



Ecological consequences of large herbivore exclusion in an African savanna: 12 years of data from the UHURU experiment

Journal:	<i>Ecology</i>
Manuscript ID	ECY21-0746.R1
Wiley - Manuscript type:	Data Papers
Date Submitted by the Author:	n/a
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Substantive Area:	<p>Population Dynamics and Life History < Population Ecology < Substantive Area, Systematics < Population Ecology < Substantive Area, Conservation < Population Ecology < Substantive Area, Community Ecology < Substantive Area, Disturbance < Community Ecology < Substantive Area, Food Webs/Trophic Structure < Community Ecology < Substantive Area, Keystone Species < Community Ecology < Substantive Area, Species Interactions < Community Ecology < Substantive Area, Herbivory < Species Interactions < Community Ecology < Substantive Area, Climate Change < Ecosystems < Substantive Area, Restoration < Management < Substantive Area, Data paper < Data < Substantive Area</p>

Organism:	Rodents < Mammals < Vertebrates < Animals, Other (specify type in field below) < Mammals < Vertebrates < Animals, Carnivores < Mammals < Vertebrates < Animals, Legumes, peas, beans < Angiosperms < Plants, Grasses < Angiosperms < Plants, Angiosperms < Plants
Habitat:	Savanna < Tropical Zone < Terrestrial < Habitat
Geographic Area:	East Africa < Africa < Geographic Area
Key words/phrases:	climate change, dik-dik (<i>Madoqua</i>), East African savannas, elephant (<i>Loxodonta africana</i>), extinction, food webs, grazing and browsing herbivores, impala (<i>Aepyceros melampus</i>), long-term ecological field experiments, plant communities, rangeland ecology, species interactions
Abstract:	<p>Diverse communities of large mammalian herbivores (LMH), once widespread, are now rare. LMH exert strong direct and indirect effects on community structure and ecosystem functions, and measuring these effects is important for testing ecological theory and for understanding past, current, and future environmental change. This in turn requires long-term experimental manipulations, owing to the slow and often nonlinear responses of populations and assemblages to LMH removal. Moreover, the effects of particular species or body-size classes within diverse LMH guilds are difficult to pinpoint, and the magnitude and even direction of these effects often depends on environmental context. Since 2008, we have maintained the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, a series of size-selective LMH exclosures replicated across a rainfall/productivity gradient in a semi-arid Kenyan savanna. The goals of the UHURU experiment are to measure the effects of removing successively smaller size classes of LMH (mimicking the process of size-biased extirpation) and to establish how these effects are shaped by spatial and temporal variation in rainfall. The UHURU experiment comprises three LMH-exclusion treatments and an unfenced control, applied to 9 randomized blocks of contiguous 1-ha plots ($n = 36$). The fenced treatments are: "MEGA" (exclusion of megaherbivores, elephant and giraffe); "MESO" (exclusion of herbivores ≥ 40 kg); and "TOTAL" (exclusion of herbivores ≥ 5 kg). Each block is replicated three times at three sites across the 20-km rainfall gradient, which has fluctuated over the course of the experiment. The first five years of data were published previously (Ecological Archives E095-064) and have been used in numerous studies. Since that publication, we have (a) continued to collect data following the original protocols, (b) improved the taxonomic resolution and accuracy of plant and small-mammal identifications, and (c) begun collecting several new data sets. Here, we present updated and extended raw data from the first 12 years of the UHURU experiment (2008–2019). Data include daily rainfall data throughout the experiment; annual surveys of understory plant communities; annual censuses of woody-plant communities; annual measurements of individually tagged woody plants; monthly monitoring of flowering and fruiting phenology; every-other-month small-mammal mark-recapture data; and quarterly large-mammal dung surveys.</p>
Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.	
DataS1.zip	

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Manuscripts

Ecological consequences of large herbivore exclusion in an African savanna: 12 years of data from the UHURU experiment

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Abstract: Diverse communities of large mammalian herbivores (LMH), once widespread, are now rare. LMH exert strong direct and indirect effects on community structure and ecosystem functions, and measuring these effects is important for testing ecological theory and for understanding past, current, and future environmental change. This in turn requires long-term experimental manipulations, owing to the slow and often nonlinear responses of populations and assemblages to LMH removal. Moreover, the effects of particular species or body-size classes within diverse LMH guilds are difficult to pinpoint, and the magnitude and even direction of these effects often depends on environmental context. Since 2008, we have maintained the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, a series of size-selective LMH exclosures replicated across a rainfall/productivity gradient in a semi-arid Kenyan savanna. The goals of the UHURU experiment are to measure the effects of removing successively smaller size classes of LMH (mimicking the process of size-biased extirpation) and to establish how these effects are shaped by spatial and temporal variation in rainfall. The UHURU experiment comprises three LMH-exclusion treatments and an unfenced control, applied to 9 randomized blocks of contiguous 1-ha plots ($n = 36$). The fenced

treatments are: “MEGA” (exclusion of megaherbivores, elephant and giraffe); “MESO” (exclusion of herbivores ≥ 40 kg); and “TOTAL” (exclusion of herbivores ≥ 5 kg). Each block is replicated three times at three sites across the 20-km rainfall gradient, which has fluctuated over the course of the experiment. The first five years of data were published previously (*Ecological Archives* E095-064) and have been used in numerous studies. Since that publication, we have (a) continued to collect data following the original protocols, (b) improved the taxonomic resolution and accuracy of plant and small-mammal identifications, and (c) begun collecting several new data sets. Here, we present updated and extended raw data from the first 12 years of the UHURU experiment (2008–2019). Data include daily rainfall data throughout the experiment; annual surveys of understory plant communities; annual censuses of woody-plant communities; annual measurements of individually tagged woody plants; monthly monitoring of flowering and fruiting phenology; every-other-month small-mammal mark-recapture data; and quarterly large-mammal dung surveys.

Key words/phrases: climate change; dik-dik (*Madoqua*); East African savannas; elephants (*Loxodonta africana*); extinction; food webs; grazing and browsing herbivores; impala (*Aepyceros melampus*); long-term ecological field experiments; plant communities; rangeland ecology; species interactions

Open Research: The complete data set is available as Supporting Information at: [*to be completed at proof stage*]. Associated data is also available at Dryad: [DOI assigned to deposited material].

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For Review Only

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Running header: Data from the UHURU experiment

Introduction

Large mammalian herbivores (≥ 5 kg; hereafter LMH) directly affect plant traits, population dynamics, community structure, and biodiversity (Huntly 1991, Milchunas and Lauenroth 1993, Anderson et al. 2007, Young et al. 2013, Staver and Bond 2014). In so doing, LMH indirectly affect the abundance, diversity, and behavior of other organisms (Keesing 1998, Pringle et al. 2007, Martin et al. 2010, Young et al. 2015, Daskin and Pringle 2016, Long et al. 2017, Guy et al. 2021). Understanding species interactions involving LMH is central to many fundamental questions in community and ecosystem ecology: To what extent do large-bodied consumers govern food-web structure and ecosystem function (van Langevelde et al. 2003, Frank 2005, Koerner et al. 2018, le Roux et al. 2020, Guy et al. 2021)? What are the legacies of Pleistocene megafauna (Janzen and Martin 1982, Guimarães et al. 2008, Smith et al. 2015) and the ecological contexts of early hominin evolution (Faith et al. 2019)? What are the consequences of large-mammal extirpation (Campbell et al. 1994, Brodie et al. 2009), and are such consequences reversible (Alston et al. 2019, Guyton et al. 2020, Lundgren et al. 2020)? How might actions taken to conserve or manage LMH populations affect the communities and ecosystems of which they are part (Walker et al. 1987, Weisberg et al. 2002, Goheen et al. 2018)?

Because large-scale, long-term field manipulations of the abundance and diversity of LMH are logistically challenging and expensive, there are few experimental data to inform two important questions linked to those listed above. First, are different size classes of LMH functionally redundant (*sensu* Walker 1992) or complementary (*sensu* Thibault et al. 2010) with respect to their effects on population-, community-, and system-level attributes? Previous work on this question has been mostly observational (but see Young et al. 2005, Staver et al. 2009, Pringle et al. 2014, Coverdale et al. 2021), making it difficult to isolate causal mechanisms.

Second, how do the direction and magnitude of LMH impacts vary across environmental gradients? Empirical tests of these questions often use meta-analysis (Chase et al. 2000, Hillebrand et al. 2007, Daskin and Pringle 2016; but see Bakker et al. 2006), which are valuable but can also confound multiple aspects of environmental variation, divergent methodologies and regional species pools, and other characteristics that inevitably differ across studies and locations (Paine 2010, Schmitz 2010). Long-term experiments that impose identical manipulations of LMH across gradients within ecosystems—but among sites with otherwise similar attributes—can bridge small-scale mechanistic studies and broad syntheses (Gruner et al. 2008).

Here, we present raw data from one of the few such experiments: the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment at the Mpala Research Centre and Conservancy in Kenya (**Fig. 1**). Initiated in 2008, the UHURU experiment selectively excludes nested subsets of a diverse LMH assemblage comprising ≥ 20 co-occurring species (Goheen et al. 2013). Three features distinguish UHURU from prior experiments: (1) selective, size-based exclusion of LMH; (2) replication across an important ecological gradient (rainfall) with minimal confounding variation in soils and species pools; and (3) plots that are sufficiently large (1 ha) to evaluate direct and indirect effects of LMH on both plants (e.g., Louthan et al. 2013, Ford et al. 2015, Coverdale et al. 2018) and smaller consumers such as invertebrates and small mammals (e.g., Young et al. 2015, Long et al. 2017, Guy et al. 2021). Several long-term LMH exclosures in Africa have recently been dismantled—including several of the Glade Legacies and Defaunation Experiment plots at Mpala (Goheen et al. 2018), plots in Hluhluwe-iMfolozi Park, South Africa (Staver and Bond 2014), and plots in Hwange National Park, Zimbabwe—underscoring the value of extended time series of data from the UHURU experiment.

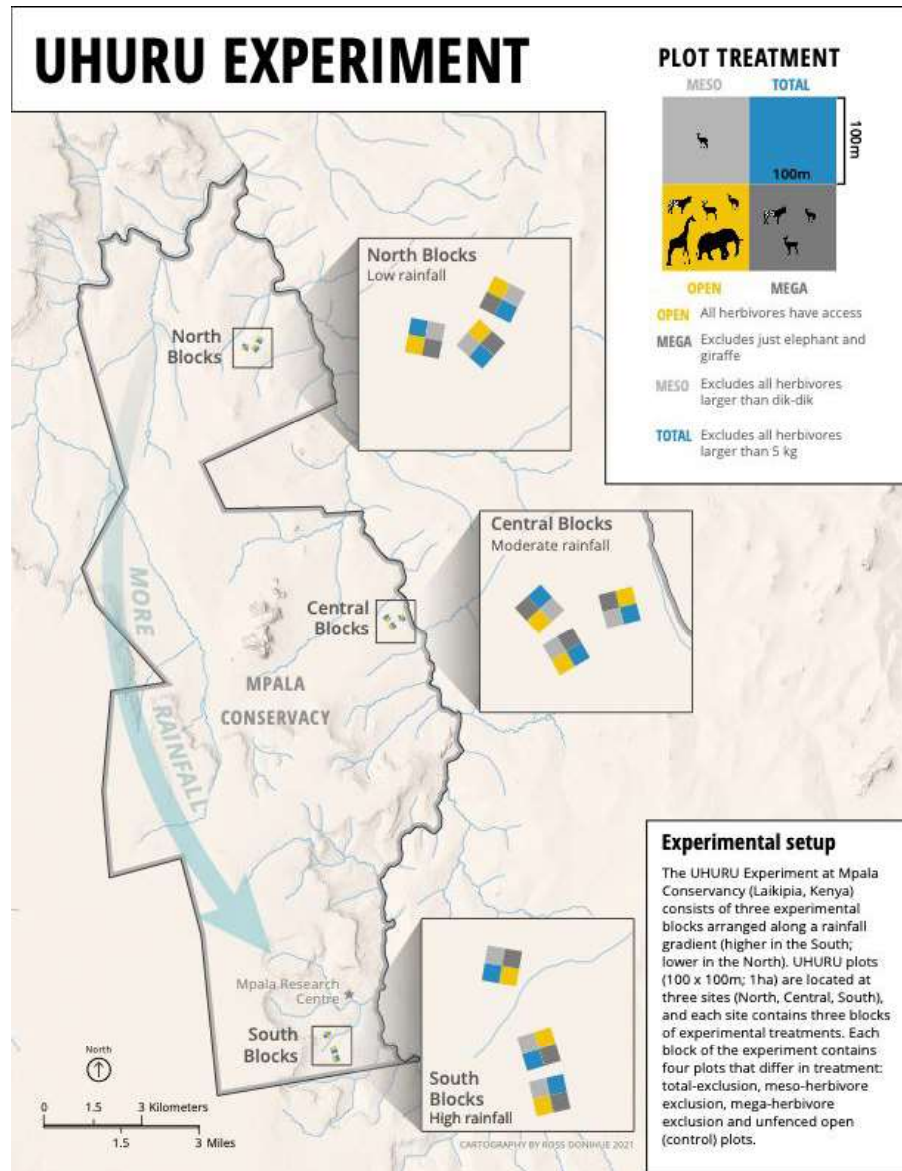


Figure 1. Schematic of the UHURU experiment at the Mpala Research Centre and Conservancy in central Kenya. The Ng'iro River runs along the eastern boundary of the property and the Narok River runs along the north. Each of the three experimental sites contains three replicate blocks, which in turn each comprise four contiguous 1-ha plots (total $n = 36$ plots, 9 per treatment).

79 The Mpala Research Centre and Conservancy are located in Laikipia County, Kenya
 80 (0°17'N, 37°52' E, 1600 m elevation), and the UHURU experiment spans the north-south axis of
 81 the property (**Fig. 1**). UHURU treatments exclude herbivores via three configurations of
 82 electrified fencing around 1-ha plots. The 'TOTAL' treatment (**Fig. 2A**) excludes all herbivores
 83 ≥ 5 kg. The 'MESO' treatment (**Fig. 2B**) excludes all megaherbivores, including African bush
 84 elephant (*Loxodonta africana*), reticulated giraffe (*Giraffa camelopardalis reticulata*), and
 85 hippopotamus (*Hippopotamus amphibius*), and mesoherbivores (> 40 kg, $< 1,000$ kg), including
 86 impala (*Aepyceros melampus*), plains zebra (*Equus quagga*), Grevy's zebra (*E. grevyi*), Defassa
 87 waterbuck (*Kobus defassa*), eland (*Taurotragus oryx*), African buffalo (*Syncerus caffer*),
 88 warthog (*Phacochoerus africanus*), and a half-dozen antelope species that are comparatively rare
 89 and occur patchily at Mpala; warthog have occasionally dug into MESO plots but are not
 90 routinely present. MESO differs from TOTAL mainly by excluding dik-dik (*Madoqua* cf. *M.*
 91 *guentheri*), which is the most abundant LMH species at Mpala (> 100 per km²; Ford and Goheen
 92 2015). In principle, three additional small antelopes are excluded by TOTAL but not MESO—
 93 bush duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), and klipspringer
 94 (*Oreotragus aureus*)—but these species are very rare in the UHURU experiment (Goheen et al.
 95 2013). The 'MEGA' (**Fig. 2C**) treatment consists of wires strung 2 m from ground level and
 96 excludes only megaherbivores ($\geq 1,000$ kg), namely elephant and reticulated giraffe;
 97 hippopotamus are not excluded by MEGA but rarely enter the plots. Unfenced 'OPEN' plots
 98 (**Fig. 2D**) serve as an unmanipulated control, accessible to all species.

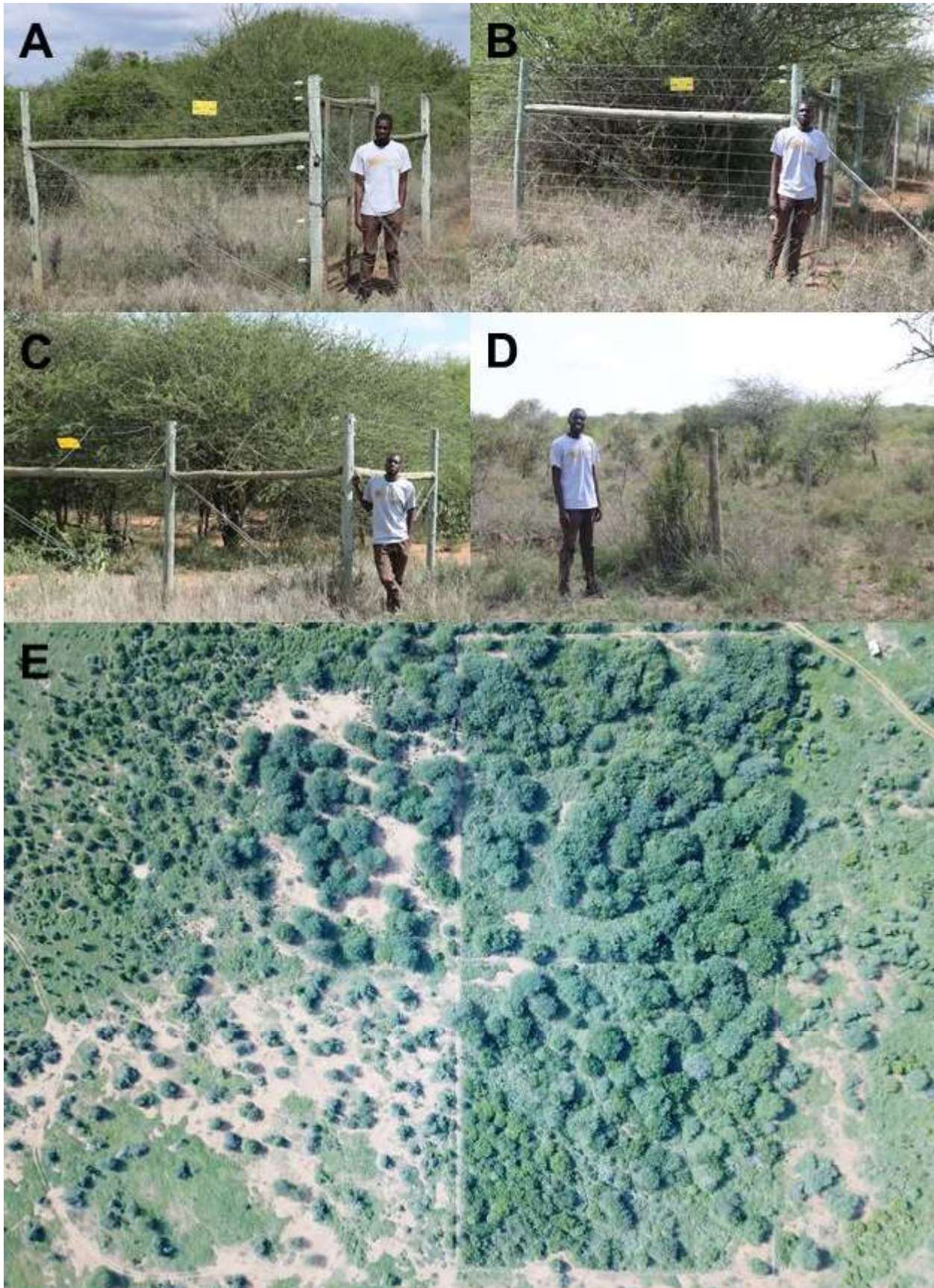
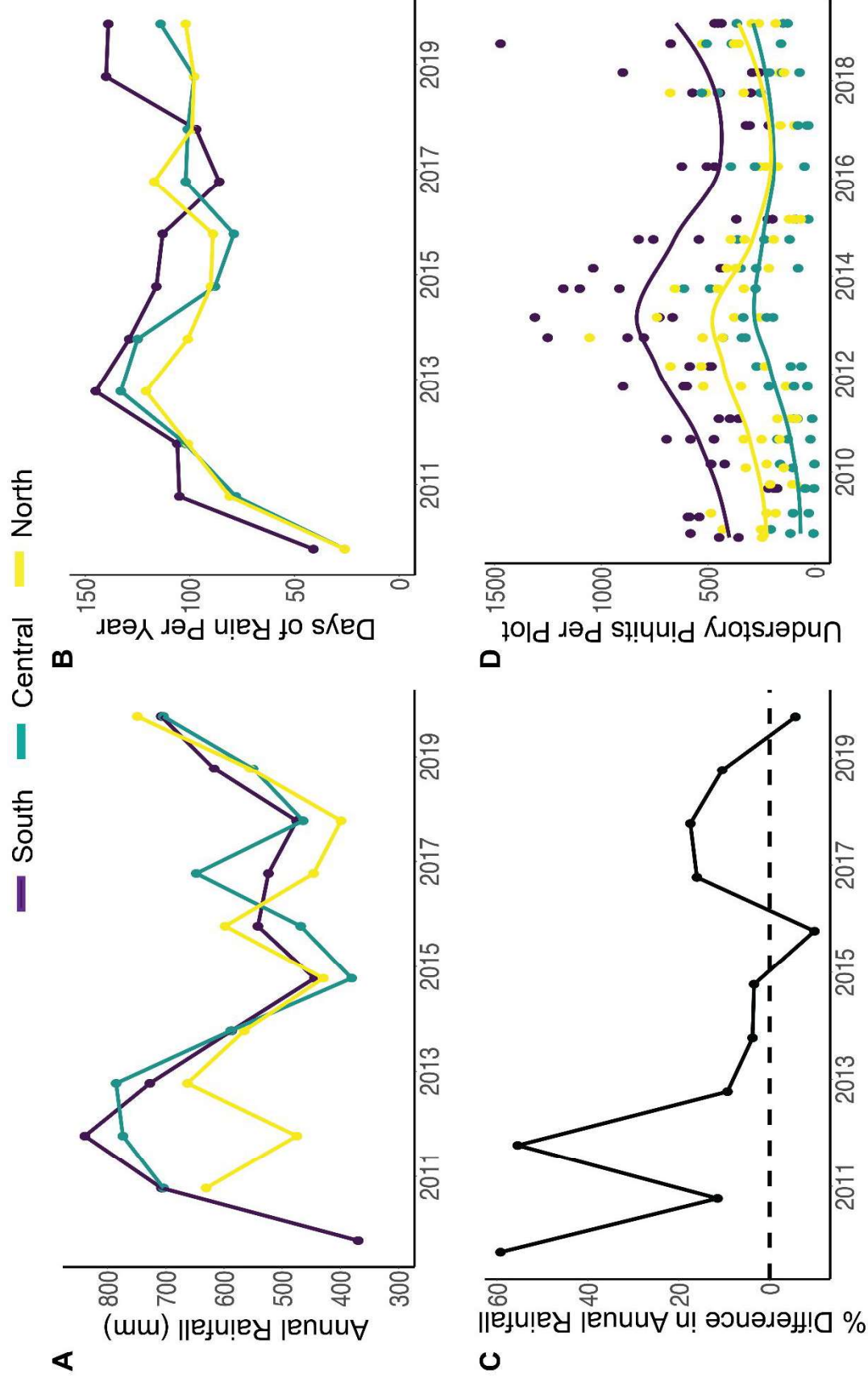


Figure 2. *Photographs of experimental treatments. (A) Total-exclusion (“TOTAL”) fences consist of 14 wires up to 2.4 m above ground level, with a 1 m high chain-link barrier at ground level. (B) Mesoherbivore-exclusion (“MESO”) fences consist of 11 parallel wires starting ~0.3 m above ground level and continuing to 2.4 m above ground level. (C) Megaherbivore-exclusion (“MEGA”) fences consist of two parallel wires starting 2 m above ground level. All fences are electrified using a solar charger and have a series of 1 m long electrified wires extending outwards to discourage large animals from contacting the fence; “TOTAL” and “MESO” fences also have a series of short vertical wires to connect the parallel horizontal wires and add structural stability. (D) “OPEN” control plots are unfenced, with boundaries demarcated by wooden posts at 10-m intervals. (E) Aerial view of a single experimental block of plots (North Block 1) in 2018; clockwise from top right: TOTAL, MESO, OPEN, and MEGA treatments. Photographs by L. Khasoha (A-D) and B. Hays (E).*

All plot types are accessible to small herbivores (e.g., hares, *Lepus* spp.) and most carnivores. Large carnivores may be partially excluded by TOTAL fences (leopards, *Panthera pardus*, and cheetahs, *Acinonyx jubatus*, have occasionally climbed in) but can access the other three treatments. These treatments have been continuously maintained (and rapidly repaired following occasional incursions and fence breakages by elephant and other species) since 2008.

Three randomized blocks—each containing one replicate of each treatment—are located at three different sites across a rainfall gradient spanning 20 km north to south (**Fig. 3**). Total annual rainfall increases from the North site (low rainfall; 2009–2019 range: 201–749 mm/y) to the Central (intermediate rainfall; 235–785 mm/y) and South sites (high rainfall; 369–839 mm/y). From 2009–2019, rainfall averaged 15% higher at the wettest site than the driest site



123

Figure 3. The UHURU experiment encompasses three sites along a 20 km north-to-south rainfall gradient. **(A)** Total annual rainfall was historically greater in the South (~640 mm/year) and Central (~580 mm/year) sites than the North (~440 mm/year) site (Goheen et al. 2013) but has increasingly converged across sites in recent years. Points show rainfall observed at each site in each year of the experiment. Data for the South site are missing 5 days (26 May – 30 May 2011). Data for the Central site are missing 23 days in Dec. 2015 and 15 days in Oct. 2016. **(B)** The South site receives more days of rain per year on average (mean \pm SD; 115 ± 23 days of rain per year) than the Central (102 ± 18 days of rain per year) and North sites (100 ± 12 days of rain per year). **(C)** Percent difference in annual rainfall between the South and North sites is positive overall (indicating greater annual rainfall at the South site) but has decreased since 2017. **(D)** Understory biomass (measured using the canopy-intercept method as pin hits per plot) has consistently been greatest in the South site (577 ± 288 pin hits per plot) and lower in the Central (189 ± 153 pin hits per plot) and North (308 ± 194 pin hits per plot) sites (which have increasingly converged since 2014). Points show pin hits per plot for each of the control plots during each semiannual understory survey; curves are smoothed lines for each site.

(range: -9 to 84%) (**Fig. 3**). Despite the trend of convergence across sites in total rainfall, the South site still receives more days of rain in a typical year (**Fig. 3B**) and supports higher biomass of understory vegetation (**Fig. 3D**) than the Central and North sites. This variation in rainfall over small spatial scales arises from Mpala's position in the rain shadow of Mt. Kenya, which lies ~60 km to the southeast. In the center of each plot, we maintain a permanent 60×60 m grid with stakes at 10 m intervals ($n = 49$ stakes) where we survey vegetation and small mammals.

Here, we present 13 data sets from the UHURU experiment, spanning 2008–2019. These raw data extend and update those from 2008–2013 provided in Kartzinel et al. (2014). These data sets include: **(1)** Geographic coordinates of the plots; **(2)** Daily rainfall at each site (2008-2019); **(3)** Semiannual pin-frame surveys of understory plant diversity and abundance at 49 stakes in each plot (2008-2019); **(4)** Semiannual surveys of understory composition within 49 small (0.25 m²) quadrats in each plot (2008-2019); **(5)** Semiannual surveys of understory composition within 49 larger (1 m²) quadrats in each plot (2008-2019); **(6)** Several canopy-intercept surveys integrating understory and woody vegetation at 49 stakes in each plot (2016-2018); **(7)** Annual size measurements of a subset of tagged and mapped trees in each plot (2009-2019); **(8)** Summaries of annual censuses of overstory plant composition for the 0.36 ha central grid in each plot (2009-2019); **(9)** Spatially explicit annual censuses of overstory plant composition for each 10×10 m cell of the 0.36 ha central grid in each plot (2009-2019); **(10)** Monthly survey of fruiting and flowering phenology in each plot (2012-2019); **(11)** Weekly seed rainfall from two dominant *Acacia* species at each site (2016-2019); **(12)** Dung surveys conducted at 2–3 month intervals in three parallel 60×5 m belt transects per plot (2009-2019); **(13)** Every-other-month mark-recapture sampling of small mammals in TOTAL and OPEN plots (2009-2019).

The associated metadata describe data collection protocols, along with refinements to these protocols that have been implemented as our understanding of the system has increased—including significant updates to plant taxonomy, supported by DNA barcodes and verification by botanical experts (Gill et al. 2019). Accordingly, the data presented here should be used preferentially over those previously published in Kartzinel et al. (2014). These data profile the annual-to-decadal scale ecological consequences of selectively excluding nested subsets of a

diverse LMH assemblage in a semi-arid African savanna ecosystem. We aim to periodically publish updated raw data throughout the (indefinite) duration of the experiment.

METADATA

Class I. Data set descriptors

A. Data set identity: Data collected from the UHURU experiment.

Title: Ecological consequences of large herbivore exclusion in an African savanna: 12 years of data from the UHURU experiment

B. Data set identification code: NA

C. Data set description:

1. Principal Investigators:

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Robert M. Pringle, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, United States of America.

Questions regarding these data may be directed to Jacob Goheen (jgoheen@uwyo.edu) and Robert Pringle (rpringle@princeton.edu).

2. Abstract: Diverse communities of large mammalian herbivores (LMH), once widespread, are now rare. LMH exert strong direct and indirect effects on community structure and ecosystem functions, and measuring these effects is important for testing ecological theory and for understanding past, current, and future environmental change. This in turn requires long-term experimental manipulations, owing to the slow and often nonlinear responses of populations and assemblages to LMH removal. Moreover, the effects of particular species or body-size classes within diverse LMH guilds are difficult to pinpoint, and the magnitude and even direction of these effects often depends on environmental context. Since 2008, we have maintained the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, a series of size-selective LMH exclosures replicated across a rainfall/productivity gradient in a semi-arid Kenyan savanna. The goals of the UHURU experiment are to measure the effects of removing successively smaller size classes of LMH (mimicking the process of size-biased extirpation) and to establish how these effects are shaped by spatial and temporal variation in rainfall. The UHURU experiment comprises three LMH-exclusion treatments and an unfenced control, applied to 9 randomized blocks of contiguous 1-ha plots ($n = 36$). The fenced treatments are: “MEGA” (exclusion of megaherbivores, elephant and giraffe); “MESO” (exclusion of herbivores ≥ 40 kg); and “TOTAL” (exclusion of herbivores ≥ 5 kg). Each block is replicated three times at three sites across the 20-km rainfall gradient, which has fluctuated over the course of the experiment. The first five years of data were published previously (*Ecological Archives* E095-064) and have been used in numerous studies. Since that publication, we have (a) continued to collect data following the original protocols, (b) improved the taxonomic resolution and accuracy of plant and small-mammal identifications, and (c) begun collecting several new data sets. Here, we present updated and extended raw data from the first 12 years of the UHURU experiment (2008–2019). Data

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218 every-other-month small-mammal mark-recapture data; and quarterly large-mammal dung
219 surveys.

220 **D. Key words:** climate change; dik-dik (*Madoqua*); East African savannas; elephants
221 (*Loxodonta africana*); extinction; food webs; grazing and browsing herbivores; impala
222 (*Aepyceros melampus*); long-term ecological field experiments; plant communities; Pleistocene
223 megafauna; rangeland ecology; species interactions

224

225 **Class II. Research origin descriptors**

226 **A. Overall project description:** The UHURU experiment excludes successively smaller-bodied
227 nested subsets of LMH (≥ 5 kg) ranging in size from dik-dik (~ 5 kg) to elephant ($\sim 3,000$ kg).

228 This design isolates the ecological impacts of different size classes of LMH and mimics the
229 effects of size-biased large-herbivore extinction. Replicates spanning a 20 km rainfall gradient
230 share similar soil characteristics and species pools. To test predictions about the independent and
231 interactive effects of LMH exclusion and rainfall variability, investigators continuously sample a
232 broad range of vegetation characteristics and animal responses.

233 **1. Identity:** Data from the UHURU experiment

234 **2. Originators:** Jacob R. Goheen, Robert M. Pringle, Todd M. Palmer.

235 **3. Period of study:** 2008–2019. Continuing. Data from 2008–2013 were published previously
236 (Kartzinel et al. 2014) but have been substantially updated (detailed descriptions of updates can
237 be found elsewhere in the metadata).

4. Objectives: To test predictions concerning the independent and interactive effects of herbivory by large mammals and rainfall variability on a broad range of ecological responses.

5. Abstract: See Section I.C.2.

6. Sources of funding: The UHURU experiment was built with seed funding from the Sherwood Family Foundation, grants from the National Sciences and Engineering Research Council of Canada, and the Universities of Florida and British Columbia. Support for maintenance and data collection has been provided by the US National Science Foundation (DEB-0709880, OISE-0852961, DEB-1355122, and IOS-1656527 to RMP; DEB-1547679, DEB-1930763, and DEB-2018405 to JRG; DEB-1930820 to TRK), the National Geographic Society, the University of Wyoming, the High Meadows Environmental Institute at Princeton University, The Nature Conservancy, and the Institute at Brown for Environment and Society. Data curation was partially funded by the Center for Advanced Systems Understanding (CASUS), which is financed by the German Federal Ministry of Education and Research (BMBF) and by the Saxon Ministry for Science, Art, and Tourism (SMWK) with tax funds on the basis of the budget approved by the Saxon State Parliament, and by the Elizabeth Gardner Norweb Summer Environmental Studies Scholarship from the Garden Club of America.

B. Research origin description

1. Site description: The UHURU experiment is located at the Mpala Research Centre and Conservancy (~200 km²) in Laikipia County, a semi-arid highland region in Kenya (0°17'N, 37°52' E, 1600 m above sea level). Mpala is in the rain shadow of Mt. Kenya, which imposes climatic variation across a relatively short distance, although the resulting rainfall gradient is unpredictable in any given year and has fluctuated over the course of the experiment. On average

from 2009-2019, total annual rainfall and number of days with rainfall were both 15% higher at the South (wettest) site than the North (driest) site.

2. Experimental design: In 2008, three fenced herbivore-exclusion treatments and an unfenced control were randomly assigned to contiguous 1 ha plots replicated three times at each of three sites along a rainfall gradient (36 total plots, 9 replicates per treatment). Although 1 ha is not large enough to detect some ecological effects of LMH, this spatial scale is adequate for documenting effects on individual-, population-, and community-level responses of plants, small mammals, and invertebrates (e.g., Goheen et al. 2013, Pringle et al. 2016, Guy et al. 2021), as well as behavioral (as opposed to numerical) responses of small mammals and mesoherbivores to the exclusion of all LMH and megaherbivores, respectively (e.g., Long et al. 2017, Wells et al. 2021). TOTAL exclosures exclude all LMH ≥ 5 kg but are accessible to hares and other smaller herbivores, as well as large (e.g., leopard, cheetah) and small (e.g., mongooses [*Ichneumia albicauda*, *Galerella sanguinea*, *Helogale parvula*], genets [*Genetta genetta*, *G. maculata*]) carnivores. These exclosures use 2.4 m high fences consisting of 14 strands of wire, electrically charged by solar-powered batteries, with a 1 m tall barrier consisting of 10 cm chain link fencing. MESO exclosures consist of 11 wires beginning 30 cm above the ground, allowing access to only the smallest LMH (predominately dik-dik), and excluding larger species. MEGA exclosures consist of two wires starting at 2 m above ground level and exclude only elephant and giraffe. OPEN plots are unfenced and demarcated by a series of 1 m tall wooden posts at 10 m intervals; these plots allow access to all LMH. On all fences, a series of 1 m long wires at 2 m height extend horizontally outward from plots to deter large herbivores from approaching the barriers. In January 2009, we added vertical connecting wires to TOTAL and MESO fences to increase security and stability. Exclosures are inspected and maintained by project personnel at

least once per week (and often more frequently). Rapid repairs are made whenever damage to the fencing is discovered. For the eight most common LMH between 2009 and 2019, mean enclosure effectiveness (assessed as the percent reduction in dung deposition between OPEN and exclusion plots) was 97% and ranged from 95% (for elephants) to 99% (for cattle/buffalo). Within each plot, a 0.36 ha grid (60×60 m) marked by 49 rebar stakes at 10 m intervals provides the spatial template for most experimental monitoring. Routine data collection (i.e., the data presented here) does not require destructive sampling. Any harvesting, as intermittently needed for individual studies, is minimized and confined to the outlying portions of each plot to avoid disturbance to the central 0.36 ha monitoring grid.

UHURU was designed to assess the effects of wild large herbivores. Mpala maintains a ranching operation with comparatively low stocking densities for the region, predominantly of cattle (1,270 head in 2021, ~6 individuals km⁻²), with smaller numbers of camel (130 head), sheep and goat (290 head), and a few donkeys. Herders are instructed and periodically reminded not to graze livestock in the plots, although camera trapping in 2010–2011 and anecdotal reports since then indicate that cattle do occasionally pass through OPEN and MEGA plots (Goheen et al. 2013); MESO and LMH plots are protected by locked gates. We do not have sufficient data to determine the exact frequency of such incursions and are unable to reliably distinguish buffalo from cattle dung in the field, but given the relatively low overall density of livestock on Mpala and the injunction against grazing in UHURU, we believe any effects of livestock are marginal. Conservatively, livestock can be interpreted as a low-density component of the diverse mesoherbivore size class, and in that respect may simulate ‘natural’ conditions of low-density pastoralism that prevailed in East African savannas for millennia. Future work in UHURU can

use camera trapping to quantify the frequency and intensity of cattle occupancy and thus refine inferences about the extent to which they contribute to net effects documented in the experiment.

3. Research methods:

Rainfall Monitoring: Rainfall has been continuously monitored since October 2008 at each of the three experimental sites (Goheen et al. 2013). At the outset of the experiment, rainfall was measured using cylindrical drip gauges (All Weather Rain Gauge, Productive Alternatives, Fergus Falls, MN). A single automated tipping-bucket rain gauge (RainLogger, Rainwise Inc., Bar Harbor, ME) was installed in one of the TOTAL plots at each site in June 2010; a second was installed in July 2011 and a third in April 2012 (Goheen et al. 2013), such that since 2012, rainfall has been logged in each of the 9 experimental blocks ($n = 3$ gauges per site). Because rainfall variability at this spatial scale is minimal, we use the average across the three gauges to characterize rainfall at each site. This design provides redundancy that is useful when rain gauges occasionally fail.

Understory Monitoring: Grasses and forbs are surveyed semiannually in February/March (dry season) and October (short rainy season). A 1 m² quadrat is placed immediately to the north of each of the 49 stakes demarcating in the center grid in each plot, and an additional 0.25 m² quadrat is placed within the larger quadrat. Species presence/absence is recorded within both quadrats. A 10-pin point frame is then positioned within the smaller quadrat, and the presence of bare soil and/or the total number of vegetation pin hits is recorded for each plant species (the canopy-intercept method; Frank and McNaughton 1990). From 2008–2012, individuals were identified to species (or to genus and morphospecies) using field guides and published species lists (Bogdan 1976, Blundell 1982, van Oudtshoorn 2009). Starting in 2012, we began a process of verifying and refining plant identifications in this data set through establishment of an

extensive collection of >1,781 herbarium reference specimens and corresponding DNA barcode data for >460 species, representing 92% of the roughly 500 vascular plants thought to occur at Mpala (Gill et al. 2019). To facilitate consistency in the face of taxonomic revisions and refinements of our own identifications, we maintain a list of voucher numbers that match each species to a reference specimen used for DNA barcoding and taxonomic verification by botanists at the National Museums of Kenya (Gill et al. 2019).

Individual Tree Monitoring: Individual-based surveys of trees focused on 10 tagged individuals per plot (or all individuals if there were less than 10 individuals per plot) of each of five common woody species, including the three dominant acacias (*Acacia* syn. *Vachellia etbaica*, *A. syn. Senegalia mellifera*, and *A. syn. Senegalia brevispica*: Fabaceae), *Croton dichogamus* (Euphorbiaceae), and *Balanites rotundifolia* (Zygophyllaceae). Plants were tagged in January 2009, and tagged individuals are resurveyed annually. The following data are recorded: survival, height (m), crown diameter (m), basal diameter (mm) and/or circumference (cm) at 15 cm from ground level, and the number of stems at ground level. Many additional trees were tagged in 2012 following the same monitoring protocol, but some of these additional trees were not monitored after 2015.

Woody Plant Censuses: Each year, a census is conducted of all trees and shrubs (i.e., species that reach ≥ 2 m tall at maturity) and large succulents (*Euphorbia* and *Opuntia* spp.) within the 0.36 ha central grids. Individuals are identified, and the number of individuals of each species are recorded for each of five height classes (<1 m, 1–2 m, 2–3 m, 3–4 m, >4 m). The first census, in 2009, omitted *Euphorbia* spp., and censuses prior to 2012 omitted *Opuntia* spp.

Phenology Surveys: Each month, the presence or absence of reproductive bodies (flowers and/or fruits) is recorded for all plant species within the 0.36 ha plot centers during a 30-minute scan of each plot. This data set was initiated in 2012 and is continuing.

Vertical Vegetation Structure: From December 2016 to December 2018, we conducted several surveys that integrate understory and overstory vegetation using a modified version of the canopy-intercept method (Frank and McNaughton 1990). At each of the 49 grid stakes in each plot, a telescoping pole was placed on the ground and extended up through the canopy (Kartzinel and Pringle 2020). All vegetation touches were recorded, along with plant species identity, height of the intercept, and whether the touch was stem or leaf. The objectives of these surveys were (a) to quantify understory and overstory vegetation simultaneously using a consistent methodology and (b) to quantify the vertical profile of vegetation biomass within the plots.

Seed Rainfall Monitoring: Seed rainfall weights were recorded weekly for two of the dominant tree species, *Acacia (Vachellia) etbaica* and *Acacia (Senegalia) mellifera* just outside of the UHURU plots at the South, Central, and North sites from 2016–2019 (**Fig. 4**). Nets were placed underneath the tree canopy, and all seeds that accumulated in the nets were weighed weekly. Three individuals per species were monitored at each site, one each from the following height classes: 2-3m, 3-4m, and >4m. Seed rainfall from 18 trees were measured in total.



Figure 4. Set-up for the *Acacia* seed rainfall monitoring, showing an *Acacia etbaica* near the Central 2 block with net for catching seeds. Seeds in the net were collected and weighed weekly. Photo by S. Kurukura.

LMH Dung Surveys: We regularly survey LMH dung (starting in 2009 at roughly quarterly intervals, later increased in 2016 to every two months) to assess the efficacy of each experimental treatment in excluding the intended classes of LMH and to provide a relative index of LMH activity levels (Goheen et al. 2013, Wells et al. 2021). In each plot, three parallel 6×60 m belt transects (spaced 30 m apart within the 0.36 ha plot centers) are walked by 2-4 observers, who count all discrete dung piles, identify the species of origin (Stuart and Stuart 2000), and crush the dung after identification to prevent recounting in subsequent surveys. Rates of dung decomposition do not differ markedly among the three sites (Goheen et al. 2013).

Small Mammal Sampling: Continuously since 2009, small mammals are live-trapped at two-month intervals in TOTAL and OPEN plots using Sherman traps baited with peanut butter and

oats (Goheen et al. 2013). In each trapping session, a single trap is set at each of the 49 grid stakes in the center of each plot, opened in the late afternoon, and checked and closed in the early morning. Trapping sessions last four consecutive days. All small mammals are fit with a numbered ear tag on each ear, with the exception of individuals in the genera *Acomys*, *Crocidura*, *Mus*, and *Steatomys*, which are too small or too fragile (Seifert et al. 2012) for ear tags. Instead, we mark individuals in these genera with permanent markers for subsequent identification within trapping sessions. Sample sizes and movement patterns by the four most commonly captured and marked small mammals (Hinde's rock rat [*Aethomys hindei*], rufous elephant shrew [*Elephantulus rufescens*], fringe-tailed gerbil [*Gerbilliscus robustus*], and Mearns' pouched mouse [*Saccostomus mearnsi*])—represented by (a) the maximum distance moved by an individual within a four-day sampling period; (b) the probability of remaining on a sampling grid between successive periods; and (c) the number of times an individual was captured on more than one plot—indicate that the 1 ha UHURU plot size is sufficiently large to measure effects of LMH exclusion on small mammals (**Table 1**). Initial misclassifications of Harrington's tateril (*Taterillus harringtoni*) as juvenile fringe-tailed gerbil (*Gerbilliscus robustus*) were identified in May 2011 via DNA barcoding (Goheen et al. 2013). We now distinguish these two species based on hindfoot length (<34 mm for *T. harringtoni*), mass (<60 g for *T. harringtoni*), and tail (tufted for *T. harringtoni*). With the aid of mitochondrial DNA barcoding, we have identified the tiny fat mouse (*Steatomys parvus*) as present in the community. We believe that there was a single misidentification of this species (for *Mus* spp. “Umus”) in Kartzin et al. 2014, which we have updated in the current data set. Mitochondrial DNA barcoding has also been used to confirm the presence of at least 3 *Mus* phylotypes in the plots that we cannot reliably distinguish in the field. Two *Crocidura* species (*C. elgonius* and *C.*

gracilipes) are morphologically indistinguishable except for size at maturity; *C. elgonius* are <7 g, while *C. gracilipes* are >7 g. We record weight, sex, age, and reproductive condition for every captured individual.

Species	Sample Size	Maximum Distance (m)	Probability of Remaining	Inter-Plot Movement
<i>Aethomys hindes</i>	2184	78.1	0.83	261
<i>Elephantulus rufescens</i>	561	67.1	0.88	49
<i>Gerbilliscus robustus</i>	1684	78.1	0.83	153
<i>Saccostomus mearnsi</i>	1125	72.1	0.93	83

Table 1. UHURU plots (1 ha) are large relative to the scale of movement by the four most commonly captured and marked small mammals within and between sampling periods. Data include the maximum distance moved within a four-day sampling bout, the probability of an individual remaining within a sampling grid between successive sampling periods, and the total number of times that any individual has been captured in more than one plot between periods.

Permit history: Kenya National Commission for Science, Technology & Innovation permits to Robert M. Pringle: NCST/5/002/R/656, NACOSTI/P/14/0592/1852, NACOSTI/P/18/0592/21481, NACOSTI/P/20/6262; University of Wyoming Institutional Animal Care and Use Committee Protocol Approval (Jacob Goheen; SKMBT_60112030515200; SKMBT_60112030515201; SKMBT_60112030515202; SKMBT_60112030515210).

C. Project personnel: In addition to the authors, the UHURU experiment team has employed several full-time Kenyan field assistants, who collected field data and maintain the experimental infrastructure. Simon Lima, Jackson Lima, Antony Eshwah (deceased), and Mohamud Mohamed have worked in this capacity.

425

426 **Class III. Data set status and accessibility**427 **A. Status**428 **1. Latest update:** December 2019.429 **2. Latest archive date:** December 2019.430 **3. Metadata status:** The metadata are current and stored with the data.

431 **4. Data verification:** Data verification was conducted by J. Alston and C. Reed, with assistance
432 from S. Kurukura, A. Hassan, L. Khasoha, S. Weiner, J. Goheen, R. Pringle, and T. Kartzinel.

433 **B. Accessibility**434 **1. Contact person(s):** Jacob Goheen, e-mail: jgoheen@uwyo.edu, phone: 307-509-0280.

435 Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA.

436 Robert Pringle, e-mail: rpringle@princeton.edu, phone 609-258-8273. Department of Ecology &
437 Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

438 **2. Storage location and medium:** Original data files exist on the authors' personal computers
439 (several of which are routinely backed up on servers housed at their home institutions) and are
440 replicated on external hard drives, Google Drive, and Dropbox in .xlsx, .csv, and .txt files. Paper
441 copies of original field data sheets are stored safely in a facility rented by Jacob Goheen and
442 Robert Pringle at the Mpala Research Centre. Data format and the programs required to access
443 and manipulate data will be kept current throughout the duration of this study.

444 **3. Copyright restrictions:** None.

445 **4. Proprietary restrictions:** Notification about when and how data are used is appreciated but
446 not mandated by the authors. Given ongoing research in the UHURU experiment and the
447 continuation of most of the data sets presented here, we strongly recommend contacting J.

Goheen and R. Pringle prior to using these data, as updated data are available at regular intervals.

We ask that users of UHURU data cite this data paper when using the data.

C. Costs: None.

Class IV. Data structural descriptors

There are 13 files that provide location, rainfall, habitat, vegetation, and animal data from the UHURU experiment. There are several column headings that identify the scale and location of sampling, appearing in many of the 13 datasets that follow.

Label	Attribute	Definition
Survey/Census	Survey or Census number	Numeric
Year	Year of sampling	2008–2019
Month	Month of sampling	Month
Site	Plot location	North (dry), Central (intermediate), South (wet)
Block	Replicate	Numeric (1–3)
Treatment	Experimental treatment type (definitions refer to the excluded LMH species)	OPEN = open plots; MEGA = megaherbivore; MESO = meso- and megaherbivore; TOTAL = all LMH excluded; OUT = near to, but outside, experimental plots (rarely used)
Plot	Unique plot identifiers	Comprises site, block, and treatment
Rebar/Section	Identity of the rebar stake within the central grid	Alphanumeric ID of rebar stakes (49 per plot). “Section” denotes the grid cell

		immediately below and to the right of a stake (e.g., 1A denotes the grid cell bounded by stakes 1A, 1B, 2A, and 2B).
Species	Species	Species of plant or animal. Some species are identified only to genus/morphospecies.

1. PLOT COORDINATES

A. Data set file

Identity: PLOT_COORDINATES.csv

Size: 4 KB

Format: CSV

Contents: Includes the name and location of all experimental plots. There are 81 lines of data, with each record providing location data for the axes of each plot.

B. Variable information

Column	Attribute	Definition
3-6	Coordinates	Columns 3 and 4 are UTM coordinates, columns 5 and 6 are decimal degree coordinates.

C. Data anomalies: None.

2. RAINFALL DATA

A. Data set file

Identity: RAINFALL_2008-2019.csv

Size: 263 KB

Contents: Daily data for each rain gauge.

B. Variable information

Column	Attribute	Definition
1	Date	Date in form of day-month-year.
2–13	Daily rainfall (mm)	Daily rain gauge readings at each block. “man” denotes manual rain gauges used early in the project, while “aut” denotes automatic rain gauges that were installed beginning in 2010.
14-16	Averages (mm)	Average rainfall across gauges at a given site.

C. Data anomalies: NA denotes days on which no data were recorded by a given gauge due to equipment failure. No gauges recorded data from the South site from 26 May 2011 to 30 May 2011, and no gauges recorded data for the Central site from 9 December 2015 to 31 December 2015 and 9 October 2016 to 23 October 2016, and therefore data is missing for these dates. No gauges recorded data for the North site from 9 December 2015 to 31 December 2015, but data from a nearby long-term hydrology study was substituted for those dates (Caylor et al. 2017).

3. VEGETATION DATA – PIN-FRAME SURVEYS

A. Data set file

Identity: UNDERSTORY_PIN_2008-2019.csv

Size: 29.1 MB

Contents: Understory pinhit vegetation data recorded within each of the smaller quadrats (0.25 m²) in each of 20 semiannual surveys from October 2008 to March 2019.

B. Variable information

Column	Attribute	Definition
9	Bare ground	Number of pins with bare ground and no vegetation
10:331	Species names	Genus and species of plant recorded in understory vegetation surveys

C. Data anomalies: Two surveys were performed per year, except for 2015, 2016, and 2019; only one survey was performed for each of those years. Notes on taxonomy, including changes across the 20 surveys, are recorded in rows 2-4. Row 2 (Notes) indicates the name that a plant was assigned during each of the 20 surveys. Row 3 (Changes) provides details on name changes, including lumping, splitting, and new identifications. Row 4 (SKS#) provides the voucher number matching each species to a specimen used to confirm identification by botanists at the National Museums of Kenya in conjunction with DNA barcoding (Gill et al. 2019). Taxonomic identities are considered provisional if labeled as morphospecies, as genus with “sp.”, or as “unknown.” Identifications of morphospecies are pending ongoing taxonomic investigation and DNA barcoding. Taxa are recorded as NA in surveys for which those taxa were not recognized. We include all 20 surveys conducted from 2008-2019 to facilitate tracking of nomenclatural updates that have been guided by detailed botanical investigations and DNA barcoding over this period (cf. Kartzinel et al. 2014). For Surveys 1-14, trees (e.g., *Acacia* spp., *Boscia angustifolia*) and other overstory species (e.g., *Opuntia stricta*, *Euphorbia* spp.) were not counted. Starting in Survey 15, seedlings and saplings of these species were included in the surveys as components of the understory. For Surveys 1-14, these species are listed as NA. Elsewhere throughout the data set, NA indicates data that are missing or suffered from transcription errors.

4. VEGETATION DATA – SMALL (0.25 m²) QUADRATS

A. Data set file

Identity: UNDERSTORY_SMQUAD_2008-2019.csv

Size: 28.7 MB

Contents: Understory vegetation data recorded in small quadrats (0.25 m²) at each rebar stake during 20 semiannual surveys from October 2008 to March 2019.

B. Variable information

Column	Attribute	Definition
9	Bare ground	Percent cover
10:331	Species names	Genus and species of plant recorded in understory vegetation surveys

C. Data anomalies: Two surveys were performed per year, except for 2015, 2016, and 2019; only one survey was performed for each of those years. Notes on taxonomy, including changes across the 20 surveys, are recorded in rows 2-4. Row 2 (Notes) indicates the name that a plant was assigned during each of the 20 surveys. Row 3 (Changes) provides details on name changes, including lumping, splitting, and new identifications. Row 4 (SKS#) provides the voucher number matching each species to a specimen used to confirm identification by botanists at the National Museums of Kenya in conjunction with DNA barcoding (Gill et al. 2019). Taxonomic identities are considered provisional if labeled as morphospecies, as genus with “sp.”, or as “unknown.” Identifications of morphospecies are pending ongoing taxonomic investigation and DNA barcoding. Taxa are recorded as NA in surveys for which those taxa were not recognized. We include all 20 surveys conducted from 2008-2019 to facilitate tracking of nomenclatural updates that have been guided by detailed botanical investigations and DNA barcoding over this

period (cf. Kartzinel et al. 2014). For Surveys 1-14, trees (e.g., *Acacia* spp., *Boscia angustifolia*) and other overstory species (e.g., *Opuntia stricta*, *Euphorbia* spp.) were not counted. Starting in Survey 15, seedlings and saplings of these species were included in the surveys as components of the understory. For Surveys 1-14, these species are listed as NA. Elsewhere throughout the data set, NA indicates data that are missing or suffered from transcription errors. For surveys 1-14, data are binary presence/absence data (values = 0 or 1), and surveys 15-20 include percent cover data.

5. VEGETATION DATA – LARGE (1 m²) QUADRATS

A. Data set file

Identity: UNDERSTORY_LGQUAD_2008-2019.csv

Size: 28.7 MB

Contents: Understory vegetation data recorded in large quadrats (1 m²) at each rebar during 20 semiannual surveys from October 2008 to March 2019.

B. Variable information

Column	Attribute	Definition
9	Bare ground	Percent cover
10:331	Species names	Genus and species of plant recorded in understory vegetation surveys

C. Data anomalies: Two surveys were performed per year, except for 2015, 2016, and 2019; only one survey was performed for each of those years. Notes on taxonomy, including changes across the 20 surveys, are recorded in rows 2-4. Row 2 (Notes) indicates the name that a plant was assigned during each of the 20 surveys. Row 3 (Changes) provides details on name changes,

including lumping, splitting, and new identifications. Row 4 (SKS#) provides the voucher number matching each species to a specimen used to confirm identification by botanists at the National Museums of Kenya in conjunction with DNA barcoding (Gill et al. 2019). Taxonomic identities are considered provisional if labeled as morphospecies, as genus with “sp.”, or as “unknown.” Identifications of morphospecies are pending ongoing taxonomic investigation and DNA barcoding. Taxa are recorded as NA in surveys for which those taxa were not recognized. We include all 20 surveys conducted from 2008-2019 to facilitate tracking of nomenclatural updates that have been guided by detailed botanical investigations and DNA barcoding over this period (cf. Kartzinel et al. 2014). For Surveys 1-14, trees (e.g., *Acacia* spp. and *Boscia angustifolia*) and other overstory species (e.g., *Opuntia stricta* and *Euphorbia* sp.) were not counted. Starting in Survey 15, seedlings and saplings of these species were included in the surveys as components of the understory. For Surveys 1-14, these species are listed as NA. Elsewhere throughout the data set, NA indicates data that are missing or suffered from transcription errors. For surveys 1-14, data are binary presence/absence data (values = 0 or 1), and surveys 15-20 include percent cover data.

6. VEGETATION DATA – VERTICAL VEGETATION STRUCTURE

A. Data set file

Identity: VERTICAL_VEGETATION_2016-2018.csv

Size: 3.8 MB

Contents: Annual surveys of vertical vegetation taken at the 49 stakes in each plot.

B. Variable information

Column	Attribute	Definition
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8	Voucher Number	Specimen number for identification at National Museums of Kenya
9	Stem	Stem (1) or non-stem (0; e.g., leaf, flower)
10	Height	Height at which plant touched tree pole (cm)

C. Data anomalies: Three vertical vegetation surveys were performed between December 2016 and December 2018. A partial survey in October 2017 (Survey 1B) includes only the South plots. During Surveys 1-2, *Achyranthes aspera* was identified to subspecies, but in Survey 3 it was identified only to species. During data curation for this publication, several species names were updated from those that have been used in previous studies from UHURU: an unknown *Eragrostis* species was identified as *Eragrostis cylindriflora*, an unknown Malvaceae was identified as *Hibiscus sparseaculeatus*, an unknown *Pavonia* species was identified as *Pavonia patens*, and an unknown *Pollichia* species was identified as *Atriplex semibaccata*. *Sida alba* was changed to *Sida ovata*, *Abutilon mauritianum* was changed to *Pavonia burchellii*, and *Cyathula cylindrica* was changed to *Cyathula orthacantha*. All instances of *Cyathula orthacantha* associated with Voucher # RRH_13_040 as described in Gill et al. (2019) were changed to *Pupalia lappacea*. Nomenclatural updates (cf. Kartzin et al. 2014) have been guided by detailed botanical investigations of voucher specimens at the National Museums of Kenya as well as DNA barcoding, and are consistent with changes made in the understory, tree census, and tree survey datasets.

7. VEGETATION DATA – LONGITUDINAL TREE SURVEYS

A. Data set file

Identity: TREE_SURVEYS_2009-2019.csv

590 **Size:** 1.3 MB

591 **Contents:** Annual tree surveys and measurements for each plot (2009–2019).

592 **B. Variable information**

Column	Attribute	Definition
9	Tag Number	Current tag number that identifies a tree.
10	Dead	Whether the tree is dead (Y = Yes; N = No).
11	Height	Tree height (m).
12	Length	Length of canopy extent (m).
13	Width	Length of canopy perpendicular to first measurement (m).
14	Circumference	Circumference of tree (cm).
15	Number of stems	Number of stems at ground level.

593

594 **C. Data anomalies:** Re-measuring tree heights and circumferences can be imprecise due to
 595 factors including variability in how high on the stem the calipers or measuring tape was placed or
 596 the inadvertent measurement of the wrong basal stem on a tagged tree. Nonetheless, tree heights
 597 and diameters can change dramatically from year to year, due to damage by elephants, drought,
 598 etc. We scrutinized data and identified all trees with changes in height or circumference greater
 599 than three standard deviations between any two consecutive surveys to identify and correct
 600 inadvertent miscalculations, transcription errors, or other verifiable mistakes; otherwise, we
 601 assumed measurements to be accurate, even when differing markedly between successive years.

No tree survey was conducted in 2018. Some trees and plots were inadvertently measured twice in the same year—these values can be used to estimate measurement error. Many additional trees were tagged in 2012 following the same monitoring protocol as the other trees, but some of these additional trees were not monitored after 2015; these trees are denoted by a tree tag number beginning with “JM”.

8. VEGETATION DATA – TREE CENSUS SUMMARY

A. Data set file

Identity: TREE_CENSUS_SUMMARY.csv

Size: 259 KB

Contents: Summary spreadsheet at the plot level showing number of individuals of each species in each size class in each year per plot (2009-2019).

B. Variable information

Column	Attribute	Definition
8–14	Size classes	Trees per size class per subplot
15	Total	Total trees per species per subplot

C. Data anomalies: No census was conducted in 2011 or 2015. No data are available for N1MESO and N3OPEN in 2019. Some data were missing for S2MESO and S3MESO in 2016, S3MESO in 2017, and C1TOTAL and C3TOTAL in 2019 (so summarized data may be meaningfully undercounted in these plots in these years). *Euphorbia* spp. were present but not

recorded in 2009; *Opuntia* spp. were present but not recorded until 2012. Otherwise, when tree species are not listed in a year, this indicates that the tree species was not present in that year.

9. VEGETATION DATA – TREE CENSUS DETAILED

A. Data set file

Identity: TREE_CENSUS_DETAILED.csv

Size: 2.7 MB

Contents: Spreadsheet showing the data for each 10 × 10 m sampled section of each plot (2009-2019).

B. Variable information

Column	Attribute	Definition
9-15	Size classes	The number of trees for the corresponding species in each size class
16	Total	The total number of trees measured.

C. Data anomalies: No census was conducted in 2011 or 2015. No data are available for N1MESO and N3OPEN in 2019. Some data were missing for S2MESO and S3MESO in 2016, S3MESO in 2017, and C1TOTAL and C3TOTAL in 2019 (so summarized data may be meaningfully undercounted in these plots in these years). *Euphorbia* spp. were present but not recorded in 2009; *Opuntia* spp. were present but not recorded until 2012. Otherwise, when tree species are not listed in a year, this indicates that the tree species was not present in that year. In some sections in some years, two rows for the same species were inadvertently recorded with

different numbers of trees. We recommend that data users average these entries to account for these data errors.

10. VEGETATION DATA - FLOWER AND FRUIT PHENOLOGY

A. Data set file

Identity: PHENOLOGY_2012-2019.csv

Size: 1.2 MB

Contents: Spreadsheet detailing the presence of flowers and fruit on species of plants at each site of the UHURU experiment.

B. Variable information

Column	Attribute	Definition
4	Flower or fruit	Whether the observation represents flowers or fruits
5-7	Presence at sites	Presence of flowers or fruits during the month and year denoted by the row (1: present, 0: absent or missing from site)

C. Data anomalies: June and December 2012 data quantified numbers of flowers and fruits for a small subset of plant species. From August 2013, monthly phenology data were collected. These data include a broader range of species than 2012 data, but only specify whether a species was flowering (not fruiting) in a given site. From January 2017, the data include the presence of both flowers and fruits (separately) for each species in each site. Zeros may indicate either that no flowers or fruits were present, or that the species itself was not present or not detected in a plot; analyses based on absence of flowering/fruiting should therefore be conducted with caution.

11. VEGETATION DATA - *ACACIA* SEED RAINFALL

A. Data set file

Identity: ACACIA_SEED_RAIN_2016-2019.csv

Size: 83 KB

Contents: Seed rain from *Acacia etbaica* and *Acacia mellifera* across the rainfall gradient from December 2016 to October 2019.

B. Variable information

Column	Attribute	Definition
2	Tree ID	Unique identifier for each tree, including species and ID number (AE = <i>Acacia etbaica</i> ; AM = <i>Acacia mellifera</i>)
3	Species	<i>Acacia</i> tree species (<i>Acacia etbaica</i> or <i>Acacia mellifera</i>)
4	Height class	Trees divided into categories based on height (2-3 m, 3-4 m, or >4 m)
6	Weight	Weight of seeds caught in net underneath tree canopy (g; marked as “not checked” if tree was not checked in a given week)

C. Data anomalies: Missing data are indicated by NA.

12. ANIMAL DATA – DUNG SURVEYS

A. Data set file

Identity: DUNG_SURVEYS.csv

Size: 532 KB

Contents: Dung count survey data, 2009–2019

B. Variable information

Column	Attribute	Definition
9	Line	Transect line number (corresponding with the tree census and small mammal trapping grid)
10-40	Source of dung	Species of origin and age (old vs. new dung assessed by color).

C. Data anomalies: Dung of several species pairs cannot be differentiated reliably in the field. These include hares (*Lepus* cf. *L. capensis* and *L. cf. L. saxatilis*; Kartzin et al. 2019), plains and Grevy’s zebra (*Equus quagga* and *E. grevyi*), African buffalo (*Syncerus caffer*) and domestic cattle (*Bos indicus*). We made no effort to differentiate predator dung (rare) according to species; instead, we lumped them within three size classes: large, medium, and small. A transcription error occurred when recording block number in the Central plots during the January 2011 survey. As a result, Block 2 and Block 3 are coded as NA to reflect the uncertainty. No data are available for the Central and South sites for Survey 19.

13. ANIMAL DATA – SMALL MAMMAL SURVEYS

A. Data set file

Identity: SMALL_MAMMALS_2009-2019.csv

Size: 2.7 MB

Contents: Small mammal captures during capture periods 1–63 (May 2009 – December 2019).

B. Variable information

Column	Attribute	Definition
10	Night	Trap night (per site per survey)
11	Species	<p> Acke = <i>Acomys kemp</i> = Kemp's spiny mouse Acpe = <i>Acomys percivali</i> = Percival's spiny mouse Aehi = <i>Aethomys hindei</i> = Hinde's rock rat Arna = <i>Arvicanthis nairobae</i> = Nairobi grass rat Arni = <i>Arvicanthis niloticus</i> = African grass rat Crel = <i>Crocidura elgonius</i> = Elgon shrew Crgr = <i>Crocidura gracilipes</i> = Peter's musk shrew Croc = <i>Crocidura</i> spp. = white-toothed shrews Dend = <i>Dendromus</i> spp. = climbing mice Elru = <i>Elephantulus rufescens</i> = rufous elephant shrew Geni = <i>Gerbiliscus nigricaudus</i> = black-tailed gerbil Gero = <i>Gerbiliscus robustus</i> = fringe-tailed gerbil Grdo = <i>Grammomys dolichurus</i> = woodland thicket rat Grmi = <i>Graphiurus microtis</i> = small-eared dormouse Mana = <i>Mastomys natalensis</i> = Natal multi-mammate rat NA = used for traps that were closed but empty as well as traps that were missing or damaged; also used for plots in which no animals were caught that night Rara = <i>Rattus rattus</i> = black rat Same = <i>Saccostomus mearnsi</i> = northern pouched mouse Stpa = <i>Steatomys parvus</i> = tiny fat mouse Taha = <i>Taterillus harringtoni</i> = Harrington's tateril Uarvi = <i>Arvicanthis</i> spp. = grass rats Umus = <i>Mus</i> spp. = pygmy mice Unkn = unknown Zehi = <i>Zelatomys hildegardae</i> = Hildegard's broad-headed stink mouse </p>
12	Capture	C = capture; R = recapture
13	Sex	F = female; M = male

14	Condition	L = lactating N = none (no reproductive condition) P = pregnant PL = pregnant and lactating S = scrotal
15	Age	A = adult; S = subadult; J = juvenile
16	Left hind foot	Length of left hind foot (mm)
17	Left tag	Tag number at survey
18	Original tag	Original tag number. Particularly useful for cross-referencing with left_tag column when a tag was missing or replaced
19	ID	Individual identifier
20	Marks	Number of paint marks left on animals without ear tags
21	Weight	Weight (g)
22	Notes	Indicate areas where individual identifications or measurement interpretations require caution. In particular, this column indicates if ID tags were lost or replaced, or if an individual escaped during evaluation. The condition of some individual captures could be consequential, such as individuals captured dead or with broken limbs. Also may indicate when a non-small mammal species is caught, such as a bird, squirrel, or dwarf mongoose.

C. Data anomalies: NA indicates no data. Based on mitochondrial DNA barcoding data, along with geographic range and morphological data, the species listed as *Mus sorella* (MUSO) on the original field data sheets is now identified as the tiny fat mouse, *Steatomys parvus* (STPA). Harrington's tateril (*Taterillus harringtoni*) was initially misclassified as juvenile fringe-tailed gerbil (*Gerbilliscus robustus*) but was identified in May 2011 via DNA barcoding (Goheen et al. 2013). We now differentiate between the two species based on hindfoot length (<34 mm for *T. harringtoni*), mass (<60 g for *T. harringtoni*), and tail (tufted for *T. harringtoni*). Mitochondrial DNA barcoding has also been used to confirm the presence of at least 3 *Mus* phylotypes in the plots that we cannot reliably distinguish in the field; all are listed as *Umus* (*Mus* spp.) in the dataset. Two *Crocidura* species (*C. elgonius* and *C. gracilipes*) are distinguished by size at maturity; *C. elgonius* are <7 g, and *C. gracilipes* are >7 g.

Class V. Supplemental descriptors

A. Data acquisition: Data can be accessed at the link located in the supporting information for this data paper.

B. Quality assurance/quality control procedures: Measures taken for quality control are detailed in each data set description above. Data were recorded in the field on paper, entered into spreadsheets via Microsoft Excel, and checked for outliers or omissions at that time, and subsequently scrutinized for similar issues during data curation for this publication. Any known data anomalies are reported with the corresponding data set. Original data sheets are stored at Mpala Research Centre.

C. Related materials: NA

D. Computer programs and data-processing algorithms: NA

713 **E. Archiving:** Data are archived at the link located in the supporting information for this data
714 paper.

715 **F. Publications**

716 Brown, B.R.P. 2021. Communities within a community: the gut microbiomes of co-occurring
717 small mammals in a Kenyan savanna. Ph.D. Thesis, Brown University.

718 Brown, B.R.P., J.R. Goheen, S.D. Newsome, R.M. Pringle, T.M. Palmer, L. Khasoha, and T.R.
719 Kartzinel. Host phylogeny and functional traits differentiate gut microbiomes in a diverse
720 natural community of small mammals. In review.

721 Coverdale, T.C. 2018. Patterns of plant defense, diversity, and fitness in an African savanna.
722 Ph.D. Thesis, Princeton University.

723 Coverdale, T.C., I.J. McGeary, R.D. O'Connell, T.M. Palmer, J.R. Goheen, M. Sankaran, D.J.
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G. History of data set usage: Data are currently in use by several of the authors on this data paper to answer research questions related to the goals of the UHURU experiment. Publications that have included data from the UHURU experiment are listed in Section V.F.

1. Data request history: Data from the UHURU experiment are frequently requested for research conducted by outside research groups. We encourage researchers to contact J. Goheen and R. Pringle to check whether more recent but as-yet-unpublished UHURU data are available.

2. Data set updates history: Data from the UHURU experiment were originally published in 2014 (Kartzinel et al. 2014). Since publication of this original data paper, we have (a) collected additional data according to the original protocols, (b) improved the taxonomic resolution and accuracy of plant and small mammal identifications, and (c) begun collecting several new data sets. Here, we present updated and extended data from the UHURU experiment (current through 2019).

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Ecological consequences of large herbivore exclusion in an African savanna: 12 years of data from the UHURU experiment

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Running header: Data from the UHURU experiment

Introduction

Large mammalian herbivores (≥ 5 kg; hereafter LMH) directly affect plant traits, population dynamics, community structure, and biodiversity (Huntly 1991, Milchunas and Lauenroth 1993, Anderson et al. 2007, Young et al. 2013, Staver and Bond 2014). In so doing, LMH indirectly affect the abundance, diversity, and behavior of other organisms (Keesing 1998, Pringle et al. 2007, Martin et al. 2010, Young et al. 2015, Daskin and Pringle 2016, Long et al. 2017, Guy et al. 2021). Understanding species interactions involving LMH is central to many fundamental questions in community and ecosystem ecology: To what extent do large-bodied consumers govern food-web structure and ecosystem function (van Langevelde et al. 2003, Frank 2005, Koerner et al. 2018, le Roux et al. 2020, Guy et al. 2021)? What are the legacies of Pleistocene megafauna (Janzen and Martin 1982, Guimarães et al. 2008, Smith et al. 2015) and the ecological contexts of early hominin evolution (Faith et al. 2019)? What are the consequences of large-mammal extirpation (Campbell et al. 1994, Brodie et al. 2009), and are such consequences reversible (Alston et al. 2019, Guyton et al. 2020, Lundgren et al. 2020)? How might actions taken to conserve or manage LMH populations affect the communities and ecosystems of which they are part (Walker et al. 1987, Weisberg et al. 2002, Goheen et al. 2018)?

Because large-scale, long-term field manipulations of the abundance and diversity of LMH are logistically challenging and expensive, there are few experimental data to inform two important questions linked to those listed above. First, are different size classes of LMH functionally redundant (*sensu* Walker 1992) or complementary (*sensu* Thibault et al. 2010) with respect to their effects on population-, community-, and system-level attributes? Previous work on this question has been mostly observational (but see Young et al. 2005, Staver et al. 2009, Pringle et al. 2014, Coverdale et al. 2021), making it difficult to isolate causal mechanisms.

Second, how do the direction and magnitude of LMH impacts vary across environmental gradients? Empirical tests of these questions often use meta-analysis (Chase et al. 2000, Hillebrand et al. 2007, Daskin and Pringle 2016; but see Bakker et al. 2006), which are valuable but can also confound multiple aspects of environmental variation, divergent methodologies and regional species pools, and other characteristics that inevitably differ across studies and locations (Paine 2010, Schmitz 2010). Long-term experiments that impose identical manipulations of LMH across gradients within ecosystems—but among sites with otherwise similar attributes—can bridge small-scale mechanistic studies and broad syntheses (Gruner et al. 2008).

Here, we present raw data from one of the few such experiments: the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment at the Mpala Research Centre and Conservancy in Kenya (**Fig. 1**). Initiated in 2008, the UHURU experiment selectively excludes nested subsets of a diverse LMH assemblage comprising ≥ 20 co-occurring species (Goheen et al. 2013). Three features distinguish UHURU from prior experiments: (1) selective, size-based exclusion of LMH; (2) replication across an important ecological gradient (rainfall) with minimal confounding variation in soils and species pools; and (3) plots that are sufficiently large (1 ha) to evaluate direct and indirect effects of LMH on both plants (e.g., Louthan et al. 2013, Ford et al. 2015, Coverdale et al. 2018) and smaller consumers such as invertebrates and small mammals (e.g., Young et al. 2015, Long et al. 2017, Guy et al. 2021). Several long-term LMH exclosures in Africa have recently been dismantled—including several of the Glade Legacies and Defaunation Experiment plots at Mpala (Goheen et al. 2018), plots in Hluhluwe-iMfolozi Park, South Africa (Staver and Bond 2014), and plots in Hwange National Park, Zimbabwe—underscoring the value of extended time series of data from the UHURU experiment.

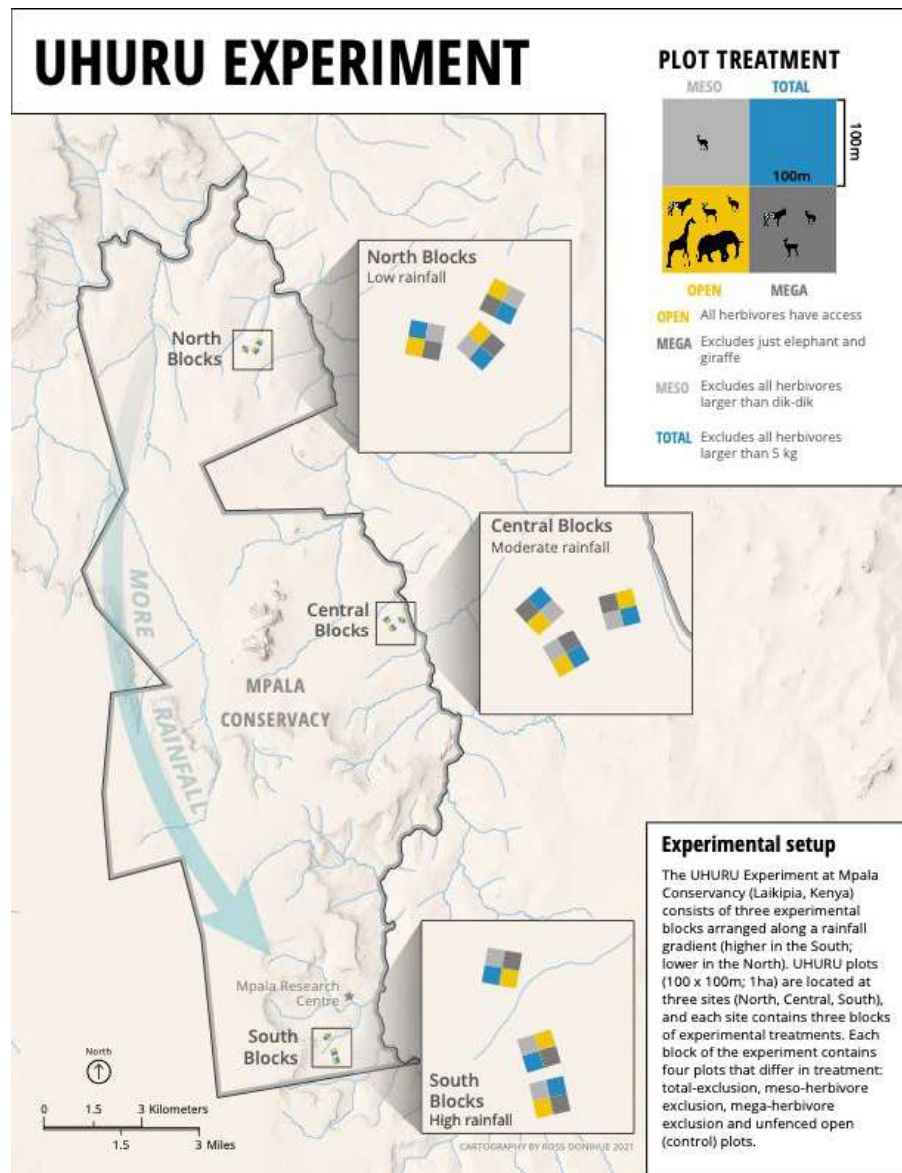


Figure 1. Schematic of the UHURU experiment at the Mpala Research Centre and Conservancy in central Kenya. The Ng'iro River runs along the eastern boundary of the property and the Narok River runs along the north. Each of the three experimental sites contains three replicate blocks, which in turn each comprise four contiguous 1-ha plots (total $n = 36$ plots, 9 per treatment).

79 The Mpala Research Centre and Conservancy are located in Laikipia County, Kenya
 80 (0°17'N, 37°52' E, 1600 m elevation), and the UHURU experiment spans the north-south axis of
 81 the property (**Fig. 1**). UHURU treatments exclude herbivores via three configurations of
 82 electrified fencing around 1-ha plots. The 'TOTAL' treatment (**Fig. 2A**) excludes all herbivores
 83 ≥ 5 kg. The 'MESO' treatment (**Fig. 2B**) excludes all megaherbivores, including African bush
 84 elephant (*Loxodonta africana*), reticulated giraffe (*Giraffa camelopardalis reticulata*), and
 85 hippopotamus (*Hippopotamus amphibius*), and mesoherbivores (> 40 kg, $< 1,000$ kg), including
 86 impala (*Aepyceros melampus*), plains zebra (*Equus quagga*), Grevy's zebra (*E. grevyi*), Defassa
 87 waterbuck (*Kobus defassa*), eland (*Taurotragus oryx*), African buffalo (*Syncerus caffer*),
 88 warthog (*Phacochoerus africanus*), and a half-dozen antelope species that are comparatively rare
 89 and occur patchily at Mpala; warthog have occasionally dug into MESO plots but are not
 90 routinely present. MESO differs from TOTAL mainly by excluding dik-dik (*Madoqua* cf. *M.*
 91 *guentheri*), which is the most abundant LMH species at Mpala (> 100 per km²; Ford and Goheen
 92 2015). In principle, three additional small antelopes are excluded by TOTAL but not MESO—
 93 bush duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), and klipspringer
 94 (*Oreotragus aureus*)—but these species are very rare in the UHURU experiment (Goheen et al.
 95 2013). The 'MEGA' (**Fig. 2C**) treatment consists of wires strung 2 m from ground level and
 96 excludes only megaherbivores ($\geq 1,000$ kg), namely elephant and reticulated giraffe;
 97 hippopotamus are not excluded by MEGA but rarely enter the plots. Unfenced 'OPEN' plots
 98 (**Fig. 2D**) serve as an unmanipulated control, accessible to all species.

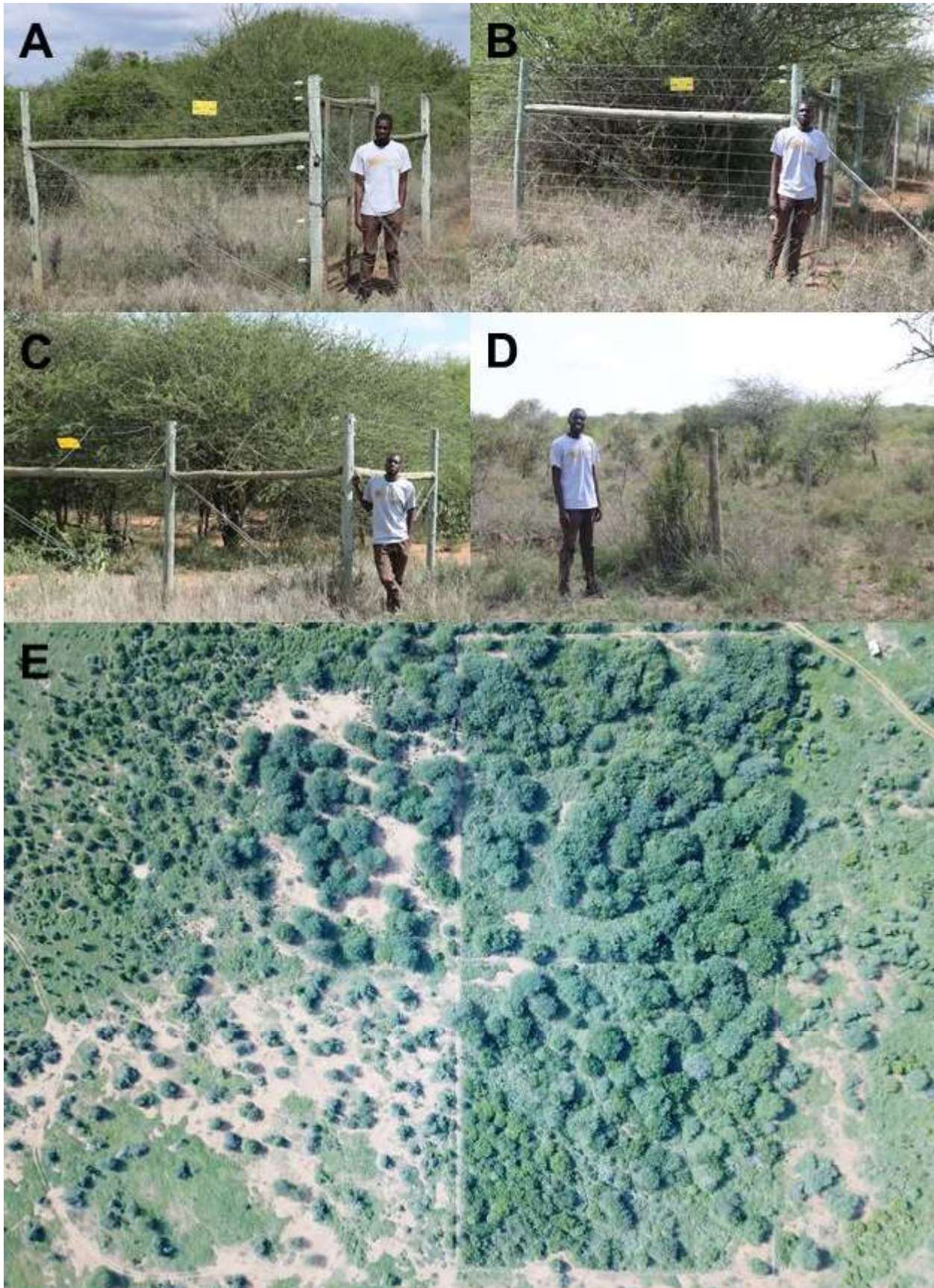


Figure 2. *Photographs of experimental treatments. (A) Total-exclusion (“TOTAL”) fences consist of 14 wires up to 2.4 m above ground level, with a 1 m high chain-link barrier at ground level. (B) Mesoherbivore-exclusion (“MESO”) fences consist of 11 parallel wires starting ~0.3 m above ground level and continuing to 2.4 m above ground level. (C) Megaherbivore-exclusion (“MEGA”) fences consist of two parallel wires starting 2 m above ground level. All fences are electrified using a solar charger and have a series of 1 m long electrified wires extending outwards to discourage large animals from contacting the fence; “TOTAL” and “MESO” fences also have a series of short vertical wires to connect the parallel horizontal wires and add structural stability. (D) “OPEN” control plots are unfenced, with boundaries demarcated by wooden posts at 10-m intervals. (E) Aerial view of a single experimental block of plots (North Block 1) in 2018; clockwise from top right: TOTAL, MESO, OPEN, and MEGA treatments. Photographs by L. Khasoha (A-D) and B. Hays (E).*

All plot types are accessible to small herbivores (e.g., hares, *Lepus* spp.) and most carnivores. Large carnivores may be partially excluded by TOTAL fences (leopards, *Panthera pardus*, and cheetahs, *Acinonyx jubatus*, have occasionally climbed in) but can access the other three treatments. These treatments have been continuously maintained (and rapidly repaired following occasional incursions and fence breakages by elephant and other species) since 2008.

Three randomized blocks—each containing one replicate of each treatment—are located at three different sites across a rainfall gradient spanning 20 km north to south (**Fig. 3**). Total annual rainfall increases from the North site (low rainfall; 2009–2019 range: 201–749 mm/y) to the Central (intermediate rainfall; 235–785 mm/y) and South sites (high rainfall; 369–839 mm/y). From 2009–2019, rainfall averaged 15% higher at the wettest site than the driest site

South Central North

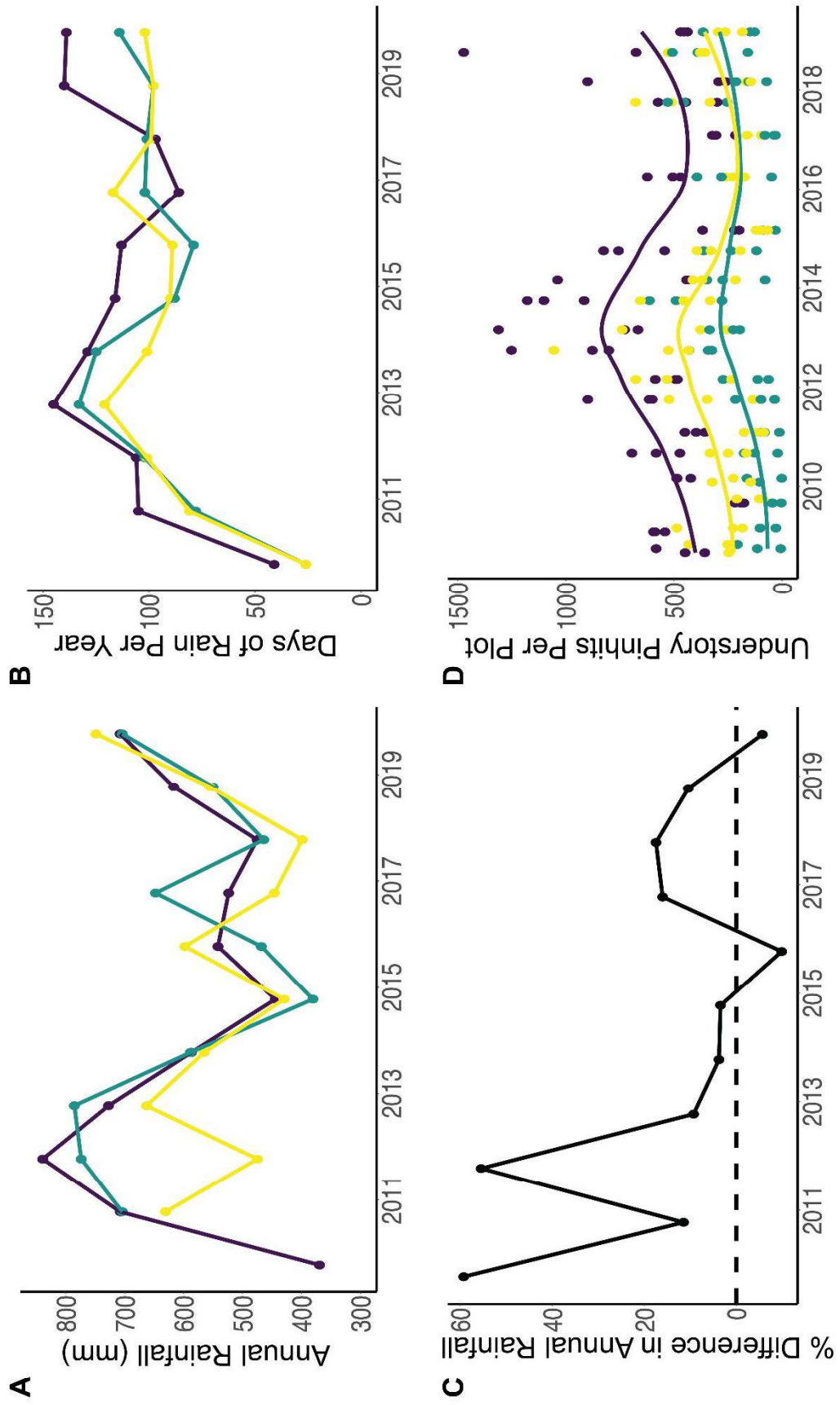


Figure 3. The UHURU experiment encompasses three sites along a 20 km north-to-south rainfall gradient. **(A)** Total annual rainfall was historically greater in the South (~640 mm/year) and Central (~580 mm/year) sites than the North (~440 mm/year) site (Goheen et al. 2013) but has increasingly converged across sites in recent years. Points show rainfall observed at each site in each year of the experiment. Data for the South site are missing 5 days (26 May – 30 May 2011). Data for the Central site are missing 23 days in Dec. 2015 and 15 days in Oct. 2016. **(B)** The South site receives more days of rain per year on average (mean \pm SD; 115 ± 23 days of rain per year) than the Central (102 ± 18 days of rain per year) and North sites (100 ± 12 days of rain per year). **(C)** Percent difference in annual rainfall between the South and North sites is positive overall (indicating greater annual rainfall at the South site) but has decreased since 2017. **(D)** Understory biomass (measured using the canopy-intercept method as pin hits per plot) has consistently been greatest in the South site (577 ± 288 pin hits per plot) and lower in the Central (189 ± 153 pin hits per plot) and North (308 ± 194 pin hits per plot) sites (which have increasingly converged since 2014). Points show pin hits per plot for each of the control plots during each semiannual understory survey; curves are smoothed lines for each site.

(range: -9 to 84%) (**Fig. 3**). Despite the trend of convergence across sites in total rainfall, the South site still receives more days of rain in a typical year (**Fig. 3B**) and supports higher biomass of understory vegetation (**Fig. 3D**) than the Central and North sites. This variation in rainfall over small spatial scales arises from Mpala's position in the rain shadow of Mt. Kenya, which lies ~60 km to the southeast. In the center of each plot, we maintain a permanent 60×60 m grid with stakes at 10 m intervals ($n = 49$ stakes) where we survey vegetation and small mammals.

Here, we present 13 data sets from the UHURU experiment, spanning 2008–2019. These raw data extend and update those from 2008–2013 provided in Kartzinel et al. (2014). These data sets include: **(1)** Geographic coordinates of the plots; **(2)** Daily rainfall at each site (2008-2019); **(3)** Semiannual pin-frame surveys of understory plant diversity and abundance at 49 stakes in each plot (2008-2019); **(4)** Semiannual surveys of understory composition within 49 small (0.25 m²) quadrats in each plot (2008-2019); **(5)** Semiannual surveys of understory composition within 49 larger (1 m²) quadrats in each plot (2008-2019); **(6)** Several canopy-intercept surveys integrating understory and woody vegetation at 49 stakes in each plot (2016-2018); **(7)** Annual size measurements of a subset of tagged and mapped trees in each plot (2009-2019); **(8)** Summaries of annual censuses of overstory plant composition for the 0.36 ha central grid in each plot (2009-2019); **(9)** Spatially explicit annual censuses of overstory plant composition for each 10×10 m cell of the 0.36 ha central grid in each plot (2009-2019); **(10)** Monthly survey of fruiting and flowering phenology in each plot (2012-2019); **(11)** Weekly seed rainfall from two dominant *Acacia* species at each site (2016-2019); **(12)** Dung surveys conducted at 2–3 month intervals in three parallel 60×5 m belt transects per plot (2009-2019); **(13)** Every-other-month mark-recapture sampling of small mammals in TOTAL and OPEN plots (2009-2019).

The associated metadata describe data collection protocols, along with refinements to these protocols that have been implemented as our understanding of the system has increased—including significant updates to plant taxonomy, supported by DNA barcodes and verification by botanical experts (Gill et al. 2019). Accordingly, the data presented here should be used preferentially over those previously published in Kartzinel et al. (2014). These data profile the annual-to-decadal scale ecological consequences of selectively excluding nested subsets of a

diverse LMH assemblage in a semi-arid African savanna ecosystem. We aim to periodically publish updated raw data throughout the (indefinite) duration of the experiment.

METADATA

Class I. Data set descriptors

A. Data set identity: Data collected from the UHURU experiment.

Title: Ecological consequences of large herbivore exclusion in an African savanna: 12 years of data from the UHURU experiment

B. Data set identification code: NA

C. Data set description:

1. Principal Investigators:

Jacob R. Goheen, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, United States of America.

Tyler R. Kartzinel, Department of Ecology and Evolutionary Biology; Institute at Brown for Environment and Society, Brown University, Providence, Rhode Island, United States of America.

Todd M. Palmer, Department of Biology, University of Florida, Gainesville, Florida, United States of America.

Robert M. Pringle, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, United States of America.

Questions regarding these data may be directed to Jacob Goheen (jgoheen@uwyo.edu) and Robert Pringle (rpringle@princeton.edu).

2. Abstract: Diverse communities of large mammalian herbivores (LMH), once widespread, are now rare. LMH exert strong direct and indirect effects on community structure and ecosystem functions, and measuring these effects is important for testing ecological theory and for understanding past, current, and future environmental change. This in turn requires long-term experimental manipulations, owing to the slow and often nonlinear responses of populations and assemblages to LMH removal. Moreover, the effects of particular species or body-size classes within diverse LMH guilds are difficult to pinpoint, and the magnitude and even direction of these effects often depends on environmental context. Since 2008, we have maintained the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, a series of size-selective LMH exclosures replicated across a rainfall/productivity gradient in a semi-arid Kenyan savanna. The goals of the UHURU experiment are to measure the effects of removing successively smaller size classes of LMH (mimicking the process of size-biased extirpation) and to establish how these effects are shaped by spatial and temporal variation in rainfall. The UHURU experiment comprises three LMH-exclusion treatments and an unfenced control, applied to 9 randomized blocks of contiguous 1-ha plots ($n = 36$). The fenced treatments are: “MEGA” (exclusion of megaherbivores, elephant and giraffe); “MESO” (exclusion of herbivores ≥ 40 kg); and “TOTAL” (exclusion of herbivores ≥ 5 kg). Each block is replicated three times at three sites across the 20-km rainfall gradient, which has fluctuated over the course of the experiment. The first five years of data were published previously (*Ecological Archives* E095-064) and have been used in numerous studies. Since that publication, we have (a) continued to collect data following the original protocols, (b) improved the taxonomic resolution and accuracy of plant and small-mammal identifications, and (c) begun collecting several new data sets. Here, we present updated and extended raw data from the first 12 years of the UHURU experiment (2008–2019). Data

include daily rainfall data throughout the experiment; annual surveys of understory plant communities; annual censuses of woody-plant communities; annual measurements of individually tagged woody plants; monthly monitoring of flowering and fruiting phenology; every-other-month small-mammal mark-recapture data; and quarterly large-mammal dung surveys.

D. Key words: climate change; dik-dik (*Madoqua*); East African savannas; elephant (*Loxodonta africana*); extinction; food webs; grazing and browsing herbivores; impala (*Aepyceros melampus*); long-term ecological field experiments; plant communities; rangeland ecology; species interactions

Class II. Research origin descriptors

A. Overall project description: The UHURU experiment excludes successively smaller-bodied nested subsets of LMH (≥ 5 kg) ranging in size from dik-dik (~ 5 kg) to elephant ($\sim 3,000$ kg). This design isolates the ecological impacts of different size classes of LMH and mimics the effects of size-biased large-herbivore extinction. Replicates spanning a 20 km rainfall gradient share similar soil characteristics and species pools. To test predictions about the independent and interactive effects of LMH exclusion and rainfall variability, investigators continuously sample a broad range of vegetation characteristics and animal responses.

1. Identity: Data from the UHURU experiment

2. Originators: Jacob R. Goheen, Robert M. Pringle, Todd M. Palmer.

3. Period of study: 2008–2019. Continuing. Data from 2008–2013 were published previously (Kartzinel et al. 2014) but have been substantially updated (detailed descriptions of updates can be found elsewhere in the metadata).

4. Objectives: To test predictions concerning the independent and interactive effects of herbivory by large mammals and rainfall variability on a broad range of ecological responses.

5. Abstract: See Section I.C.2.

6. Sources of funding: The UHURU experiment was built with seed funding from the Sherwood Family Foundation, grants from the National Sciences and Engineering Research Council of Canada, and the Universities of Florida and British Columbia. Support for maintenance and data collection has been provided by the US National Science Foundation (DEB-0709880, OISE-0852961, DEB-1355122, and IOS-1656527 to RMP; DEB-1547679, DEB-1930763, and DEB-2018405 to JRG; DEB-1930820 to TRK), the National Geographic Society, the University of Wyoming, the High Meadows Environmental Institute at Princeton University, The Nature Conservancy, and the Institute at Brown for Environment and Society. Data curation was partially funded by the Center for Advanced Systems Understanding (CASUS), which is financed by the German Federal Ministry of Education and Research (BMBF) and by the Saxon Ministry for Science, Art, and Tourism (SMWK) with tax funds on the basis of the budget approved by the Saxon State Parliament, and by the Elizabeth Gardner Norweb Summer Environmental Studies Scholarship from the Garden Club of America.

B. Research origin description

1. Site description: The UHURU experiment is located at the Mpala Research Centre and Conservancy (~200 km²) in Laikipia County, a semi-arid highland region in Kenya (0°17'N, 37°52' E, 1600 m above sea level). Mpala is in the rain shadow of Mt. Kenya, which imposes climatic variation across a relatively short distance, although the resulting rainfall gradient is unpredictable in any given year and has fluctuated over the course of the experiment. On average

from 2009-2019, total annual rainfall and number of days with rainfall were both 15% higher at the South (wettest) site than the North (driest) site.

2. Experimental design: In 2008, three fenced herbivore-exclusion treatments and an unfenced control were randomly assigned to contiguous 1 ha plots replicated three times at each of three sites along a rainfall gradient (36 total plots, 9 replicates per treatment). Although 1 ha is not large enough to detect some ecological effects of LMH, this spatial scale is adequate for documenting effects on individual-, population-, and community-level responses of plants, small mammals, and invertebrates (e.g., Goheen et al. 2013, Pringle et al. 2016, Guy et al. 2021), as well as behavioral (as opposed to numerical) responses of small mammals and mesoherbivores to the exclusion of all LMH and megaherbivores, respectively (e.g., Long et al. 2017, Wells et al. 2021). TOTAL exclosures exclude all LMH ≥ 5 kg but are accessible to hares and other smaller herbivores, as well as large (e.g., leopard, cheetah) and small (e.g., mongooses [*Ichneumia albicauda*, *Galerella sanguinea*, *Helogale parvula*], genets [*Genetta genetta*, *G. maculata*]) carnivores. These exclosures use 2.4 m high fences consisting of 14 strands of wire, electrically charged by solar-powered batteries, with a 1 m tall barrier consisting of 10 cm chain link fencing. MESO exclosures consist of 11 wires beginning 30 cm above the ground, allowing access to only the smallest LMH (predominately dik-dik), and excluding larger species. MEGA exclosures consist of two wires starting at 2 m above ground level and exclude only elephant and giraffe. OPEN plots are unfenced and demarcated by a series of 1 m tall wooden posts at 10 m intervals; these plots allow access to all LMH. On all fences, a series of 1 m long wires at 2 m height extend horizontally outward from plots to deter large herbivores from approaching the barriers. In January 2009, we added vertical connecting wires to TOTAL and MESO fences to increase security and stability. Exclosures are inspected and maintained by project personnel at

least once per week (and often more frequently). Rapid repairs are made whenever damage to the fencing is discovered. For the eight most common LMH between 2009 and 2019, mean enclosure effectiveness (assessed as the percent reduction in dung deposition between OPEN and exclusion plots) was 97% and ranged from 95% (for elephants) to 99% (for cattle/buffalo). Within each plot, a 0.36 ha grid (60×60 m) marked by 49 rebar stakes at 10 m intervals provides the spatial template for most experimental monitoring. Routine data collection (i.e., the data presented here) does not require destructive sampling. Any harvesting, as intermittently needed for individual studies, is minimized and confined to the outlying portions of each plot to avoid disturbance to the central 0.36 ha monitoring grid.

UHURU was designed to assess the effects of wild large herbivores. Mpala maintains a ranching operation with comparatively low stocking densities for the region, predominantly of cattle (1,270 head in 2021, ~6 individuals km⁻²), with smaller numbers of camel (130 head), sheep and goat (290 head), and a few donkeys. Herders are instructed and periodically reminded not to graze livestock in the plots, although camera trapping in 2010–2011 and anecdotal reports since then indicate that cattle do occasionally pass through OPEN and MEGA plots (Goheen et al. 2013); MESO and LMH plots are protected by locked gates. We do not have sufficient data to determine the exact frequency of such incursions and are unable to reliably distinguish buffalo from cattle dung in the field, but given the relatively low overall density of livestock on Mpala and the injunction against grazing in UHURU, we believe any effects of livestock are marginal. Conservatively, livestock can be interpreted as a low-density component of the diverse mesoherbivore size class, and in that respect may simulate ‘natural’ conditions of low-density pastoralism that prevailed in East African savannas for millennia. Future work in UHURU can

use camera trapping to quantify the frequency and intensity of cattle occupancy and thus refine inferences about the extent to which they contribute to net effects documented in the experiment.

3. Research methods:

Rainfall Monitoring: Rainfall has been continuously monitored since October 2008 at each of the three experimental sites (Goheen et al. 2013). At the outset of the experiment, rainfall was measured using cylindrical drip gauges (All Weather Rain Gauge, Productive Alternatives, Fergus Falls, MN). A single automated tipping-bucket rain gauge (RainLogger, Rainwise Inc., Bar Harbor, ME) was installed in one of the TOTAL plots at each site in June 2010; a second was installed in July 2011 and a third in April 2012 (Goheen et al. 2013), such that since 2012, rainfall has been logged in each of the 9 experimental blocks ($n = 3$ gauges per site). Because rainfall variability at this spatial scale is minimal, we use the average across the three gauges to characterize rainfall at each site. This design provides redundancy that is useful when rain gauges occasionally fail.

Understory Monitoring: Grasses and forbs are surveyed semiannually in February/March (dry season) and October (short rainy season). A 1 m² quadrat is placed immediately to the north of each of the 49 stakes demarcating in the center grid in each plot, and an additional 0.25 m² quadrat is placed within the larger quadrat. Species presence/absence is recorded within both quadrats. A 10-pin point frame is then positioned within the smaller quadrat, and the presence of bare soil and/or the total number of vegetation pin hits is recorded for each plant species (the canopy-intercept method; Frank and McNaughton 1990). From 2008–2012, individuals were identified to species (or to genus and morphospecies) using field guides and published species lists (Bogdan 1976, Blundell 1982, van Oudtshoorn 2009). Starting in 2012, we began a process of verifying and refining plant identifications in this data set through establishment of an

extensive collection of >1,781 herbarium reference specimens and corresponding DNA barcode data for >460 species, representing 92% of the roughly 500 vascular plants thought to occur at Mpala (Gill et al. 2019). To facilitate consistency in the face of taxonomic revisions and refinements of our own identifications, we maintain a list of voucher numbers that match each species to a reference specimen used for DNA barcoding and taxonomic verification by botanists at the National Museums of Kenya (Gill et al. 2019).

Individual Tree Monitoring: Individual-based surveys of trees focused on 10 tagged individuals per plot (or all individuals if there were less than 10 individuals per plot) of each of five common woody species, including the three dominant acacias (*Acacia* syn. *Vachellia etbaica*, *A. syn. Senegalia mellifera*, and *A. syn. Senegalia brevispica*: Fabaceae), *Croton dichogamus* (Euphorbiaceae), and *Balanites rotundifolia* (Zygophyllaceae). Plants were tagged in January 2009, and tagged individuals are resurveyed annually. The following data are recorded: survival, height (m), crown diameter (m), basal diameter (mm) and/or circumference (cm) at 15 cm from ground level, and the number of stems at ground level. Many additional trees were tagged in 2012 following the same monitoring protocol, but some of these additional trees were not monitored after 2015.

Woody Plant Censuses: Each year, a census is conducted of all trees and shrubs (i.e., species that reach ≥ 2 m tall at maturity) and large succulents (*Euphorbia* and *Opuntia* spp.) within the 0.36 ha central grids. Individuals are identified, and the number of individuals of each species are recorded for each of five height classes (<1 m, 1–2 m, 2–3 m, 3–4 m, >4 m). The first census, in 2009, omitted *Euphorbia* spp., and censuses prior to 2012 omitted *Opuntia* spp.

Phenology Surveys: Each month, the presence or absence of reproductive bodies (flowers and/or fruits) is recorded for all plant species within the 0.36 ha plot centers during a 30-minute scan of each plot. This data set was initiated in 2012 and is continuing.

Vertical Vegetation Structure: From December 2016 to December 2018, we conducted several surveys that integrate understory and overstory vegetation using a modified version of the canopy-intercept method (Frank and McNaughton 1990). At each of the 49 grid stakes in each plot, a telescoping pole was placed on the ground and extended up through the canopy (Kartzinel and Pringle 2020). All vegetation touches were recorded, along with plant species identity, height of the intercept, and whether the touch was stem or leaf. The objectives of these surveys were (a) to quantify understory and overstory vegetation simultaneously using a consistent methodology and (b) to quantify the vertical profile of vegetation biomass within the plots.

Seed Rainfall Monitoring: Seed rainfall weights were recorded weekly for two of the dominant tree species, *Acacia (Vachellia) etbaica* and *Acacia (Senegalia) mellifera* just outside of the UHURU plots at the South, Central, and North sites from 2016–2019 (**Fig. 4**). Nets were placed underneath the tree canopy, and all seeds that accumulated in the nets were weighed weekly. Three individuals per species were monitored at each site, one each from the following height classes: 2-3m, 3-4m, and >4m. Seed rainfall from 18 trees were measured in total.



Figure 4. Set-up for the *Acacia* seed rainfall monitoring, showing an *Acacia etbaica* near the Central 2 block with net for catching seeds. Seeds in the net were collected and weighed weekly. Photo by S. Kurukura.

LMH Dung Surveys: We regularly survey LMH dung (starting in 2009 at roughly quarterly intervals, later increased in 2016 to every two months) to assess the efficacy of each experimental treatment in excluding the intended classes of LMH and to provide a relative index of LMH activity levels (Goheen et al. 2013, Wells et al. 2021). In each plot, three parallel 6×60 m belt transects (spaced 30 m apart within the 0.36 ha plot centers) are walked by 2-4 observers, who count all discrete dung piles, identify the species of origin (Stuart and Stuart 2000), and crush the dung after identification to prevent recounting in subsequent surveys. Rates of dung decomposition do not differ markedly among the three sites (Goheen et al. 2013).

Small Mammal Sampling: Continuously since 2009, small mammals are live-trapped at two-month intervals in TOTAL and OPEN plots using Sherman traps baited with peanut butter and

oats (Goheen et al. 2013). In each trapping session, a single trap is set at each of the 49 grid stakes in the center of each plot, opened in the late afternoon, and checked and closed in the early morning. Trapping sessions last four consecutive days. All small mammals are fit with a numbered ear tag on each ear, with the exception of individuals in the genera *Acomys*, *Crocidura*, *Mus*, and *Steatomys*, which are too small or too fragile (Seifert et al. 2012) for ear tags. Instead, we mark individuals in these genera with permanent markers for subsequent identification within trapping sessions. Sample sizes and movement patterns by the four most commonly captured and marked small mammals (Hinde's rock rat [*Aethomys hindei*], rufous elephant shrew [*Elephantulus rufescens*], fringe-tailed gerbil [*Gerbilliscus robustus*], and Mearns' pouched mouse [*Saccostomus mearnsi*])—represented by (a) the maximum distance moved by an individual within a four-day sampling period; (b) the probability of remaining on a sampling grid between successive periods; and (c) the number of times an individual was captured on more than one plot—indicate that the 1 ha UHURU plot size is sufficiently large to measure effects of LMH exclusion on small mammals (**Table 1**). Initial misclassifications of Harrington's tateril (*Taterillus harringtoni*) as juvenile fringe-tailed gerbil (*Gerbilliscus robustus*) were identified in May 2011 via DNA barcoding (Goheen et al. 2013). We now distinguish these two species based on hindfoot length (<34 mm for *T. harringtoni*), mass (<60 g for *T. harringtoni*), and tail (tufted for *T. harringtoni*). With the aid of mitochondrial DNA barcoding, we have identified the tiny fat mouse (*Steatomys parvus*) as present in the community. We believe that there was a single misidentification of this species (for *Mus* spp. “Umus”) in Kartzin et al. 2014, which we have updated in the current data set. Mitochondrial DNA barcoding has also been used to confirm the presence of at least 3 *Mus* phylotypes in the plots that we cannot reliably distinguish in the field. Two *Crocidura* species (*C. elgonius* and *C.*

gracilipes) are morphologically indistinguishable except for size at maturity; *C. elgonius* are <7 g, while *C. gracilipes* are >7 g. We record weight, sex, age, and reproductive condition for every captured individual.

Species	Sample Size	Maximum Distance (m)	Probability of Remaining	Inter-Plot Movement
<i>Aethomys hindai</i>	2184	78.1	0.83	261
<i>Elephantulus rufescens</i>	561	67.1	0.88	49
<i>Gerbilliscus robustus</i>	1684	78.1	0.83	153
<i>Saccostomus mearnsi</i>	1125	72.1	0.93	83

Table 1. UHURU plots (1 ha) are large relative to the scale of movement by the four most commonly captured and marked small mammals within and between sampling periods. Data include the maximum distance moved within a four-day sampling bout, the probability of an individual remaining within a sampling grid between successive sampling periods, and the total number of times that any individual has been captured in more than one plot between periods.

Permit history: Kenya National Commission for Science, Technology & Innovation permits to Robert M. Pringle: NCST/5/002/R/656, NACOSTI/P/14/0592/1852, NACOSTI/P/18/0592/21481, NACOSTI/P/20/6262; University of Wyoming Institutional Animal Care and Use Committee Protocol Approval (Jacob Goheen; SKMBT_60112030515200; SKMBT_60112030515201; SKMBT_60112030515202; SKMBT_60112030515210).

C. Project personnel: In addition to the authors, the UHURU experiment team has employed several full-time Kenyan field assistants, who collected field data and maintain the experimental infrastructure. Simon Lima, Jackson Lima, Antony Eshwah (deceased), and Mohamud Mohamed have worked in this capacity.

Class III. Data set status and accessibility

A. Status

1. Latest update: December 2019.

2. Latest archive date: December 2019.

3. Metadata status: The metadata are current and stored with the data.

4. Data verification: Data verification was conducted by J. Alston and C. Reed, with assistance from S. Kurukura, A. Hassan, L. Khasoha, S. Weiner, J. Goheen, R. Pringle, and T. Kartzinel.

B. Accessibility

1. Contact person(s): Jacob Goheen, e-mail: jgoheen@uwyo.edu, phone: 307-509-0280.

Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA.

Robert Pringle, e-mail: rpringle@princeton.edu, phone 609-258-8273. Department of Ecology & Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

2. Storage location and medium: Original data files exist on the authors' personal computers (several of which are routinely backed up on servers housed at their home institutions) and are replicated on external hard drives, Google Drive, and Dropbox in .xlsx, .csv, and .txt files. Paper copies of original field data sheets are stored safely in a facility rented by Jacob Goheen and Robert Pringle at the Mpala Research Centre. Data format and the programs required to access and manipulate data will be kept current throughout the duration of this study.

3. Copyright restrictions: None.

4. Proprietary restrictions: Notification about when and how data are used is appreciated but not mandated by the authors. Given ongoing research in the UHURU experiment and the continuation of most of the data sets presented here, we strongly recommend contacting J.

Goheen and R. Pringle prior to using these data, as updated data are available at regular intervals.

We ask that users of UHURU data cite this data paper when using the data.

C. Costs: None.

Class IV. Data structural descriptors

There are 13 files that provide location, rainfall, habitat, vegetation, and animal data from the UHURU experiment. There are several column headings that identify the scale and location of sampling, appearing in many of the 13 datasets that follow.

Label	Attribute	Definition
Survey/Census	Survey or Census number	Numeric
Year	Year of sampling	2008–2019
Month	Month of sampling	Month
Site	Plot location	North (dry), Central (intermediate), South (wet)
Block	Replicate	Numeric (1–3)
Treatment	Experimental treatment type (definitions refer to the excluded LMH species)	OPEN = open plots; MEGA = megaherbivore; MESO = meso- and megaherbivore; TOTAL = all LMH excluded; OUT = near to, but outside, experimental plots (rarely used)
Plot	Unique plot identifiers	Comprises site, block, and treatment
Rebar/Section	Identity of the rebar stake within the central grid	Alphanumeric ID of rebar stakes (49 per plot). “Section” denotes the grid cell

		immediately below and to the right of a stake (e.g., 1A denotes the grid cell bounded by stakes 1A, 1B, 2A, and 2B).
Species	Species	Species of plant or animal. Some species are identified only to genus/morphospecies.

1. PLOT COORDINATES

A. Data set file

Identity: PLOT_COORDINATES.csv

Size: 4 KB

Format: CSV

Contents: Includes the name and location of all experimental plots. There are 81 lines of data, with each record providing location data for the axes of each plot.

B. Variable information

Column	Attribute	Definition
3-6	Coordinates	Columns 3 and 4 are UTM coordinates, columns 5 and 6 are decimal degree coordinates.

C. Data anomalies: None.

2. RAINFALL DATA

A. Data set file

Identity: RAINFALL_2008-2019.csv

Size: 263 KB

Contents: Daily data for each rain gauge.

B. Variable information

Column	Attribute	Definition
1	Date	Date in form of day-month-year.
2–13	Daily rainfall (mm)	Daily rain gauge readings at each block. “man” denotes manual rain gauges used early in the project, while “aut” denotes automatic rain gauges that were installed beginning in 2010.
14-16	Averages (mm)	Average rainfall across gauges at a given site.

C. Data anomalies: NA denotes days on which no data were recorded by a given gauge due to equipment failure. No gauges recorded data from the South site from 26 May 2011 to 30 May 2011, and no gauges recorded data for the Central site from 9 December 2015 to 31 December 2015 and 9 October 2016 to 23 October 2016, and therefore data is missing for these dates. No gauges recorded data for the North site from 9 December 2015 to 31 December 2015, but data from a nearby long-term hydrology study was substituted for those dates (Caylor et al. 2017).

3. VEGETATION DATA – PIN-FRAME SURVEYS

A. Data set file

Identity: UNDERSTORY_PIN_2008-2019.csv

Size: 29.1 MB

Contents: Understory pinhit vegetation data recorded within each of the smaller quadrats (0.25 m²) in each of 20 semiannual surveys from October 2008 to March 2019.

B. Variable information

Column	Attribute	Definition
9	Bare ground	Number of pins with bare ground and no vegetation
10:331	Species names	Genus and species of plant recorded in understory vegetation surveys

C. Data anomalies: Two surveys were performed per year, except for 2015, 2016, and 2019; only one survey was performed for each of those years. Notes on taxonomy, including changes across the 20 surveys, are recorded in rows 2-4. Row 2 (Notes) indicates the name that a plant was assigned during each of the 20 surveys. Row 3 (Changes) provides details on name changes, including lumping, splitting, and new identifications. Row 4 (SKS#) provides the voucher number matching each species to a specimen used to confirm identification by botanists at the National Museums of Kenya in conjunction with DNA barcoding (Gill et al. 2019). Taxonomic identities are considered provisional if labeled as morphospecies, as genus with “sp.”, or as “unknown.” Identifications of morphospecies are pending ongoing taxonomic investigation and DNA barcoding. Taxa are recorded as NA in surveys for which those taxa were not recognized. We include all 20 surveys conducted from 2008-2019 to facilitate tracking of nomenclatural updates that have been guided by detailed botanical investigations and DNA barcoding over this period (cf. Kartzinel et al. 2014). For Surveys 1-14, trees (e.g., *Acacia* spp., *Boscia angustifolia*) and other overstory species (e.g., *Opuntia stricta*, *Euphorbia* spp.) were not counted. Starting in Survey 15, seedlings and saplings of these species were included in the surveys as components of the understory. For Surveys 1-14, these species are listed as NA. Elsewhere throughout the data set, NA indicates data that are missing or suffered from transcription errors.

4. VEGETATION DATA – SMALL (0.25 m²) QUADRATS

A. Data set file

Identity: UNDERSTORY_SMQUAD_2008-2019.csv

Size: 28.7 MB

Contents: Understory vegetation data recorded in small quadrats (0.25 m²) at each rebar stake during 20 semiannual surveys from October 2008 to March 2019.

B. Variable information

Column	Attribute	Definition
9	Bare ground	Percent cover
10:331	Species names	Genus and species of plant recorded in understory vegetation surveys

C. Data anomalies: Two surveys were performed per year, except for 2015, 2016, and 2019; only one survey was performed for each of those years. Notes on taxonomy, including changes across the 20 surveys, are recorded in rows 2-4. Row 2 (Notes) indicates the name that a plant was assigned during each of the 20 surveys. Row 3 (Changes) provides details on name changes, including lumping, splitting, and new identifications. Row 4 (SKS#) provides the voucher number matching each species to a specimen used to confirm identification by botanists at the National Museums of Kenya in conjunction with DNA barcoding (Gill et al. 2019). Taxonomic identities are considered provisional if labeled as morphospecies, as genus with “sp.”, or as “unknown.” Identifications of morphospecies are pending ongoing taxonomic investigation and DNA barcoding. Taxa are recorded as NA in surveys for which those taxa were not recognized. We include all 20 surveys conducted from 2008-2019 to facilitate tracking of nomenclatural updates that have been guided by detailed botanical investigations and DNA barcoding over this

period (cf. Kartzinel et al. 2014). For Surveys 1-14, trees (e.g., *Acacia* spp., *Boscia angustifolia*) and other overstory species (e.g., *Opuntia stricta*, *Euphorbia* spp.) were not counted. Starting in Survey 15, seedlings and saplings of these species were included in the surveys as components of the understory. For Surveys 1-14, these species are listed as NA. Elsewhere throughout the data set, NA indicates data that are missing or suffered from transcription errors. For surveys 1-14, data are binary presence/absence data (values = 0 or 1), and surveys 15-20 include percent cover data.

5. VEGETATION DATA – LARGE (1 m²) QUADRATS

A. Data set file

Identity: UNDERSTORY_LGQUAD_2008-2019.csv

Size: 28.7 MB

Contents: Understory vegetation data recorded in large quadrats (1 m²) at each rebar during 20 semiannual surveys from October 2008 to March 2019.

B. Variable information

Column	Attribute	Definition
9	Bare ground	Percent cover
10:331	Species names	Genus and species of plant recorded in understory vegetation surveys

C. Data anomalies: Two surveys were performed per year, except for 2015, 2016, and 2019; only one survey was performed for each of those years. Notes on taxonomy, including changes across the 20 surveys, are recorded in rows 2-4. Row 2 (Notes) indicates the name that a plant was assigned during each of the 20 surveys. Row 3 (Changes) provides details on name changes,

including lumping, splitting, and new identifications. Row 4 (SKS#) provides the voucher number matching each species to a specimen used to confirm identification by botanists at the National Museums of Kenya in conjunction with DNA barcoding (Gill et al. 2019). Taxonomic identities are considered provisional if labeled as morphospecies, as genus with “sp.”, or as “unknown.” Identifications of morphospecies are pending ongoing taxonomic investigation and DNA barcoding. Taxa are recorded as NA in surveys for which those taxa were not recognized. We include all 20 surveys conducted from 2008-2019 to facilitate tracking of nomenclatural updates that have been guided by detailed botanical investigations and DNA barcoding over this period (cf. Kartzin et al. 2014). For Surveys 1-14, trees (e.g., *Acacia* spp. and *Boscia angustifolia*) and other overstory species (e.g., *Opuntia stricta* and *Euphorbia* sp.) were not counted. Starting in Survey 15, seedlings and saplings of these species were included in the surveys as components of the understory. For Surveys 1-14, these species are listed as NA. Elsewhere throughout the data set, NA indicates data that are missing or suffered from transcription errors. For surveys 1-14, data are binary presence/absence data (values = 0 or 1), and surveys 15-20 include percent cover data.

6. VEGETATION DATA – VERTICAL VEGETATION STRUCTURE

A. Data set file

Identity: VERTICAL_VEGETATION_2016-2018.csv

Size: 3.8 MB

Contents: Annual surveys of vertical vegetation taken at the 49 stakes in each plot.

B. Variable information

Column	Attribute	Definition
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8	Voucher Number	Specimen number for identification at National Museums of Kenya
9	Stem	Stem (1) or non-stem (0; e.g., leaf, flower)
10	Height	Height at which plant touched tree pole (cm)

C. Data anomalies: Three vertical vegetation surveys were performed between December 2016 and December 2018. A partial survey in October 2017 (Survey 1B) includes only the South plots. During Surveys 1-2, *Achyranthes aspera* was identified to subspecies, but in Survey 3 it was identified only to species. During data curation for this publication, several species names were updated from those that have been used in previous studies from UHURU: an unknown *Eragrostis* species was identified as *Eragrostis cylindriflora*, an unknown Malvaceae was identified as *Hibiscus sparseaculeatus*, an unknown *Pavonia* species was identified as *Pavonia patens*, and an unknown *Pollichia* species was identified as *Atriplex semibaccata*. *Sida alba* was changed to *Sida ovata*, *Abutilon mauritianum* was changed to *Pavonia burchellii*, and *Cyathula cylindrica* was changed to *Cyathula orthacantha*. All instances of *Cyathula orthacantha* associated with Voucher # RRH_13_040 as described in Gill et al. (2019) were changed to *Pupalia lappacea*. Nomenclatural updates (cf. Kartzin et al. 2014) have been guided by detailed botanical investigations of voucher specimens at the National Museums of Kenya as well as DNA barcoding, and are consistent with changes made in the understory, tree census, and tree survey datasets.

7. VEGETATION DATA – LONGITUDINAL TREE SURVEYS

A. Data set file

Identity: TREE_SURVEYS_2009-2019.csv

590 **Size:** 1.3 MB

591 **Contents:** Annual tree surveys and measurements for each plot (2009–2019).

592 **B. Variable information**

Column	Attribute	Definition
9	Tag Number	Current tag number that identifies a tree.
10	Dead	Whether the tree is dead (Y = Yes; N = No).
11	Height	Tree height (m).
12	Length	Length of canopy extent (m).
13	Width	Length of canopy perpendicular to first measurement (m).
14	Circumference	Circumference of tree (cm).
15	Number of stems	Number of stems at ground level.

593

594 **C. Data anomalies:** Re-measuring tree heights and circumferences can be imprecise due to
 595 factors including variability in how high on the stem the calipers or measuring tape was placed or
 596 the inadvertent measurement of the wrong basal stem on a tagged tree. Nonetheless, tree heights
 597 and diameters can change dramatically from year to year, due to damage by elephants, drought,
 598 etc. We scrutinized data and identified all trees with changes in height or circumference greater
 599 than three standard deviations between any two consecutive surveys to identify and correct
 600 inadvertent miscalculations, transcription errors, or other verifiable mistakes; otherwise, we
 601 assumed measurements to be accurate, even when differing markedly between successive years.

No tree survey was conducted in 2018. Some trees and plots were inadvertently measured twice in the same year—these values can be used to estimate measurement error. Many additional trees were tagged in 2012 following the same monitoring protocol as the other trees, but some of these additional trees were not monitored after 2015; these trees are denoted by a tree tag number beginning with “JM”.

8. VEGETATION DATA – TREE CENSUS SUMMARY

A. Data set file

Identity: TREE_CENSUS_SUMMARY.csv

Size: 259 KB

Contents: Summary spreadsheet at the plot level showing number of individuals of each species in each size class in each year per plot (2009-2019).

B. Variable information

Column	Attribute	Definition
8–14	Size classes	Trees per size class per subplot
15	Total	Total trees per species per subplot

C. Data anomalies: No census was conducted in 2011 or 2015. No data are available for N1MESO and N3OPEN in 2019. Some data were missing for S2MESO and S3MESO in 2016, S3MESO in 2017, and C1TOTAL and C3TOTAL in 2019 (so summarized data may be meaningfully undercounted in these plots in these years). *Euphorbia* spp. were present but not

recorded in 2009; *Opuntia* spp. were present but not recorded until 2012. Otherwise, when tree species are not listed in a year, this indicates that the tree species was not present in that year.

9. VEGETATION DATA – TREE CENSUS DETAILED

A. Data set file

Identity: TREE_CENSUS_DETAILED.csv

Size: 2.7 MB

Contents: Spreadsheet showing the data for each 10 × 10 m sampled section of each plot (2009-2019).

B. Variable information

Column	Attribute	Definition
9-15	Size classes	The number of trees for the corresponding species in each size class
16	Total	The total number of trees measured.

C. Data anomalies: No census was conducted in 2011 or 2015. No data are available for N1MESO and N3OPEN in 2019. Some data were missing for S2MESO and S3MESO in 2016, S3MESO in 2017, and C1TOTAL and C3TOTAL in 2019 (so summarized data may be meaningfully undercounted in these plots in these years). *Euphorbia* spp. were present but not recorded in 2009; *Opuntia* spp. were present but not recorded until 2012. Otherwise, when tree species are not listed in a year, this indicates that the tree species was not present in that year. In some sections in some years, two rows for the same species were inadvertently recorded with

different numbers of trees. We recommend that data users average these entries to account for these data errors.

10. VEGETATION DATA - FLOWER AND FRUIT PHENOLOGY

A. Data set file

Identity: PHENOLOGY_2012-2019.csv

Size: 1.2 MB

Contents: Spreadsheet detailing the presence of flowers and fruit on species of plants at each site of the UHURU experiment.

B. Variable information

Column	Attribute	Definition
4	Flower or fruit	Whether the observation represents flowers or fruits
5-7	Presence at sites	Presence of flowers or fruits during the month and year denoted by the row (1: present, 0: absent or missing from site)

C. Data anomalies: June and December 2012 data quantified numbers of flowers and fruits for a small subset of plant species. From August 2013, monthly phenology data were collected. These data include a broader range of species than 2012 data, but only specify whether a species was flowering (not fruiting) in a given site. From January 2017, the data include the presence of both flowers and fruits (separately) for each species in each site. Zeros may indicate either that no flowers or fruits were present, or that the species itself was not present or not detected in a plot; analyses based on absence of flowering/fruiting should therefore be conducted with caution.

11. VEGETATION DATA - *ACACIA* SEED RAINFALL

A. Data set file

Identity: ACACIA_SEED_RAIN_2016-2019.csv

Size: 83 KB

Contents: Seed rain from *Acacia etbaica* and *Acacia mellifera* across the rainfall gradient from December 2016 to October 2019.

B. Variable information

Column	Attribute	Definition
2	Tree ID	Unique identifier for each tree, including species and ID number (AE = <i>Acacia etbaica</i> ; AM = <i>Acacia mellifera</i>)
3	Species	<i>Acacia</i> tree species (<i>Acacia etbaica</i> or <i>Acacia mellifera</i>)
4	Height class	Trees divided into categories based on height (2-3 m, 3-4 m, or >4 m)
6	Weight	Weight of seeds caught in net underneath tree canopy (g; marked as “not checked” if tree was not checked in a given week)

C. Data anomalies: Missing data are indicated by NA.

12. ANIMAL DATA – DUNG SURVEYS

A. Data set file

Identity: DUNG_SURVEYS.csv

Size: 532 KB

Contents: Dung count survey data, 2009–2019

B. Variable information

Column	Attribute	Definition
9	Line	Transect line number (corresponding with the tree census and small mammal trapping grid)
10-40	Source of dung	Species of origin and age (old vs. new dung assessed by color).

C. Data anomalies: Dung of several species pairs cannot be differentiated reliably in the field. These include hares (*Lepus* cf. *L. capensis* and *L. cf. L. saxatilis*; Kartzin et al. 2019), plains and Grevy’s zebra (*Equus quagga* and *E. grevyi*), African buffalo (*Syncerus caffer*) and domestic cattle (*Bos indicus*). We made no effort to differentiate predator dung (rare) according to species; instead, we lumped them within three size classes: large, medium, and small. A transcription error occurred when recording block number in the Central plots during the January 2011 survey. As a result, Block 2 and Block 3 are coded as NA to reflect the uncertainty. No data are available for the Central and South sites for Survey 19.

13. ANIMAL DATA – SMALL MAMMAL SURVEYS

A. Data set file

Identity: SMALL_MAMMALS_2009-2019.csv

Size: 2.7 MB

Contents: Small mammal captures during capture periods 1–63 (May 2009 – December 2019).

B. Variable information

Column	Attribute	Definition
10	Night	Trap night (per site per survey)
11	Species	<p> Acke = <i>Acomys kemp</i> = Kemp's spiny mouse Acpe = <i>Acomys percivali</i> = Percival's spiny mouse Aehi = <i>Aethomys hindei</i> = Hinde's rock rat Arna = <i>Arvicanthis nairobae</i> = Nairobi grass rat Arni = <i>Arvicanthis niloticus</i> = African grass rat Crel = <i>Crocidura elgonius</i> = Elgon shrew Crgr = <i>Crocidura gracilipes</i> = Peter's musk shrew Croc = <i>Crocidura</i> spp. = white-toothed shrews Dend = <i>Dendromus</i> spp. = climbing mice Elru = <i>Elephantulus rufescens</i> = rufous elephant shrew Geni = <i>Gerbiliscus nigricaudus</i> = black-tailed gerbil Gero = <i>Gerbilliscus robustus</i> = fringe-tailed gerbil Grdo = <i>Grammomys dolichurus</i> = woodland thicket rat Grmi = <i>Graphiurus microtis</i> = small-eared dormouse Mana = <i>Mastomys natalensis</i> = Natal multi-mammate rat NA = used for traps that were closed but empty as well as traps that were missing or damaged; also used for plots in which no animals were caught that night Rara = <i>Rattus rattus</i> = black rat Same = <i>Saccostomus mearnsi</i> = northern pouched mouse Stpa = <i>Steatomys parvus</i> = tiny fat mouse Taha = <i>Taterillus harringtoni</i> = Harrington's tateril Uarvi = <i>Arvicanthis</i> spp. = grass rats Umus = <i>Mus</i> spp. = pygmy mice Unkn = unknown Zehi = <i>Zelatomys hildegardae</i> = Hildegard's broad-headed stink mouse </p>
12	Capture	C = capture; R = recapture
13	Sex	F = female; M = male

14	Condition	L = lactating N = none (no reproductive condition) P = pregnant PL = pregnant and lactating S = scrotal
15	Age	A = adult; S = subadult; J = juvenile
16	Left hind foot	Length of left hind foot (mm)
17	Left tag	Tag number at survey
18	Original tag	Original tag number. Particularly useful for cross-referencing with left_tag column when a tag was missing or replaced
19	ID	Individual identifier
20	Marks	Number of paint marks left on animals without ear tags
21	Weight	Weight (g)
22	Notes	Indicate areas where individual identifications or measurement interpretations require caution. In particular, this column indicates if ID tags were lost or replaced, or if an individual escaped during evaluation. The condition of some individual captures could be consequential, such as individuals captured dead or with broken limbs. Also may indicate when a non-small mammal species is caught, such as a bird, squirrel, or dwarf mongoose.

C. Data anomalies: NA indicates no data. Based on mitochondrial DNA barcoding data, along with geographic range and morphological data, the species listed as *Mus sorella* (MUSO) on the original field data sheets is now identified as the tiny fat mouse, *Steatomys parvus* (STPA). Harrington's tateril (*Taterillus harringtoni*) was initially misclassified as juvenile fringe-tailed gerbil (*Gerbilliscus robustus*) but was identified in May 2011 via DNA barcoding (Goheen et al. 2013). We now differentiate between the two species based on hindfoot length (<34 mm for *T. harringtoni*), mass (<60 g for *T. harringtoni*), and tail (tufted for *T. harringtoni*). Mitochondrial DNA barcoding has also been used to confirm the presence of at least 3 *Mus* phylotypes in the plots that we cannot reliably distinguish in the field; all are listed as *Umus* (*Mus* spp.) in the dataset. Two *Crocidura* species (*C. elgonius* and *C. gracilipes*) are distinguished by size at maturity; *C. elgonius* are <7 g, and *C. gracilipes* are >7 g.

Class V. Supplemental descriptors

A. Data acquisition: Data can be accessed at the link located in the supporting information for this data paper.

B. Quality assurance/quality control procedures: Measures taken for quality control are detailed in each data set description above. Data were recorded in the field on paper, entered into spreadsheets via Microsoft Excel, and checked for outliers or omissions at that time, and subsequently scrutinized for similar issues during data curation for this publication. Any known data anomalies are reported with the corresponding data set. Original data sheets are stored at Mpala Research Centre.

C. Related materials: NA

D. Computer programs and data-processing algorithms: NA

713 **E. Archiving:** Data are archived at the link located in the supporting information for this data
 714 paper.

715 **F. Publications**

716 Brown, B.R.P. 2021. Communities within a community: the gut microbiomes of co-occurring
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718 Brown, B.R.P., J.R. Goheen, S.D. Newsome, R.M. Pringle, T.M. Palmer, L. Khasoha, and T.R.
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- 867 **G. History of data set usage:** Data are currently in use by several of the authors on this data
 868 paper to answer research questions related to the goals of the UHURU experiment. Publications
 869 that have included data from the UHURU experiment are listed in Section V.F.

1. Data request history: Data from the UHURU experiment are frequently requested for research conducted by outside research groups. We encourage researchers to contact J. Goheen and R. Pringle to check whether more recent but as-yet-unpublished UHURU data are available.

2. Data set updates history: Data from the UHURU experiment were originally published in 2014 (Kartzinel et al. 2014). Since publication of this original data paper, we have (a) collected additional data according to the original protocols, (b) improved the taxonomic resolution and accuracy of plant and small mammal identifications, and (c) begun collecting several new data sets. Here, we present updated and extended data from the UHURU experiment (current through 2019).

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