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Original research article

Impacts of anthropogenic habitat modification on mammalian diversity in the Mau Forest Complex, Kenya

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ABSTRACT

Habitat destruction is a major driver of biodiversity loss, especially in the tropics. We investigated changes in the diversity and occupancy of forest-dwelling mammals in response to habitat loss, alteration, and degradation at the Mau Forest Complex (MFC), southwestern Kenya. Using a systematic camera trapping grid, we estimated patterns of mammalian diversity, occupancy of small carnivores, and detection rates of functional mammalian groups across three habitat types (primary forests, secondary forests, and cultivated habitats). Between March 2019 and October 2021, 246 camera traps were deployed across 181 locations representing 5509 sampling days, resulting in 47,345 images of 52 mammalian species in nine mammalian orders. Alpha diversity differed among treatments, with primary forests having the highest diversity, and cultivated habitats the lowest, though results were not statistically significant. Beta diversity differed significantly among treatments, indicating differences in community composition as well as species richness. Overall occupancy for small carnivores was highest in primary forests and lowest in cultivated habitats, with some species specializing in primary forests while others were able to occupy more degraded habitats. Among functional groups, detection rates only differed significantly for large rodents, primates, and ungulates. Our results indicate that although functional groups and species may respond differently to habitat loss and alteration at the MFC, overall species diversity of specialist mammals was highest in the less-disturbed primary forests. Specialist, forest-dependent species are likely most affected by human activities, making them especially vulnerable to habitat loss at the MFC.

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1. Introduction

Biodiversity loss represents one of the most critical current environmental problems facing global ecosystems (Barnosky et al., 2011; Ceballos et al., 2010; Mace et al., 2012). The loss of biodiversity can negatively affect the ability of an ecosystem to maintain health and essential functions in the face of changing environmental conditions by eliminating entire functional groups (Flynn et al., 2009). When this happens, ecosystems can become homogenized (McKinney and Lockwood, 2001) and prone to invasions (Elton, 1958), disease (Swaddle and Calos, 2008), and further degradation. Many global species' losses or declines can be linked directly to rapid habitat loss because of human-induced factors (Crooks et al., 2011; Schipper et al., 2008). At least 70 % of land has been modified by humans through a myriad of anthropogenic activities (Díaz et al., 2019). Consequently, land-use change resulting in habitat loss has become a major global driver affecting terrestrial and freshwater systems (Lake et al., 2000), with particularly strong impacts reported for terrestrial mammals (Kuipers et al., 2021; Schipper et al., 2008).

Although the effects of habitat loss on mammals is well-documented for large species (i.e., defaunation, Galetti and Dirzo, 2013; Torres-Romero et al., 2020), information on the impacts of such losses on small and medium-sized mammals, especially for tropical forests, is just now being realized (Bovendorp et al., 2019; Carreira et al., 2020). Small and medium-sized mammals, including small carnivores (Prugh et al., 2009), provide a number of key ecosystem services, including balancing herbivore populations, seed dispersal, and controlling agricultural pests (Do Linh San et al., 2022; Marneweck et al., 2021, 2022). Thus, understanding factors affecting these mammalian groups in the context of the entire mammalian community is critical to establishing conservation baselines as anthropogenic impacts increase across the globe. Understanding the impacts of habitat loss on these and other mammals is particularly important for tropical forests and pathways by which deforestation directly and indirectly affects wildlife remain poorly understood, especially for elusive forest-dependent species such as arboreal mammals (Cudney-Valenzuela et al., 2022).

Camera traps are a key tool used to study mammals in a wide range of habitats, with a wealth of studies in the humid tropics (Rovero and De Luca, 2007; Tobler et al., 2008). More appropriate for cryptic, forest-dwelling species than other metrics such as tracks, scats, and burrows, camera trapping is an excellent non-invasive tool to monitor mammals in the face of habitat loss in tropical forests (Caravaggi et al., 2017; Hofmeester et al., 2019; Rowcliffe et al., 2008; Silveira et al., 2003; Weingarth et al., 2013; Yasuda, 2004). A recent meta-analysis identified tropical moist forests as experiencing the highest number of mammal-focused camera trap studies, although tropical African countries had a lower probability of such studies (Mugerwa et al., 2023). This study found a total of 28 camera trap studies of Kenyan mammals between 1900 and 2019, with Cordier et al. (2022) reporting 22 studies. A majority of these studies were concentrated in central Kenya's Laikipia County, with forest-focused camera trap studies mostly restricted to coastal or montane areas (see references in Cordier et al., 2022). Camera trapping in the Mau Forest has been limited to targeted surveys for the mountain bongo (*Traagelaphus eurycerus isaaci*) in the Maasai Mau (Sandri et al., 2023) and eight sites for a total of 576 hours in the Kiptunga Forest of the northern Mau (Albertazzi et al., 2018).

While tropical forests play important roles in biodiversity conservation, carbon storage, and climate regulation (Bonan, 2008), rapid global expansion of agricultural land and urban areas (Craigie et al., 2010; Seto et al., 2012) continue to confine many mammalian species to protected areas. While the cores of these protected areas may contain intact forests, they are typically surrounded by increasing levels of human encroachment (Geldmann et al., 2019; Mutugi and Kiiru, 2015), creating a gradient of human disturbance which increases farther from the protected area core (Pickett et al., 2011). This creates a natural experiment for testing the intermediate disturbance hypothesis (IDH), which predicts that species diversity is maximal at an intermediate level of disturbance (Connell, 1978; Moi et al., 2020; Wilkinson, 1999). Tests of the IDH in tropical forests remain scarce, small in scale, and contentious (Burslem and Whitmore, 1999; Roxburgh et al., 2004; Shea et al., 2004), with many studies finding lower species diversity at intermediate levels of disturbance, counter to predicted patterns under IDH (Fox, 2013). In tropical forests, the validity of IDH is unclear, especially for small and medium-sized species, a fact further complicated by limited biodiversity inventories of these species (Rovero et al., 2014).

The African continent is home to some of the most extensive protected areas on the planet, including tropical forests. East Africa (Burundi, Kenya, Rwanda, Tanzania, and Uganda) alone has 1776 nationally designated protected areas, covering more than 27 % of the terrestrial area of the region (Riggio et al., 2019). East Africa is also one of the most biodiverse regions of the planet, however, it faces unprecedented anthropogenic-driven loss of wildlife habitat, with human population growth having increased by nearly 2.7 % per year for the last five years (Worldometer, 2023). Despite the abundance of protected forests, high levels of human disturbance, and rich mammalian communities, many of East Africa's protected areas have been understudied (Rovero et al., 2014), especially in the context of human disturbance effects on mammalian biodiversity. The paucity of data for some East African forests may represent areas that are difficult to access but are nevertheless key to understanding the ecological impacts of anthropogenic influences across the globe (Bowman et al., 2011; Kairo et al., 2001).

One particular East African forest that has received relatively little study despite its ecological importance is the Mau Forest Complex (MFC). Located in southwest Kenya, a megadiverse country with >400 known mammals (Musila et al., 2019) representing approximately one-third of the 1116 mammalian species recorded in Africa (Kingdon et al., 2013; Shorrocks, 2013), the MFC represents the largest indigenous montane forest in East Africa (Chrisphine et al., 2016). The MFC also serves as Kenya's most important water catchment, with ecological services provided by the forest estimated at USD 1.84 billion per annum (Langat et al., 2021). However, human encroachment threatens the persistence of the MFC and its wildlife, including several mammals of conservation concern – in particular the last remaining wild populations of critically endangered mountain bongo and the eastern-most records of the vulnerable African golden cat (*Caracal aurata*) (Butynski et al., 2012; Svengren et al., 2017). For the MFC, no systematic survey of mammals presently exists, partially as a result of the difficult terrain and accessibility. Using systematic camera trap surveys, this study targeted predominantly medium to large-sized mammals, along a gradient of human disturbance at the MFC. Specifically, we tested

the intermediate disturbance hypothesis (IDH), comparing diversity and relative abundance between tracts of primary forests (low disturbance), secondary forests (intermediate disturbance), and cultivated habitats (areas completely converted to agriculture -high disturbance). If the IDH is supported, we predicted the highest levels of diversity in secondary forests. However, because of differences in individual species tolerances to humans (i.e., generalists vs. forest specialists), we expected variation in relative abundances and occupancy rates across species at each level of human disturbance.

2. Materials and methods

2.1. Study area

The Mau Forest Complex (MFC) lies across the equator between $00^{\circ} 1' 0''$ and $00^{\circ} 55' 0''$ N and between the longitudes of $35^{\circ} 15' 0''$ and $36^{\circ} 15' 0''$ E in Kenya's Rift Valley. The MFC is the largest surviving closed canopy forest block in East Africa, covering an area of over 400,000 ha (Jebiwott et al., 2021). It is classified as a montane forest below 2300 m transitioning to bamboo (*Arundinaria alpina*) thickets interspersed with forest and grassland as the altitude increases. It extends further to the montane sclerophyllous forest next to the escarpment crest (Key Biodiversity Areas Partnership, 2023).

The MFC consists of 23 forest blocks spread across Narok, Bomet, Kericho, Nandi, Uasin Gishu, Elgeyo Marakwet, Baringo, and Nakuru Counties, of which 22 are designated as forest reserves (Mwiu et al., 2021). For this study, we focused on two forest blocks, the Masaai Mau (Narok County) and Transmara (Bomet County). The Masaai Mau covers an approximate area of 46,000 ha that is yet ungazetted since it is a trust land forest under the management of Narok County, while the Transmara covers approximately 34,400 ha (Key Biodiversity Areas Partnership, 2023).

2.2. Experimental design

Generally, the MFC has difficult terrain for designing a systematic survey method, with accessibility being a major challenge. In this study, we deployed 1×1 km grids of camera traps to record mammals within two randomly selected forest blocks of MFC (Transmara and Masaai Mau). Within each of the forest blocks, we stratified sampling among three study treatments: primary forests, secondary forests, and cultivated habitats. Camera trapping focused on the region's dry season at Masaai Mau (January-February-March-April) and during August-September-October-November at Transmara because of logistical constraints of reaching difficult-to-access regions of the forest (i.e., primary forest sites) during the rainy season (May-June-July). Camera trap images were used to analyse patterns of alpha and beta diversity for all detected mammals together with occupancy and detection rates for subsets of the regions' mammalian fauna, most notably small carnivores.

2.3. Grid-based camera surveys

We used trail camera traps (Browning Trail Cameras, Strike Force HD Pro X/Model BTC-5HDF, and Strike Force HD Pro/Model BTC-5HDP) to record mammals. Detections were defined as independent images separated by 60 seconds. Studies by Parsons et al. (2016) and Kays and Parsons (2014) demonstrated that at a 60-second cutoff, camera trapping temporal correlation becomes negligible. Camera trap locations were stratified in two forest blocks (Masaai Mau and Transmara) among three treatments (primary forests, secondary forests, and cultivated habitats). The primary forest was defined as an area that had experienced minimal human disturbance [e.g., absence of charcoal kilns, tree harvesting (e.g., no cut tree stumps), and closed canopy from satellite imagery as viewed by eye]. Secondary forest was defined as areas of transition between primary forests that had clear signs of forest re-growth after

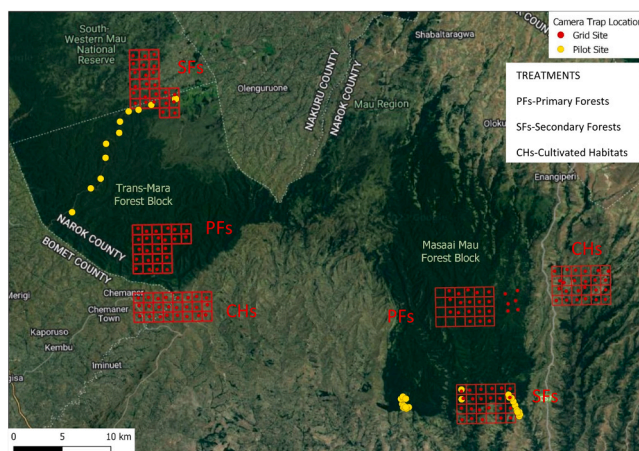


Fig. 1. Map showing the location of sampling grids (red dots) and pilot locations (yellow dots) for the Transmara and Masaai Mau forest blocks.

human-induced disturbances (e.g., cut tree stumps/forest logging or clearing for agriculture). Cultivated habitat was areas within the community lands, typically at the periphery of the MFC, and characterized by extreme levels of human activity, including clearing of all forests, with the exception of narrow strips along riparian corridors, for row-crop agriculture.

Camera locations were selected by creating a 1×1 km grid across the study area, distinguishing treatments from satellite imagery provided by Google Earth (Imagery obtained on 23/10/2020; Fig. 1), and selecting centroids from these grid cells using QGIS (Fig. 1). BaseCamp software vs. 4.6.2 (Garmin Ltd., USA) was used to load pre-set locations to handheld GPS units (eTrex® 20x and GPSMAP® 60CSx). The handheld GPS receivers were then used to locate camera trapping points in the centre of each grid cell. Camera traps were placed within a 200-m radius of the grid centroid, targeting wildlife trails or riparian areas when available.

We sampled a total of 72 camera locations in each forest block for a minimum of 21 days per camera. No camera location was surveyed twice to avoid possible double recording. We deployed 24 camera traps in each treatment, for at least 21 continuous days each. Because of the limited number of camera traps available, twelve camera traps were deployed systematically in each treatment ($n = 36$ camera traps deployed at one time) within one forest block at a time. After twenty-one days, camera traps were moved to the next camera locations in that forest block until a total of 24 camera trap locations per treatment was achieved, after which the same procedure was followed for the other forest block. Following Zungu et al. (2020), camera traps were attached to trees at 15–25 cm high and set to take a burst of three photographs with a one-second delay between bursts. The three-burst option and one-second delay were chosen to maximize opportunities to photograph fast-moving and smaller species. At low light levels in the daytime and night, pictures were taken using an infrared flash. All camera traps were baited (bananas, chicken, and rounded peanut butter oat clusters) to ensure as many mammalian detections as possible (Coronel-Arellano et al., 2018), with bait placed 1.5 m from the camera on day one of each setup but never refreshed. The vegetation cover in front of each camera was cleared within the view range to allow for maximum camera sensor optimal range and also to avoid blank shots (Zungu et al., 2020). We used the Wildlife Insights (WI) platform (www.wildlifeinsights.org) to manage camera trap images and for identification of recorded species. Ambiguous records were flagged and verified by additional authors or outside experts for accurate identification.

2.4. Pilot camera trap surveys

Prior to implementing systematic, grid-based sampling, both forest blocks were surveyed haphazardly during a pilot period. A total of 37 pilot locations were surveyed, this included 19 sampling locations at the Maasai Mau and 18 locations at the Transmara before the implementation of the grid system (Fig. 1, yellow dots). Camera settings and baiting techniques followed protocols for the grid-based camera traps as described above.

2.5. Statistical analyses

All statistical analyses were conducted using combined results from the grid-based and pilot camera trap surveys.

2.6. Alpha diversity

The effective number of all mammalian species was measured in a community using a combination of Hill numbers (e.g., the exponential of Shannon's entropy; Chao et al., 2014) and rarefaction curves to account for uneven sampling efforts. Hill numbers allow simultaneous accounting of differences in richness (total number of unique species) and evenness (relative abundance) and have historically been used to quantify the species diversity of a congregation because they represent an intuitive and statistically rigorous alternative to other diversity indices (Chao et al., 2014). Using the iNEXT package (Hsieh et al., 2022) in the program R version 4.2.1, rarefaction curves were constructed for each treatment (primary forests, secondary forests, and cultivated habitat) to assess differences in asymptotic alpha diversity.

2.7. Beta diversity

To assess statistical differences in beta diversity or compositional similarity or dissimilarity between communities, Jaccard distances (Hao et al., 2019) were calculated among the species presence data for each treatment and forest block along principal component (PCA) axes. A permutational-based analysis of variance (PERMANOVA) via the *adonis* routine in the *vegan* package (Oksanen et al., 2017) in program R was used to test significance levels.

2.8. Occupancy patterns of small carnivores

To assess the occupancy of small carnivores, a single-season occupancy modelling framework of MacKenzie et al. (2006) was used to estimate detection probability (p), defined as the probability of detecting an occurring species at a camera site, and occupancy (ψ), defined as the probability that a given camera site is occupied. Occupancy modelling was applied to small carnivore species (≤ 15 kg) that had at least 30 detections across all surveyed treatments. A model was constructed using the *unmarked* package in Program R (Fiske and Chandler, 2011), with p allowed to remain constant over occasions and ψ allowed to vary with treatment. Akaike's Information Criterion (AIC) was used to verify that our model performed better than an intercept-only model. The model was used to estimate ψ and associated 95 % confidence intervals for each species.

Table 1
Detection rates of different mammals at Mau Forest Complex, March 2019– October 2021.

Order	Family	Species	Maasai Mau Forest Block			Transmara Forest Block			Total
			Primary	Secondary	Cultivated	Primary	Secondary	Cultivated	
Artiodactyla	Bovidae	<i>Cephalophus</i> spp.	7	5	0	3	0	0	15
		Yellow-backed duiker (<i>Cephalophus silvicultor</i>)	6	11	0	18	0	0	35
		Weyns's duiker (<i>Cephalophus weynsi</i>)	44	68	0	16	0	0	128
		Waterbuck (<i>Kobus ellipsiprymnus</i>)	9	1	0	0	0	0	10
		African buffalo (<i>Syncerus caffer</i>) *	0	2	0	0	0	0	2
		Kirk's dik-dik (<i>Madoqua kirkii</i>)	0	13	9	0	0	0	22
		Blue duiker (<i>Philantomba monticola</i>)	62	41	0	66	12	0	181
		Common duiker (<i>Sylvicapra grimmia</i>)	0	1	3	0	15	0	19
		Mountain bongo (<i>Tragelaphus eurycerus isaaci</i>)	2	0	0	0	0	0	2
		Bushbuck (<i>Tragelaphus scriptus</i>)	84	22	0	25	9	0	140
		Domestic goat (<i>Capra aegagrus hircus</i>) **	0	41	330	0	0	95	466
		Domestic sheep (<i>Ovis aries</i>) **	0	15	398	0	5	52	470
		Domestic cattle (<i>Bos taurus</i>) **	22	178	175	7	429	832	1465
		Giant forest hog (<i>Hylochoerus meinertzhageni</i>)	3	0	0	9	0	0	12
		Bushpig (<i>Potamochoerus larvatus</i>)	6	1	0	1	1	0	9
		Domestic donkey (<i>Equus asinus</i>) **	0	10	42	0	0	472	524
		Carnivora	Canidae	<i>Canis</i> spp.	0	0	0	0	0
Domestic dog (<i>Canis familiaris</i>) **	46			41	261	15	151	292	806
Side-striped jackal (<i>Canis adustus</i>)	0			0	4	0	0	3	7
Felidae	Caracal (<i>Caracal</i> spp.)		0	1	0	0	0	0	1
	Caracal (<i>Caracal caracal</i>)		0	3	0	0	0	0	3
	Domestic cat (<i>Felis catus</i>) **		0	0	2	0	0	22	24
	African wild cat (<i>Felis silvestris lybica</i>)		0	0	1	0	0	0	1
	<i>Felis</i> spp.		0	0	0	0	0	3	3
Leopard (<i>Panthera pardus</i>) *	1		0	0	0	0	0	1	
Serval (<i>Leptailurus serval</i>)	0		2	1	3	2	3	11	
Herpestidae	Marsh mongoose (<i>Atilax paludinosus</i>)		0	0	0	6	4	0	10
	Jackson's mongoose (<i>Bdeogale jacksoni</i>)		32	36	2	21	1	0	92
	Egyptian mongoose (<i>Herpestes ichneumon</i>)		3	0	2	7	1	1	14
	Slender mongoose (<i>Herpestes sanguineus</i>)		13	9	0	1	1	0	24
	<i>Herpestes</i> spp.		8	1	16	0	0	0	25
	White-tailed mongoose (<i>Ichneumia albicauda</i>)		0	2	4	0	0	20	26
	Spotted hyena (<i>Crocuta crocuta</i>)		0	0	0	1	2	0	3
	Zorilla (<i>Ictonyx striatus</i>)	12	20	1	3	0	0	36	
	Honey badger/Ratel (<i>Mellivora capensis</i>)	4	0	0	3	1	0	8	
	African clawless otter (<i>Aonyx capensis</i>) *	0	0	0	1	0	0	1	
Nandinidae	African palm civet (<i>Nandinia binotata</i>)	0	0	0	2	0	3	5	
	Viverridae	African civet (<i>Civettictis civetta</i>)	0	8	1	0	1	1	11
		Large-spotted genet (<i>Genetta maculata</i>)	60	92	44	5	13	28	242
Hyracoidea	Procavidae	Servaline genet (<i>Genetta servalina</i>)	0	0	0	59	0	0	59
		<i>Genetta</i> spp.	7	5	3	2	5	1	23
		Southern tree hyrax (<i>Dendrohyrax arboreus</i>)	11	6	7	25	3	0	52

(continued on next page)

Table 1 (continued)

Order	Family	Species	Maasai Mau Forest Block			Transmara Forest Block			Total	
			Primary	Secondary	Cultivated	Primary	Secondary	Cultivated		
Lagomorpha	Leporidae	<i>Lepus</i> spp.	0	15	6	0	0	12	33	
Primates	Cercopithecidae	Red-tailed monkey (<i>Cercopithecus ascanius</i>)	1	0	0	12	5	0	18	
		Blue monkey (<i>Cercopithecus mitis</i>)	115	34	6	56	25	0	236	
		<i>Cercopithecus</i> spp.	1	6	0	12	10	0	29	
		Guereza (<i>Colobus guereza</i>)	0	3	0	8	1	0	12	
		Olive baboon (<i>Papio anubis</i>)	0	5	5	1	0	0	11	
	Hominidae	Human resident (<i>Homo sapiens</i>) *	7	67	225	54	68	137	558	
	Galagidae	Brown greater galago (<i>Otolemur crassicaudatus</i>) *	0	13	0	0	0	0	13	
	Rodentia	Gliridae	Dormouse (<i>Graphiurus</i> spp.)	0	5	0	0	2	0	7
		Hystricidae	Cape porcupine (<i>Hystrix africaeaustralis</i>)	0	3	0	0	16	2	21
			Muridae	Striped mouse (<i>Lemniscomys</i> spp.)	0	0	0	1	0	1
		Crested rat (<i>Lophiomyys imhausi</i>)	3	1	0	5	0	0	9	
		Brush-furred mouse (<i>Lophuromys</i> spp.)	0	0	0	2	2	0	4	
Nesomyidae		Gambian pouched rat (<i>Cricetomys ansorgei</i>)	0	2	1	84	22	52	161	
Sciuridae		Red-legged sun squirrel (<i>Heliosciurus rufobrachium</i>)	0	1	0	1	0	0	2	
Proboscidea	Thryonomyidae	Cane rat (<i>Thryonomys</i> spp.)	0	1	0	0	6	0	7	
	Elephantidae	African elephant (<i>Loxodonta africana</i>) *	0	0	6	1	0	0	7	
	Tubulidentata	Orycteropidae	Aardvark (<i>Orycteropus afer</i>) *	0	9	0	0	0	9	
Aves	Galliformes	Domestic chicken (<i>Gallus domesticus</i>) **	0	0	338	0	0	1327	1665	
Total detections			493	424	118	458	160	154	1807	
Species richness (S)			22	32	19	30	24	15	48	

Note:

A single Asterisk (*) shows species that were excluded from the analyses, as they had too few detections.

Double Asterisk (**) are domestic animals, to show human activities at the various treatments, these species were also excluded from the analyses.

2.9. Detection rates of functional groups

To understand how different groups of ecologically similar or phylogenetically related mammals respond to habitat degradation (treatments), wild mammalian species were grouped into six functional groups (Afrotheria, carnivores, large rodents, small rodents, primates, and ungulates). Afrotherian mammals included the ecologically distinct but phylogenetically related species, including the southern tree hyrax (*Dendrohyrax arboreus*), the African elephant (*Loxodonta africana*), and the aardvark (*Orycteropus afer*). Carnivores included 18 of 20 species of the Order Carnivora detected during the study, the spotted hyena (*Crocuta crocuta*), and leopard (*Panthera pardus*) were excluded since they are considered as large carnivores, additionally, the leopard had too few detections (Table 1). Large rodents included the African pouched rat (*Cricetomys ansorgei*), red-legged sun squirrel (*Heliosciurus rufobrachium*), African crested porcupine (*Hystrix africaeaustralis*), cane rat (*Thryonomys* spp.) and the African crested or manned rat (*Lophiomyys imhausi*). Small rodents included three genera that could be readily identified from photographs (e.g., *Graphiurus*, *Lemniscomys*, and *Lophuromys*). Primates included six monkey species and ungulates included 12 species of hoofed mammals (Order Artiodactyla) detected during the study. Using these groupings, detection rates (count/day) were calculated for each functional group at each camera site, then averaged (with associated standard error) within each treatment, considering groups in which standard errors did not overlap to be statistically different.

3. Results

3.1. Pilot camera trap surveys

Between 19th March 2019 and 28th August 2020, 38 camera trap locations were sampled with 102 camera deployments totalling 2485 camera trap days. These sampling efforts resulted in 33,986 total images, 58 % (19,723) were of non-human, mammalian species. From the pilot survey, the brown greater galago (*Otolemur crassicaudatus*), African clawless otter (*Aonyx capensis*), and the Cape buffalo (*Syncerus caffer caffer*) were unique observations since they were not recorded in the grid-based surveys.

3.2. Grid-based camera trap surveys

Between 11th January 2021 and 10th October 2021, 143 camera trap locations were sampled with 144 camera deployments totalling 3024 camera trap days. Camera traps were deployed for an average of 30 days (21–39) owing to accessibility issues during camera retrieval. This sampling effort resulted in 269,011 total images, including 74 % (199,068) of non-human, mammalian species. The mountain bongo, leopard, and marsh mongoose (*Atilax paludinosus*) were unique observations since they were not recorded in the earlier pilot survey.

3.3. Camera trapping effort and species richness

From 181 camera trap locations (143 grid-based locations + 38 pilot locations), we had 246 camera deployments and 5509 sampling days. A total of 302,997 images (33,986 images from the pilot and 269,011 from grid-based surveys, respectively) were captured (Fig. 2), and out of these, 47,345 images (15.6 %) were of wildlife species. Overall, 52 non-human, mammalian species were recorded. Of the 52 species, leopard ($n=1$ detection), Cape buffalo ($n=2$ detections), and African savanna elephant ($n=7$ detections), had too few detections and were thus excluded from further analyses.

We recorded the highest detections of mammals in primary forests ($n = 952$), followed by secondary forests ($n = 584$) and cultivated habitats ($n = 272$). Detections included nine Orders of mammals: 20 species of Carnivora of 7 families (two Canidae, five Felidae, five Herpestidae, three Mustelidae, three Viverridae, one Hyaenidae, and one Nandinidae), 15 species of Artiodactyla of two families (12 species of family Bovidae, two species of family Suidae), one species of the Order Lagomorpha, nine species of Order Rodentia, seven species of Order Primates and one species each of the orders Hyracoidea, Perissodactyla, Proboscidea, and Tubulidentata. In general, the Maasai Mau Forest Block had the highest detections ($n = 1036$) compared with the Transmara Forest Block ($n = 772$; Table 1). However, in terms of treatments, detection rates in both forest blocks followed a similar pattern.

3.4. Alpha diversity

Although not statistically significant, the mean alpha diversity of small to medium-sized mammals, as measured by Shannon's entropy, was lower in cultivated habitats than in both secondary and primary forests. Similarly, we recorded a higher diversity of mammals in primary forests than in secondary forests, but this result was not statistically significant (Fig. 2).

3.5. Beta diversity

The community composition of mammals differed significantly between primary and secondary forests ($F = 4.27$, $df = 1$, $p = 0.001$), primary forests and cultivated habitats ($F = 6.99$, $df = 1$, $p = 0.001$), cultivated habitats and secondary forests ($F = 4.65$, $df = 1$, $p = 0.001$). Differences were especially apparent when comparing cultivated to both primary and secondary forests (Fig. 3).

3.6. Small carnivore abundance and occupancy

The overall number of detections of small carnivores varied among species (Fig. 4) and treatments (Fig. 5). Large spotted genets (*Genetta maculata*) had the greatest number of detections ($n = 344$), followed by Jackson's mongoose (*Bdeogale jacksoni*; $n = 158$), and servaline genet (*Genetta servalina*; $n = 123$). The African wild cat (*Felis silvestris libyca*) had the fewest detections with a single individual reported from cultivated habitats.

Four species of small carnivores were each detected in only a single treatment, with African wild cat in a cultivated farmland at

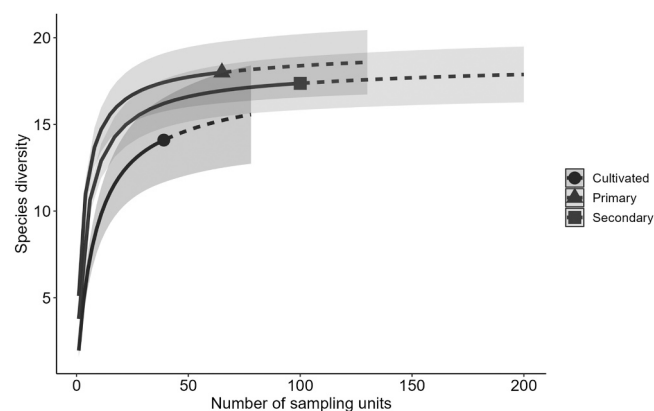


Fig. 2. Alpha diversity, as shown by the exponential of Shannon's entropy, for mammalian species between cultivated habitats, primary forests, and secondary forests in the Mau Forest Complex, Kenya.

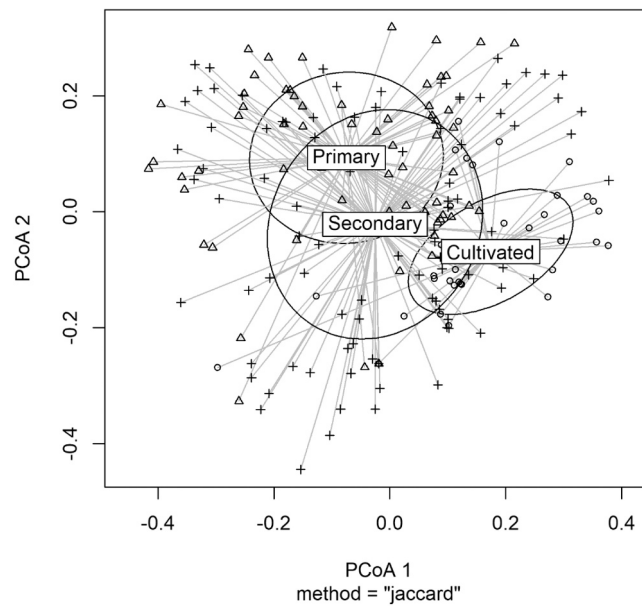


Fig. 3. Differences in mammalian community composition between cultivated, primary, and secondary forests as assessed by Jaccard distances and principal components analysis.

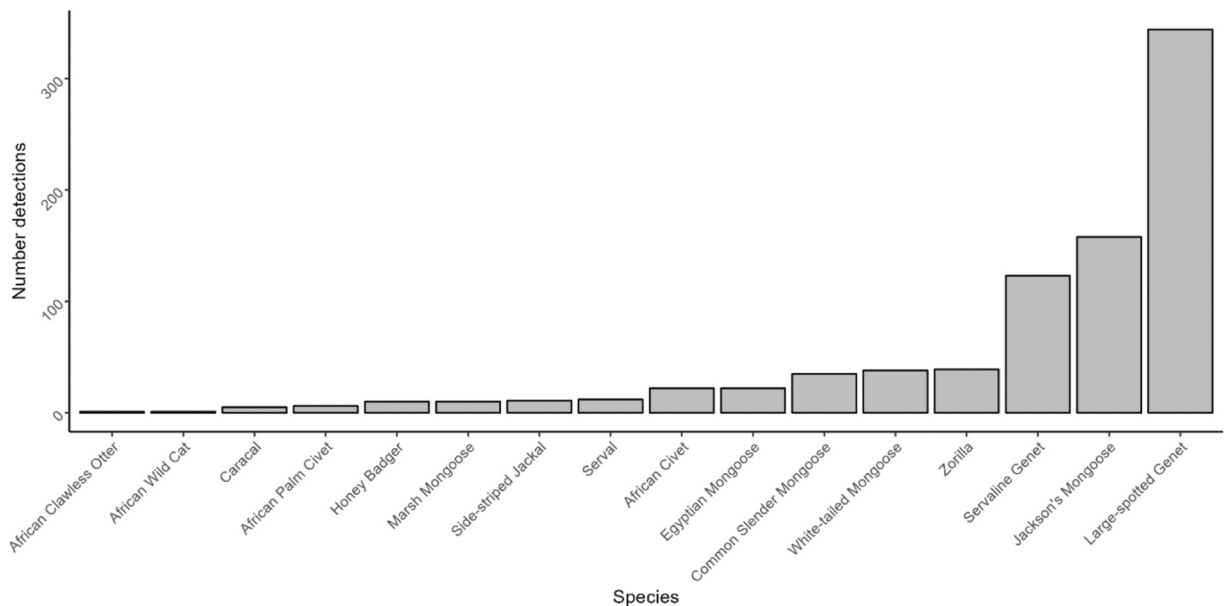


Fig. 4. The number of detections captured of each of the 16 species of small carnivores from 246 camera trap locations within the two forest blocks studied between January 2021 and October 2021.

Maasai Mau, caracal (*Caracal caracal*) in a secondary forest at Maasai Mau, side-striped jackal (*Canis adustus*) in a cultivated farmland at Transmara, and servaline genet in the primary forests of Transmara (Fig. 5).

The large-spotted genet had significantly higher occupancy (mean $\psi = 0.56$, 95 %CI=0.44–0.68) in secondary forests when compared with primary (mean $\psi = 0.26$, 95 %CI=0.16 – 0.39) and cultivated habitats (mean $\psi = 0.32$, 95 %CI=0.21 – 0.46) (Fig. 6). The Jackson's mongoose, a known forest specialist, had higher occupancy in both primary (mean $\psi = 0.32$, 95 %CI=0.21 – 0.46) and secondary (mean $\psi = 0.28$, 95 %CI=0.20–0.40) forests when compared with cultivated habitats (mean $\psi = 0.04$, 95 %CI=0.01 – 0.14) (Fig. 6). Some species, such as the slender mongoose (*Herpestes sanguineus*), servaline genet, and white-tailed mongoose (*Ichneumia albicauda*), had no detections in one or more treatments (Fig. 5). Thus, occupancy probabilities associated with those habitats for such species could not be estimated (Fig. 6).

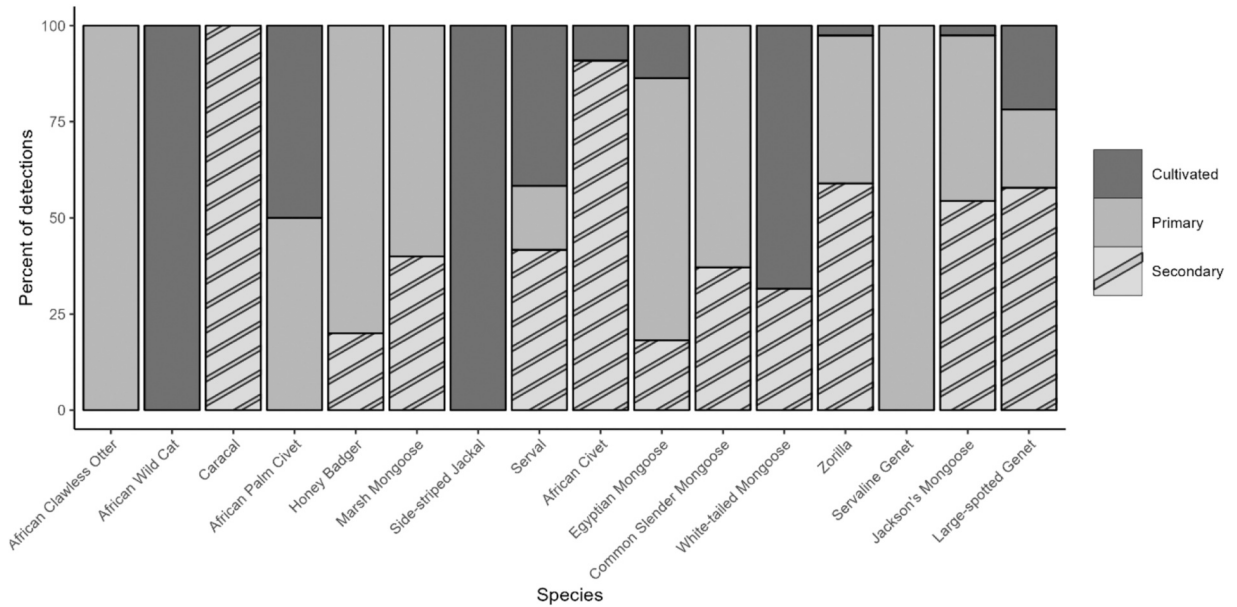


Fig. 5. The percentage of total detections of the 16 small carnivore species located in cultivated habitats, or primary or secondary forests of two Mau forest complex's studied forest block between January 2021 and October 2021.

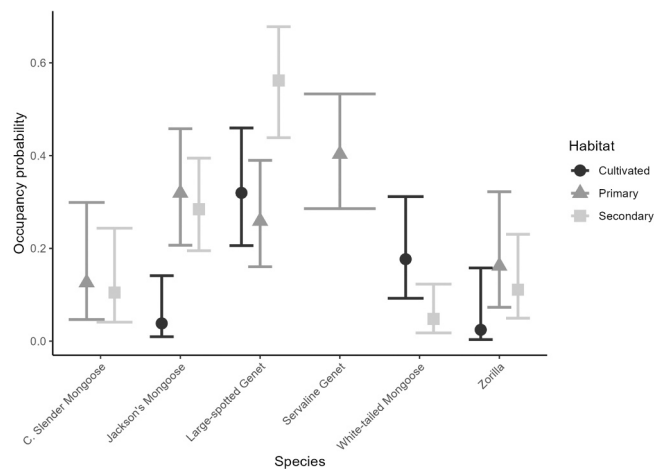


Fig. 6. The probability of occupancy for six small carnivore species in cultivated habitats, and in primary and secondary forests, respectively. Points are means and bars are at 95 % confidence intervals.

3.7. Functional group detection rates

Detection rates were similar across treatments for Afrotherians, Carnivora, and small rodents, but differed significantly for large rodents, primates, and ungulates (Fig. 7). Both primates and ungulates had higher detection rates in primary forests followed by secondary forests, and lastly cultivated habitats. Large rodents had the highest detection rates in primary forests, but their detection rates did not differ between cultivated habitats and secondary forests.

4. Discussion

This is the first study of species-specific and assemblage-wide responses of non-volant small to medium-sized mammals, including small carnivores, to forest loss, degradation, and alteration in Mau Forest Complex, Kenya. We detected 48 species of mammals at the MFC, including 18 small-medium carnivores and a critically endangered species, the mountain bongo (IUCN 2017 C2a(i)). Human disturbance negatively affected the abundance and species richness of mammals, with only 15 % of all detections (272/1807) in cultivated areas compared with 32.3 % and 52.5 % in secondary and primary forests respectively, supporting similar studies in Asia

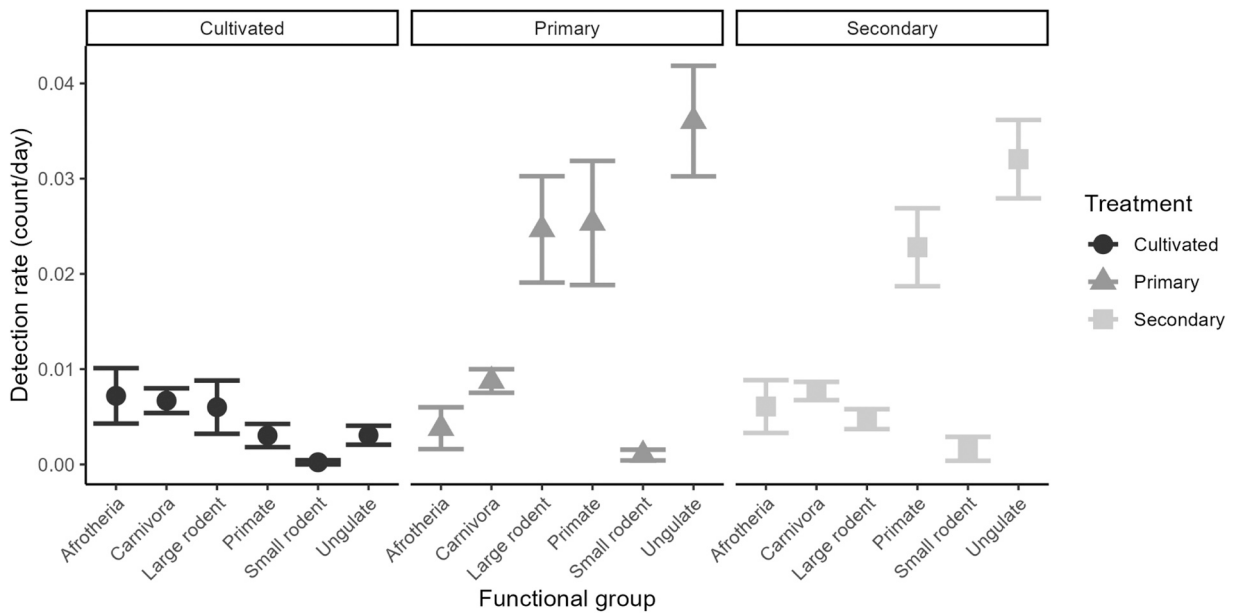


Fig. 7. Detection rate (count/day) of six functional groups of small to medium-sized mammals in cultivated habitats, and in primary and secondary forests. Points represent mean detection rates and bars 95 % confidence intervals.

and South America (Sponchiado et al., 2012; Xingyuan et al., 2015). In general, primary forests supported the highest relative abundance and species richness, including the richness of forest specialists, compared with the more disturbed secondary forests and cultivated habitats, which were inhabited more by generalists.

Our findings did not support the intermediate disturbance hypothesis (Connell, 1978; Moi et al., 2020; Wilkinson, 1999). On the contrary, though not statistically significant, primary forests were more diverse than both secondary forests and cultivated areas, consistent with primary forests being more species-rich than disturbed forests and other modified habitats (Barlow et al., 2007), and counter to the IDH. The rejection of the IDH by this study is consistent with other empirical studies that rarely found higher species diversity at intermediate levels of disturbance (Fox, 2013). While the IDH posits that intermediate levels of disturbance create more niches to facilitate the coexistence of competitors, thus predicting higher levels of diversity (Connell, 1978), it is likely that the disturbance experienced by mammals in secondary forests at the MFC is prolonged and not variable enough to provide the diversity of niches necessary to support both specialist and generalist species. Thus, species that are either obligate forest-dwellers or disturbance intolerant may be unable to occupy secondary forests (Ferreira and Van Aarde, 2000), thereby reducing the diversity of these tracts in which solely generalists and/or tolerant species can persist (e.g., Webala et al., 2019). Indeed, the mountain bongo and some carnivores such as the Jackson's mongoose were only or primarily detected in primary forests in this study, similar to patterns for other forest-dwelling small carnivores in Uganda (Mills et al., 2019).

Although our alpha diversity results indicated that the species richness was similar between disturbance levels, beta diversity, analogous to community composition, was significantly different between disturbance levels. This is indicative of different communities of mammals occupying different levels of disturbance, even if the overall number (richness/alpha diversity) of species remains the same. Indeed, several species were only detected in primary forests (mountain bongo, giant forest hog, African clawless otter, servaline genet), others only in secondary forests (caracal), and others only in cultivated areas (African wild cat, side-striped jackal). The African wild cat had a single individual reported from cultivated habitats, however, given the similarity of these wild cats with their domestic counterparts and their ability to hybridize, these results should be interpreted with caution. Although servaline genets were only recorded in primary forests in Transmara in this study, other studies have observed them capable of occupying secondary forests as well (Gaubert et al., 2015). Kenya and Tanzania represent the easternmost limits of the servaline genet's range, likely contributing to different levels of tolerance to disturbance compared with other regions (Gereau et al., 2016). These findings further highlight the community-level consequences of human disturbance, where some species will be favoured and others lost from areas dominated by humans (Williams et al., 2019).

We found that small rodents and Afrotherians exhibited similar detection rates across the three treatments, suggesting relatively low sensitivity to human disturbance across these functional groups. However, long-term studies may reveal different responses for disparate species within these functional groups. For carnivores, although mean detection rates were not statistically different between disturbance levels, they were marginally higher in primary forests compared with cultivated habitats. Mean detection rates for carnivores in cultivated habitats were driven predominantly by white-tailed mongoose and large-spotted genet. Large-spotted genets generally prefer secondary growth with sufficient hiding places (Angelici and Gaubert, 2013), and indeed occupancy levels for this species were highest in secondary forests. However, detection rates were relatively high in cultivated habitats as well, possibly because of their need for open corridors to facilitate movements (Angelici and Gaubert, 2013). Moreover, a study by Roberts et al. (2007) found

the large-spotted genet to maintain an opportunistic, generalist diet, explaining their preference of cultivated habitats with a variety of dietary options. White-tailed mongoose also exhibited higher occupancy levels in cultivated habitats, perhaps because the species is disturbance tolerant and may select for habitats occupied by domestic livestock (Ramesh and Downs, 2015; Simon et al., 2020).

Primates and ungulates showed the highest sensitivity to human disturbance, with significantly higher detection rates in the primary compared with both secondary forests and the highly disturbed cultivated habitats. Since primates and ungulates tend to rely on trees for shelter, movement, and foraging (Thaker et al., 2011), their association with primary forests is not surprising. Primary forests provide tall trees, ample cover, and complexity in vertical stratification which promotes diversity of forage (Oliveira and Scheffers, 2018). For these two functional groups, the loss of forests may drive them to local extinction if the level of human encroachment and forest loss at the Mau Forest Complex continues unabated, with possible impacts on ecosystem functioning. Primates and ungulates function as primary consumers, predators, and prey to other animal species, and therefore their decline may lead to the decline or loss of other more disturbance-intolerant functional groups. Additionally, some primates and ungulates can influence ecosystem structure, function, and resilience since they are mutualist species in food webs (Koné et al. 2008, Lambert and Garber 1998). Primates are also important pollinators because of their opportunistic non-destructive feeding on flowers and nectar (Chapman et al., 2013; Heymann, 2011).

5. Conclusions

This study provides an important systematic assessment of MFC mammals, offering insight into potential threats from human disturbance to forest-dwelling species. Mammalian communities of the MFC differed across the surveyed disturbance gradient, with primary forests maintaining the highest diversity. The MFC represents the eastern-most, largely isolated range of several forest-dependent species of conservation concern including the critically endangered mountain bongo, near threatened yellow-backed duiker and Jackson's mongoose, and the vulnerable African golden cat. This study recorded the presence of three of these four species, with the exception of the African golden cat which was not recorded despite records indicating its presence at the MFC (Hatfield et al., 2019; Butynski et al., 2012). While we did not sample arboreal species, this type of sampling may be warranted for the MFC in the future. Arboreal species tend to be highly vulnerable to forest canopy destruction but are severely under-sampled by traditional methods, including terrestrial camera trapping (Whitworth et al., 2019), but see (Ehlers Smith et al., 2018, 2020 and Sosibo et al., 2022). Thus, future camera-trap surveys at the MFC incorporating arboreal camera trapping could reveal further undocumented diversity in the mammalian community, but this may be undermined by limited accessibility, rugged terrain, and insufficient investment in personnel and equipment. The findings of this study shed light on the unique species-level and functional group responses of mammals to habitat loss, alteration, and degradation at the MFC. With limited formal protection and a growing human population, conservationists will need to work collaboratively with government officials and communities to ensure the protection of this unique and diverse forest.

Ethics approval

Data collection used remotely set camera traps and, therefore, did not involve direct contact or interaction with the targeted mammalian community in the study area. Fieldwork was conducted under access and research permits from the relevant authorities: The National Commission for Science, Technology, and Innovation (NACOSTI Licence No: NACOSTI/P/20/4694), the Kenya Wildlife Service (KWS/BRP/5001) and the Kenya Forest Service (REF: NO. RESEA/1/KFS/VOL.IV (6).

Code availability

Not applicable.

Consent to participate

All authors declare to have participated in this study.

Consent for publication

All authors agree on the publication of the data and results presented in this article.

Supplementary Material

CSV output used for analyses

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CRediT authorship contribution statement

The first draft of the manuscript was written by Evance O. Ouya and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. Author contributions following CRediT taxonomy were as follows: Conceptualization: Adam W. Ferguson, Paul W. Webala | Data Curation: Evance O. Ouya, Brian O. Otiego, Adam W. Ferguson, Arielle W. Parsons | Formal Analysis: Evance O. Ouya, Brian O. Otiego, Arielle W. Parson | Funding Acquisition: Adam W. Ferguson, Paul W. Webala | Investigation: Evance O. Ouya, Brian O. Otiego, Paul W. Webala, Adam W. Ferguson | Methodology: Paul W. Webala, Arielle W. Parsons, Adam W. Ferguson | Project Administration: Johnstone K. Kimanzi, Paul W. Webala, Adam W. Ferguson | Software: NA | Supervision: Johnstone K. Kimanzi, Paul W. Webala, Arielle W. Parsons, Adam W. Ferguson | Validation: Evance O. Ouya, Brian O. Otiego, Johnstone K. Kimanzi, Paul W. Webala, Arielle W. Parsons, Adam W. Ferguson | Visualization: Arielle W. Parsons | Writing-Original Draft: Evance O. Ouya, Brian O. Otiego | Writing- Review & Editing: Evance O. Ouya, Brian O. Otiego, Johnstone K. Kimanzi, Paul W. Webala, Arielle W. Parsons, Adam W. Ferguson

Declaration of Competing Interest

All authors declare no conflict of interest.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03066](https://doi.org/10.1016/j.gecco.2024.e03066).

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