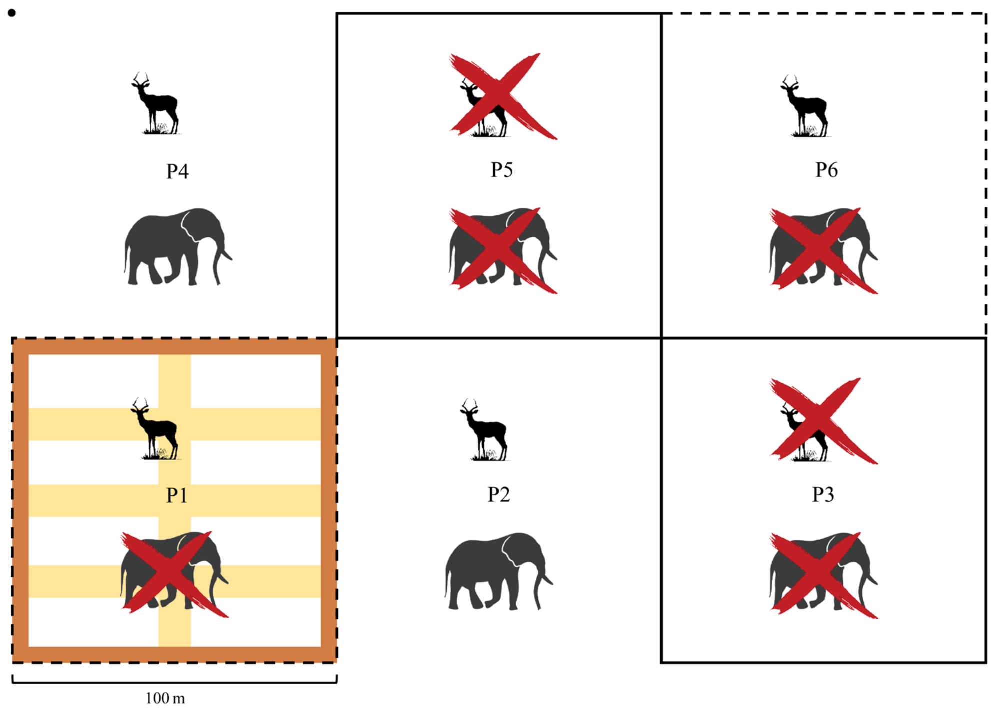

FIGURE 2 | Schematic design of a block of the Lapalala Elephant Landscape Experiment with three treatment levels in random spatial configuration: (i) full exclosures (P3, P5); (ii) mega-herbivore exclosures (P1, P6); and (iii) open plots (P2, P4). Note that plot borders are shared and that open plots always have four corner posts. For each 1-ha plot, dung piles and animal tracks were recorded in a 5-m buffer inside the plot border, while additional dropping observations were recorded in 10 × 100 m transects, as exemplified in P1.

spaced 10–15 cm apart, forming a 245-cm high barrier, with five additional electrified wires positioned 30 cm parallel to the main fence on one side (Figure S1).

ii. Mega-herbivore exclosure plots ($N = 16$) excluded elephants and giraffes using three electrified wires set at 160, 200 and 240 cm heights (Figure 3; Figure S2). The lowest wire aims to prevent young elephants from entering (and their mothers from following). Actual fence height of the lowest wire varied with terrain.

iii. Open plots ($N = 16$) were accessible to all species, marked only by corner posts. Each open plot bordered at least one full or elephant exclosure plot due to the spatial configuration of the blocks.

All plot borders were kept clear of woody vegetation within a 0.5 m buffer zone on each side of the fence line as part of regular maintenance. This regime was also applied to open plot borders.

2.3 | Data Collection

Evidence of animal presence was determined in the field from dung piles and animal tracks. Prior to fieldwork, two data collectors (MRP, TJ) received extensive training in dung identification and spoor tracking from a local professional (Malosi Nkhumane, certified game tracker at Lapalala Wilderness). Dung piles and animal tracks were identified to species or species group (sensu Hoare 1992). All uncertain observations—mostly dung piles—were collected or photographed for identification by local game trackers and confirmed using relevant literature (Murray 2011; Stuart and Stuart 2013; Van den Heever et al. 2017). To enable a posteriori identification correction, all uncertain observations were uploaded to a customised iNaturalist project (https://www.inaturalist.org/projects/dung-count-lele-lapalala). Data curation was done in ArcGIS Pro 2.8.0 (ESRI 2021).

To quantify non-target species abundance through dung, we identified and mapped dung piles in two transect types: (i) border transects: four transects of 5 × 100 m along plot borders; and (ii) interior transects: four transects of 10 × 100 m within each plot (384 transects in total; Figure 2). A dung sample was collected to confirm the species identification if deemed necessary. Dung piles in animal latrines (here: mainly white rhinoceros, impala, common duiker, blue wildebeest defecated in middens) were counted by estimated defecation events (sensu Kimuyu et al. 2017).

To quantify animal track abundance in border transects, each track crossing a plot border was mapped, including the direction of movement. Multiple crossings by a single individual were not controlled for; this was unlikely to significantly affect results (Keeping and Pelletier 2014). To control for the impact of vegetation and substrate on animal track detection probability, we also estimated transect suitability as the proportion where tracks would be visible. Animal track age was estimated based on the number of days since precipitation (> 10 mm/day) as maximum age. Local precipitation was recorded using six rain collectors across the area (Figure 1).

Field data were collected from December 2021 to March 2022. To minimise temporal variation, all transects within a block were mapped for dung piles or animal tracks on the same day. Dung pile mapping was done once only, while animal track mapping was generally conducted three times. Animal track mapping was repeated after a rain event. Blocks with many or

FIGURE 3 | Data collector MRP is recording the position of a corner fence post of a mega-herbivore enclosure using a Global Navigation Satellite System (GNSS) sensor.

few animal tracks were sampled two or four times, respectively. The minimum realised height of the mega-herbivore fence was measured for each fence and corner post at vertical resolution of 5 cm, with locations determined using a handheld GNSS sensor (ppm10xx GNSS Sensor, ppm GmbH, Penzberg, Germany; Figure 3) at a horizontal accuracy 0.01–1.00 m.

To collect supporting data on animal behaviour such as avoidance of mega-herbivore fences, wildlife camera traps (Primos Proofcam 03 or Spypoint Solar Dark) were used. Cameras were mounted at 1.3 m on fence posts or nearby trees (following Bernard et al. 2023), and recorded 30-s videos upon activation. Cameras were deployed for all plots in each block for six consecutive days.

2.4 | Statistical Analysis

Dung piles and animal tracks were summarised as the number of observations per species per plot, excluding unidentifiable observations (1.3% of dung piles; 0.1% of animal tracks). Due to the absence of animal track observations in full exclosure plots, this treatment was excluded from the analysis. We used generalised linear mixed-effects models (GLMM) using a log link to analyse dung pile and animal track data for each species (Zuur et al. 2009), with fence type as a fixed effect and block as a random variable (sensu Bolker et al. 2009). For larger non-target species (greater kudu, blue wildebeest and plains zebra), we also tested if fence height affected species movement. Data normality was visually assessed using qq-plots, and homogeneity of variance and zero inflation were checked using *DHARMa* (Hartig 2022). Overdispersion of residuals was accounted for using a negative binomial error distribution (Hilbe 2011). GLMMs were fitted using *glmmTMB* (Brooks et al. 2017), with post hoc pairwise comparisons conducted via *multcomp* (Hothorn et al. 2008). All statistical analyses were performed in R (version 4.2.2; R Core Team 2022).

3 | Results

We recorded 2485 identifiable dung piles and 5352 animal tracks, most of which were identified with a high level of confidence. A total of 452 observations were uploaded to the iNaturalist project, with 137 identified to species level and the rest conservatively identified to a higher taxonomic level. Dung piles and tracks of mega-herbivores—elephants and giraffes—were consistently observed in open plots (Figure 4) but never in mega-herbivore or full-exclosure plots. Camera trap footage confirmed that elephants entered open plots only (Figure S3).

Among non-target herbivores, dung pile counts showed similar abundance in both mega-herbivore exclosures and open plots, but were virtually absent from full exclosures (Table S1). This was also largely true for the track data for most species. However, significantly fewer tracks at plot level were recorded for plains zebra (54% less, $p < 0.001$) and greater kudu (43% less, $p = 0.004$) in mega-herbivore exclosures compared to open plots (Figure 4B; Table S2). Similar patterns were observed at plot border level and outer plot borders, respectively (Tables S3 and S4). Variations in minimum realised height of mega-herbivore fence (150–170 cm) generally did not significantly contribute to the GLMM models ($p = 0.190$), except for greater kudu (GLMM estimate $= -0.032$, $p = 0.034$). We did not have sufficient dung pile and animal track observations for African buffalo (*Syncerus caffer*) and rhinos for a reliable interpretation of the GLMM models.

Wildlife camera traps were active for 513 trap days. In total, we recorded 129 camera-days at open plots, 275 at mega-herbivore exclosures and 109 at full exclosures, capturing 19 species, including African buffalo and rhinos. A total of 572 specimens cautiously—displaying heightened alertness—passed under the mega-herbivore fences, with most species, such as male kudus, needing to lower their heads and horns to cross (Figure S3). The camera traps recorded only one deterrent event, involving a young kudu. Most interactions involved a specimen grazing, sniffing or defecating under the fence. Camera traps confirmed mega-herbivores visiting open plots (giraffe: 3 observations; elephant: 6 observations), while carnivores, mainly hyaenas and black-backed jackal (*Lupulella mesomelas*), were observed in mega-herbivore exclosures and open plots. We documented four fence breaches by non-target species. Full exclosures effectively prevented animals from crossing, with few exceptions, such as common duiker (*Sylvicapra grimmia*) and Cape genet (*Genetta tigrina*). Notably, these small species are not typically considered crucial for wildlife management and conservation.

4 | Discussion

Mega-herbivore fences effectively excluded mega-herbivores (elephant and giraffe), while non-target species were largely unaffected, with the exception (for track data only) of plains zebra and greater kudu. Both of these species were less abundant in mega-herbivore plots compared to open plots, suggesting a species-specific or individual size-related effect. Interestingly, non-target species that were even larger, like white rhinoceros and African buffalo, appeared unaffected by the fences. These differences might be attributed to predator behaviour near fences (Dupuis-Desormeaux et al. 2016), species-specific responses to novel landscape structures (Hoare 1992), and physical interactions as a result of individual size relative to fence properties (Liefting et al. 2018). Below, we discuss these potential explanations in detail.

Mega-herbivore fences can affect predator hunting success in various ways. For example, vegetation protected from mega-herbivory becomes denser over time—providing concealment for predators—and can increase hunting success (Dupuis-Desormeaux et al. 2016). However, given the recent reintroduction of only a small herd of elephants, it is unlikely that vegetation density has already changed enough to affect predator–prey interaction, although this may change over time (Valeix et al. 2011). Fences can also act as a physical barrier, facilitating predators in encircling or trapping prey (Van Dijk et al. 2017; Van Dyk and Slotow 2003). While we observed some fence damage linked to animal activity, we have no direct evidence, for example carcasses or fresh predator tracks, to confirm a change in predator hunting behaviour. Indeed, breaches in game fences are a common occurrence shortly after their construction (Kesch et al. 2014, 2015). Although the spatial configuration of

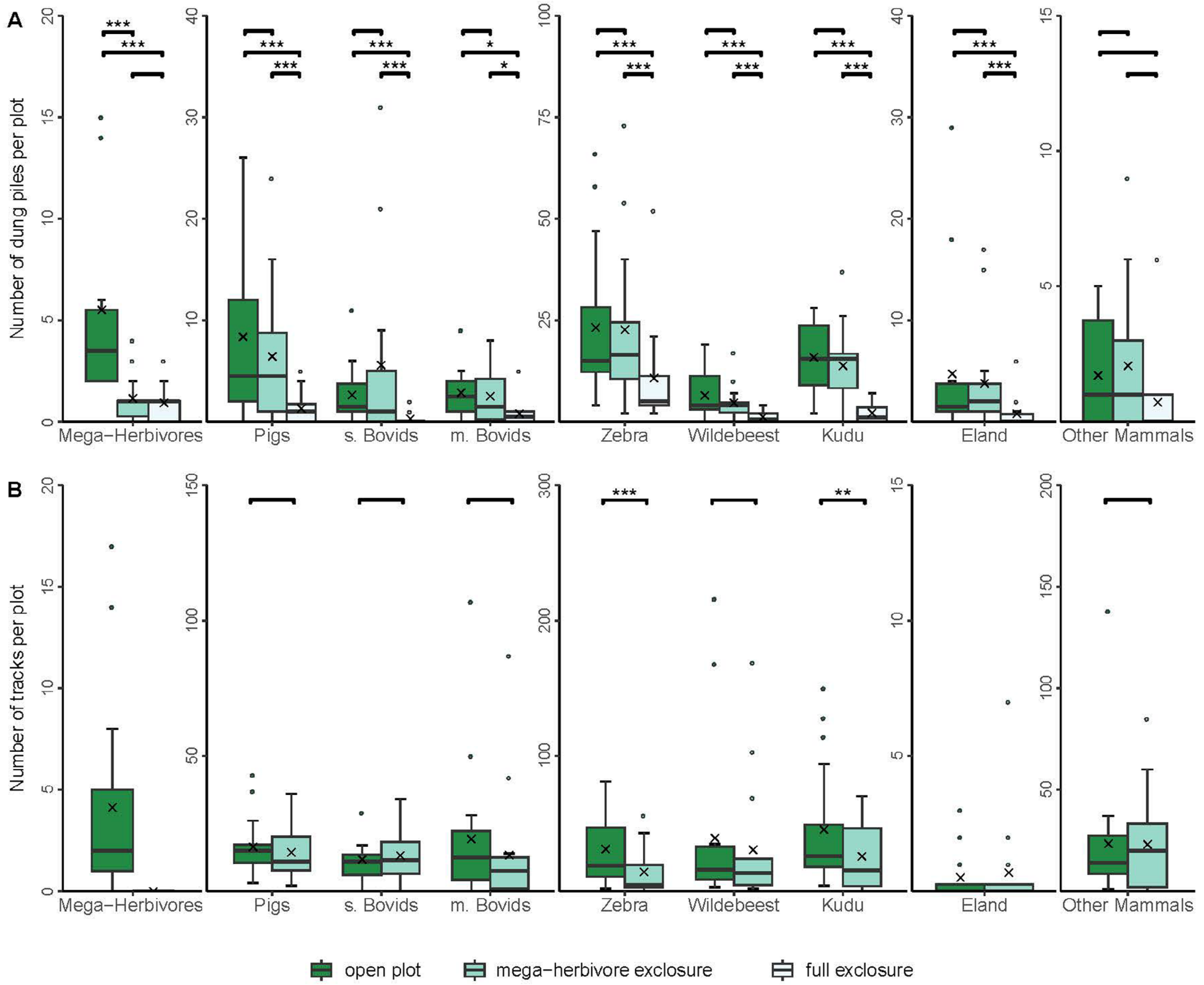

FIGURE 4 | Boxplots depicting the amount of dung piles (panel A) and animal tracks (panel B) for each species group (s = small; m = medium) and the 1-ha plot type. Crosses indicate mean values. Asterisks indicate the level of statistical significance between groups (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The box colours correspond to the plot treatment: open plots are depicted in deep-earthy green, mega-herbivore exclosures in mint green, and full exclosures in very light blue.

the experimental blocks has the potential to benefit predators (but see Dupuis-Desormeaux et al. 2016), the recent erection of the LELE project fences makes it unlikely that a change in predator hunting behaviour explains the lower abundance of plains zebra and greater kudu in mega-herbivore plots.

Mega-herbivore fences vary in design, with the height of the electrified wires playing a major role (Liefting et al. 2018; Scholes and Mennell 2008). The mega-herbivore fences of the LELE project had a minimum height of approximately 1.6 m, lower than comparable experiments such as KLEE (2 m with 0.5-m dangling wires; Young et al. 1998), UHURU (2 m without dangling wires; Goheen et al. 2013), and the Nkuhlu exclosure in Kruger National Park (1.8 m; O'Keefe and Alard 2002). Despite the seemingly low minimum height of the LELE mega-herbivore fences, we found no dung pile evidence that large non-target species were unable or unwilling to access mega-herbivore exclosure plots, or that minimum fence height affected their abundance. However, since we did not experimentally test the impact of minimum fence height, we lack an adequate dataset to determine a relationship between species abundance and minimum fence height. The lower abundance of two medium-sized non-target species (plains zebra and greater kudu) suggests that the impact of mega-herbivore fences was species-specific rather than determined by fence height.

Plains zebra, and to a lesser extent greater kudu, crossed mega-herbivore fences less frequently than expected, while similar-sized species (e.g., blue wildebeest) or larger species (e.g., rhinos and African buffalo) showed no difference. A possible explanation is that certain species exhibit cautious behaviour. Zebra species are particularly vigilant near habitats or objects that are potentially associated with increased predation risk (Chen et al. 2021; Yiu et al. 2021). Such behaviour is likely to diminish over time as the population learns that the mega-herbivore fences pose no threat (Fischhoff et al. 2007). Interestingly, the camera traps showed that some large non-target specimen crossed the mega-herbivore fence, in spite of being taller than the minimum fence height (Figure S3), but we have insufficient data to draw any definitive conclusions. We suspect that brief contact with an electric wire using low-conductivity body parts such as greater kudu's horns or rhinoceros' withers, reduces the likelihood of a deterring electrical pulse (Kubisz 2001). Rhino skin, although thick, is rather sensitive to electrical pulses (Reilly 2005). Therefore, we expect larger non-target specimen to increasingly avoid mega-herbivore fences as they eventually experience the deterring effect of an electrical pulse.

Dropping counts inside full exclosures were higher than expected. A plausible explanation is that some dung piles were present before the fences were built and became enclosed, thus representing baseline pre-fence activity. Since dung decomposition and recognisability vary greatly between species, accurately determining their age is challenging (Laing et al. 2003; Sitters et al. 2014). To gather enough data in this low-density system, we recorded all visible droppings, including deposits. Moreover, surface runoff during heavy precipitation may have washed dung into fenced plots (Goheen et al. 2013). These factors suggest that dung indicates cumulative activity over an extended period, while tracks, which degrade faster and accumulate over shorter durations, represent more recent presence (Winterbach et al. 2016). Such temporal mismatch explains the discrepancy between dung and track data.

Our study primarily relied on a unique combination of dung pile mapping and animal track observations during a 3-month field season. A follow-up study is needed to assess temporal changes in species movement patterns (Yiu et al. 2021). To complement our short-term observations, which are less effective for detecting low-density species (Barnes 2001; Funston et al. 2010), we supplemented our dataset with camera trapping, which provided valuable additional information. For rare species, however, extended sampling remains advantageous (Stander 1998). Wildlife observations are affected by observer bias (Gielen et al. 2024). To reduce this bias in identifying dung piles and animal tracks (Loosen et al. 2022), fieldwork was always conducted by two observers. To further improve data quality, observers used accurate GPS devices and ESRI's ArcGIS Pro apps (Field Maps and QuickCapture) for data capture. This digital approach facilitated data curation and sharing, including via an iNaturalist project, and allowed for transparent a posteriori correction. We recommend adopting an online data curation system to optimise data quality and accessibility, irrespective of the type of natural data collected.

Mega-herbivore fences have three main advantages: (i) an effective barrier for elephants and giraffes, (ii) permeable for non-target species and (iii) cost effective when compared to traditional multistrand fences. However, we showed that permeability for non-target species is lower than assumed, primarily affecting vigilant and larger species. Raising the minimum fence height could enable young elephants to cross, which may lead to fence breaks as herds follow (Slotow 2012). Attaching conspicuous objects to increase mega-herbivore fence visibility, a common practice to prevent species from running into new fences (Hoare 1992; McKillop and Sibly 1988), might inadvertently deter non-target species altogether. Although a mega-herbivore fence has short-term impacts on certain non-target species, medium- to long-term impacts may decrease due to habituation (Blumstein 2016; Malherbe et al. 2021).

5 | Conclusions

Mega-herbivore fences are effective barriers for elephants and giraffes. However, the assumption that non-target species are entirely unaffected had mixed support from our results. Monitoring of newly erected fences is essential to determine whether their impact on non-target species aligns with management objectives.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code are available at https://github.com/TimoJaeger/LELE_Fence and at https://www.inaturalist.org/projects/dung-count-lele-lapalala.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.