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Effects of forest degradation on bats at the South and North Nandi Forests, Western Kenya

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Abstract. Habitat loss and degradation pose significant threats to biodiversity, especially in tropical regions characterized by high biodiversity levels and elevated deforestation rates. However, there is a lack of sufficient information concerning the effects of such disturbances on bats (Mammalia: Chiroptera) in tropical Africa. This research investigated the impact of habitat degradation on bat communities in two forests of varying sizes, South Nandi and North Nandi, located in western Kenya, through bat capture methods. Tree density and forest human use intensity served as predictors for relative bat abundance and species richness. A total of 6,003 bats were recorded, representing 21 species across seven families, during a comprehensive study involving 5,322 hours of mist-netting and 4,224 hours of harp trapping. A progressive decline in species richness (S) was observed from the forest interiors ($S = 17$) to the edges ($S = 16$) and the matrices ($S = 12$) at both forests. Fruit bats ($n = 3427$; 61.7%) were predominantly detected at the edges and within the matrices, with a limited presence in the forest interior. Conversely, forest-interior insectivorous bats and those foraging in confined spaces ($n = 260$; 58.6%) were primarily recorded within the forest interiors. Forest specialists exhibited significant correlations with tree density, whereas frugivores and edge- and open-space foraging species showed positive responses to human activity indicators, including cut stumps, charcoal kilns, and footpaths in highly degraded matrices and along forest edges. Consequently, specialized bat species are particularly vulnerable to habitat loss and degradation.

Keywords: habitat degradation, tropical forest, bat conservation.

INTRODUCTION

Bats (Mammalia: Chiroptera), with more than 1,500 known species globally (Simmons and Cirranello 2026), represent one of the most diverse mammalian groups, surpassed only by rodents (Mammal Diversity Database 2026), and provide critical ecosystem services such as pollination, seed dispersal, and insect population control (Kunz *et al.* 2011). Their high sensitivity to environmental change makes them effective bioindicators of ecosystem integrity (Jones *et al.* 2009). Yet, across the tropics, bat populations are increasingly threatened by habitat loss, fragmentation, and degradation, with African tropical forests under particularly intense pressure (Meyer *et al.* 2016).

In sub-Saharan Africa, agricultural expansion, logging, and other anthropogenic activities are major drivers of forest degradation (Newmark 2008). These disturbances reduce canopy cover, simplify vegetation structure, and alter microclimates, changes that can strongly influence bat diversity and assemblage composition (Fahr and Kalko 2011). Although studies from West and Central Africa have shown that forest disturbance reshapes bat communities (Cosson *et al.* 1999), similar works in East African forests remain scarce, limiting understanding of the regional conservation priorities.

Kenya is home to at least 100 known bat species (belonging to 11 families) (Patterson and Webala 2012; Musila *et al.* 2019a). In some forests like Kakamega, where many large mammals have been extirpated, bats arguably comprise up to 50% of the local mammal fauna. Recent systematic analyses in Kenya have revealed substantial cryptic diversity across many bat genera, with numerous lineages yet to be formally described (Demos *et al.* 2018, 2019a, 2019b, 2019c, 2023; Patterson *et al.* 2019, 2020, 2025; Monadjem *et al.* 2021). In such cases, genetically distinct but morphologically similar taxa are often provisionally designated using numbered labels or clade identifiers (e.g., *species A*, *clade 1*) to distinguish evolutionary lineages pending formal taxonomic description. These designations are used throughout this study to reflect underlying genetic diversity where species-level resolution remains incomplete. Information on the current trends of bats in Kenya is scarce. This can be attributed to scanty ecological studies, with a few exceptions from Meru National Park (Webala *et al.* 2004), Lake Turkana (Webala *et al.* 2009), Taita Hills (López Baucells *et al.* 2016), Lake Bogoria (Wechuli *et al.* 2017), Arabuko Sokoke forest (Musila *et al.* 2019b), and Kakamega forest (Webala *et al.* 2019). While the museum voucher specimens provide valuable systematic and biogeographic information, their applicability for evaluating current

population trends is restricted by the absence of recent ecological data. As a result, current information is scarce regarding the impact of habitat loss and fragmentation on bat communities in Kenya, with only a handful of studies specifically addressing this issue (e.g., Webala *et al.* 2019).

The Nandi Forests, located in western Kenya, comprising South and North Nandi, represent remnants of the Guineo-Congolian rainforest and are integral to the Eastern Afrotropics biodiversity hotspot (Mitchell *et al.* 2009). Both forests, despite their significant conservation importance, are currently experiencing threats from human encroachment, selective logging, and agricultural conversion (Kenya Forest Service 2018). However, few studies in the region have given much attention to bats and how they might respond to these habitat perturbations (e.g., Webala *et al.* 2019).

This study investigated the impact of forest degradation on bats in the South and North Nandi Forests. Our objectives were to (i) compare vegetation structure and human disturbance indicators across the matrix, forest edge, and forest interior of both forests in relation to bat occurrence; (ii) compare bat relative abundance and species richness along the degradation gradient; and (iii) assess how human disturbance influences different bat species and foraging ensembles. We hypothesised that

structurally complex sites with dense canopy cover would exhibit higher bat species diversity, including forest specialists, while generalist and edge- and open-space insectivorous species would be more prevalent in degraded sites.

MATERIAL AND METHODS

Study area and sampling design

The South (24,683 ha) and North Nandi (10,500 ha) forests experience a relatively cool-to-moderate climate, with mean annual temperatures ranging from 17°C to 20°C and annual rainfall between 1600 mm and 2000 mm. The Nandi forests are characterised by a closed canopy and permanent freshwater streams that provide favourable habitats for bats, including stable microclimatic conditions, potentially abundant and diverse insect prey, protected commuting and foraging corridors, and reliable drinking sites essential for thermoregulation and daily water balance (Fig. 1). The primary forest environment, and this is defined as sites at least 200 m from the forest/non-forest boundary, is the forest interior (South Nandi: 225 ± 5.62 m; North Nandi: 243 ± 2.43 m), which is the largest part of the

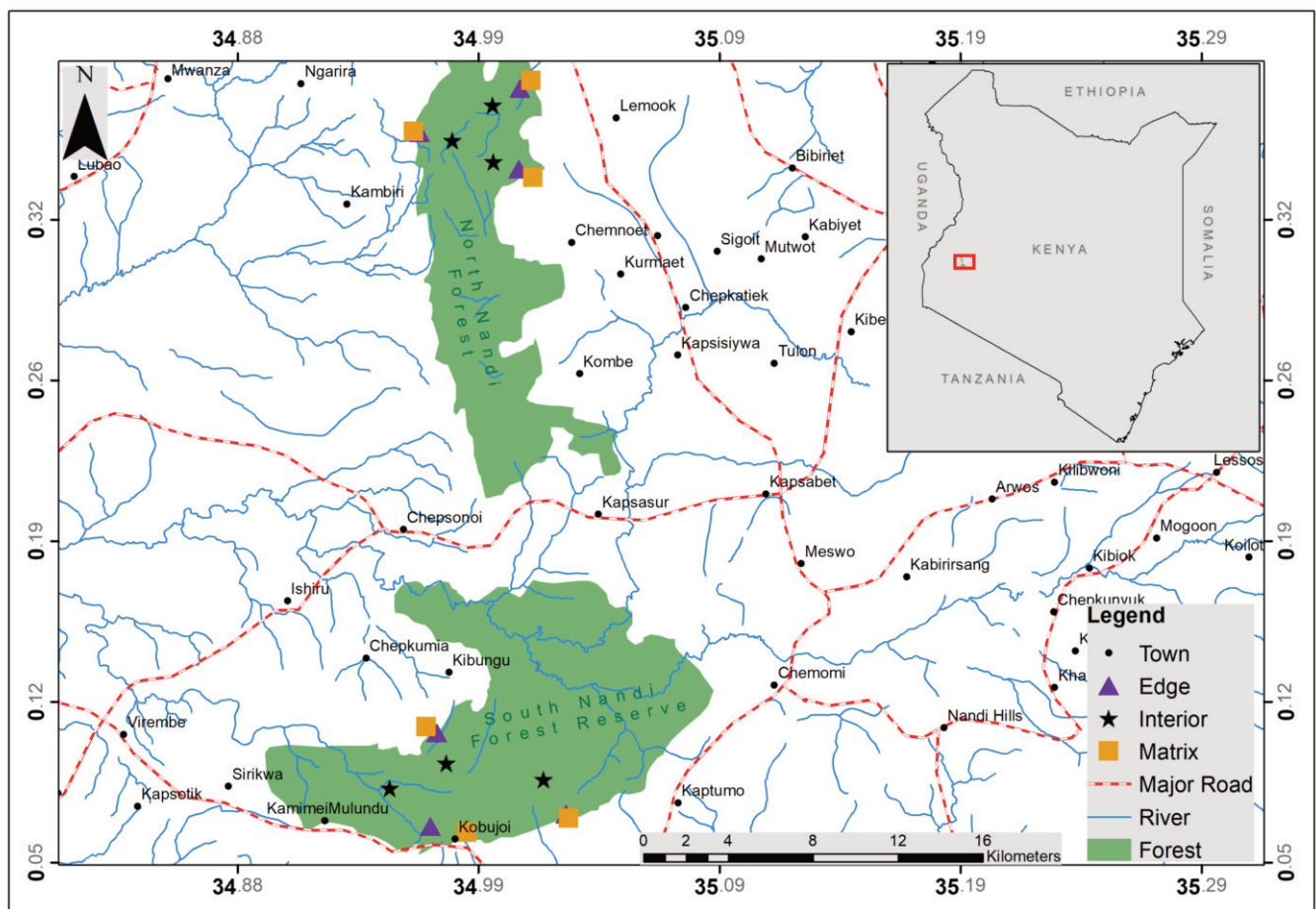


Figure 1. Map of South and North Nandi Forests in western Kenya showing sampling locations (stars, triangle and squares) and an inset map of Kenya indicating the study area.

research area and adjoins the forest edge. The forest edge comprised the outer boundary, defined as the area within 200–500 m of disturbances such as agricultural fields, pastures, or roads. The surrounding matrix consisted mainly of agricultural land, human settlements, and occasional agroforestry systems defined here as land-use practices that integrate trees with crops and/or livestock (e.g., scattered indigenous or planted trees within farms or along field boundaries), sometimes overlapping with tea buffer zones. Tea buffer zones refer to areas of tea (*Camellia sinensis*) plantations established adjacent to forest edges, often serving as transitional zones between natural forest and agricultural land while also acting as partial barriers to human encroachment. The matrix was sampled within 1 km of the forest border. Three replicated sites were established in each forest, named after neighbouring villages: Chepkumia, Resio, and Kapkitany in South Nandi; and Kipsamoite, Septonok, and Kipsuswai in North Nandi. Fieldwork was conducted over one year, from July 2019 to June 2020, totalling 188 sampling nights. At each replicated site, relative abundance and species richness via captures were assessed across the three habitat types. This design allowed comparisons of bat communities along a gradient of forest degradation, from the surrounding matrix through the edge and into the interior of both forests.

Field methods

To evaluate the influence of habitat characteristics on bat communities, vegetation structure and human disturbance indicators were quantified in three 20 × 20 m plots at each sampling site in both forests. Trees ≥ 10 cm diameter at breast height (dbh) were counted to characterise vegetation structure, while forest degradation was assessed by recording cut stumps, active or recently used sawpits, charcoal kilns, and footpaths as indicators of human access and forest use intensity. Footpaths were recorded solely as indicators of human presence, independent of sampling-site placement. These variables provided measures of habitat quality and disturbance intensity, which were subsequently related to patterns of bat relative abundance and species richness across the matrix, edge, and interior habitats. Bats were sampled by capture, with sites visited in random order to minimise bias based on weather, prey availability, or seasonality.

Bat captures

Six monofilament mist nets (6 × 2.5 m or 9 × 2.5 m, mesh 16 × 16 mm — Ecotone, Poland) and two harp traps (two-bank, 4.2 m² — Austbat Research Equipment, Australia) were installed along bat flyways such as trails, stream corridors, canopy gaps, and natural forest openings identified during preliminary surveys. Although selected trapping locations along likely flyways may introduce bias, this approach was adopted to maximize capture success while ensuring standardised

effort across habitats. Traps and nets were deployed across multiple microhabitats within each site and rotated between sampling sessions to reduce bias. Mist nets were set with the bottom shelf at ground level and extended vertically to approximately 2.5 m, targeting species commuting within the understory. All traps were spaced at 50 m intervals. Nets were deployed from 18:30 to 23:00 hours and inspected every 15 minutes to prevent bat injuries, predation, or net damage. Harp traps were left open from 18:30 to 06:00 h, with checks occurring every 30 minutes until 23:00 h and again at 05:00 h. Sampling at each site occurred over two consecutive nights, with a minimum interval of two weeks, while avoiding nights with rain and a full moon (Saldaña-Vázquez and Munguía-Rosas 2013; Appel *et al.* 2017). Bats were identified through external morphological characters following Patterson and Webala (2012) and Happold (2013), while taxonomy followed ACR (2019), with standard morphometric measurements recorded for all captured individuals. While most individuals were identified to species level, morphologically cryptic genera such as *Miniopterus* and *Scotophilus* were treated conservatively, and individuals lacking clear diagnostic features were identified to the genus level (Demos *et al.* 2018, 2019a, 2019b, 2019c, 2020, 2023; Patterson *et al.* 2019, 2020, 2025; Monadjem *et al.* 2021). Genetic or acoustic analyses, which can improve taxonomic resolution, were beyond the logistical scope of this field-based study, and identification therefore relied on established morphological protocols commonly applied in bat surveys. Voucher specimens were deposited at the National Museums of Kenya following established guidelines (Russo 2017) to support verification of species identifications, particularly in taxa with known cryptic diversity, and to provide a permanent reference for the records reported in this study. Bats were captured and handled in accordance with the guidelines approved by the American Society of Mammalogists (Sikes *et al.* 2016). Capture data yielded direct estimates of relative abundance, species richness, and ensemble composition, with a focus on frugivores and gleaning insectivores, which are less likely to be detected acoustically.

Data analyses

All data were log-transformed [$\ln(x+1)$] and tested for normality (Shapiro–Wilk). Means are presented as ± SE. Vegetation structure (tree density) and disturbance indicators (cut stumps, saw pits, footpaths, charcoal kilns) were compared among matrix, edge, and interior habitats using MANOVA, with forest block and habitat location as fixed factors. Tukey tests were applied post hoc. These variables were then related to bat responses to assess how habitat structure and human activity shape community patterns.

Bat diversity was quantified using species richness and Shannon's index (H'). Sample-based rarefaction and extrapolation were conducted with Hill numbers

($q = 0, 1$) in iNEXT, using 100 bootstrap replications for 95% confidence intervals, to allow comparisons across habitats and forests at equal sampling coverage. The relative abundance of common species ($n > 30$) was compared between forests and habitat types using ANOVA.

Finally, Canonical Correspondence Analysis (CCA) using the CANOCO 4.5 software (Microcomputer Power, Ithaca, USA) was performed to examine how bat activity and captures were influenced by vegetation and disturbance variables. Predictor significance was tested with Monte Carlo permutation tests ($n = 999$) using forward selection. All statistical analyses were conducted using R version 4.1.3 (R Core Team 2021) and Real Statistics Resource Package (Zaiontz 2025).

RESULTS

Vegetation and forest-use intensity characteristics

Tree density and saw pits were associated with the interiors of both forests, whereas footpaths, charcoal kilns, and cut stumps were predominantly found at the edges and matrices (Fig. 2). The analysis of pooled data from both forests revealed significant variations in measured vegetation and human disturbance parameters across

treatments. Specifically, tree density showed a significant effect ($F = 224.9, p < 0.001$), as did footpaths ($F = 21.3, p = 0.002$), cut stumps ($F = 23.1, p = 0.002$), charcoal kilns ($F = 48.8, p < 0.001$), and saw pits ($F = 6.1, p = 0.036$; in all cases $d.f. = 2$ and 8 — Fig. 3). As expected, matrices and edges differed from interiors in all parameters ($p < 0.001$). Between matrices and edges, tree density, footpaths, and cut stumps showed no significant variation ($p > 0.05$), whereas charcoal kilns and saw pits differed significantly ($p < 0.05$) (Fig. 3).

When examined separately, vegetation and human disturbance parameters differed significantly among treatments at both forests. In South Nandi, tree density ($F = 107.1, p < 0.001$), footpaths ($F = 28.0, p = 0.001$), cut stumps ($F = 27.7, p = 0.001$), charcoal kilns ($F = 15.3, p = 0.004$), and saw pits ($F = 6.1, p = 0.031$) varied significantly, with matrices and edges generally more disturbed than interiors. In North Nandi, comparable patterns were noted for tree density ($F = 77.1, p < 0.001$), footpaths ($F = 10.5, p = 0.011$), cut stumps ($F = 10.7, p = 0.011$), charcoal kilns ($F = 9.8, p = 0.013$), and saw pits ($F = 5.4, p = 0.046$; in all cases $d.f. = 2$ and 8), indicating that interiors were consistently less disturbed. South Nandi displayed more pronounced contrasts between matrices and edges, whereas North Nandi exhibited a more uniform pattern, characterised by less disturbed interiors and largely comparable edges and matrices.

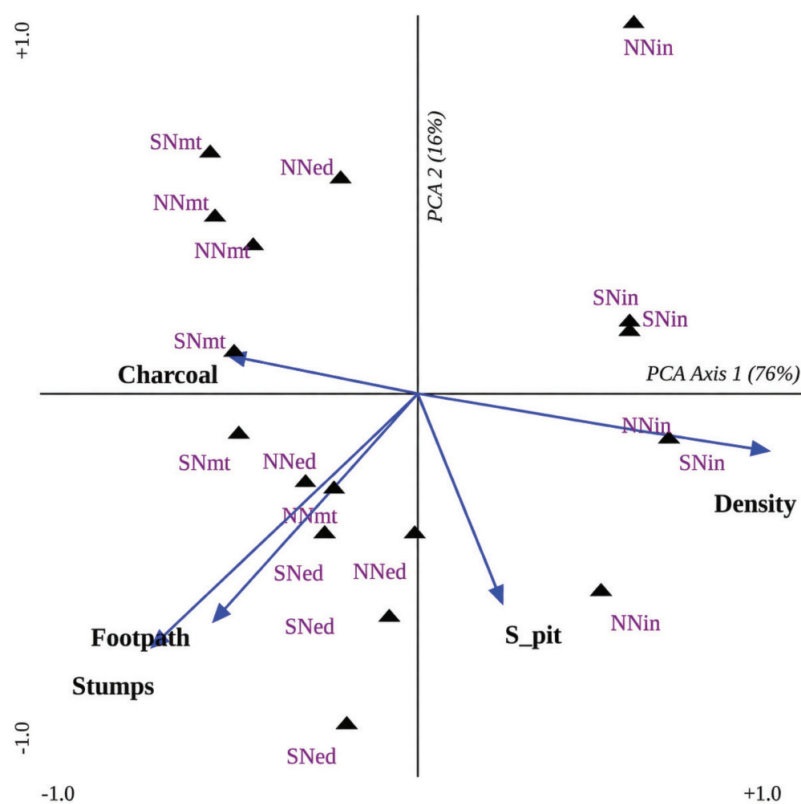


Figure 2. Principal Component Analysis (PCA) biplot showing relationships between vegetation and human disturbance variables (tree density, footpaths, charcoal kilns, cut tree stumps, and sawpits) across habitat types (matrix, edge, and interior) in South and North Nandi Forests, Kenya, sampled between July 2019 and June 2020. Arrows represent the direction and strength of the variables, while filled triangles represent sampling sites. Site codes indicate forest and habitat type: SN = South Nandi; NN = North Nandi; mt = matrix; ed = edge; in = interior. The first two principal components (PC1 and PC2) explain most of the variation in the data.

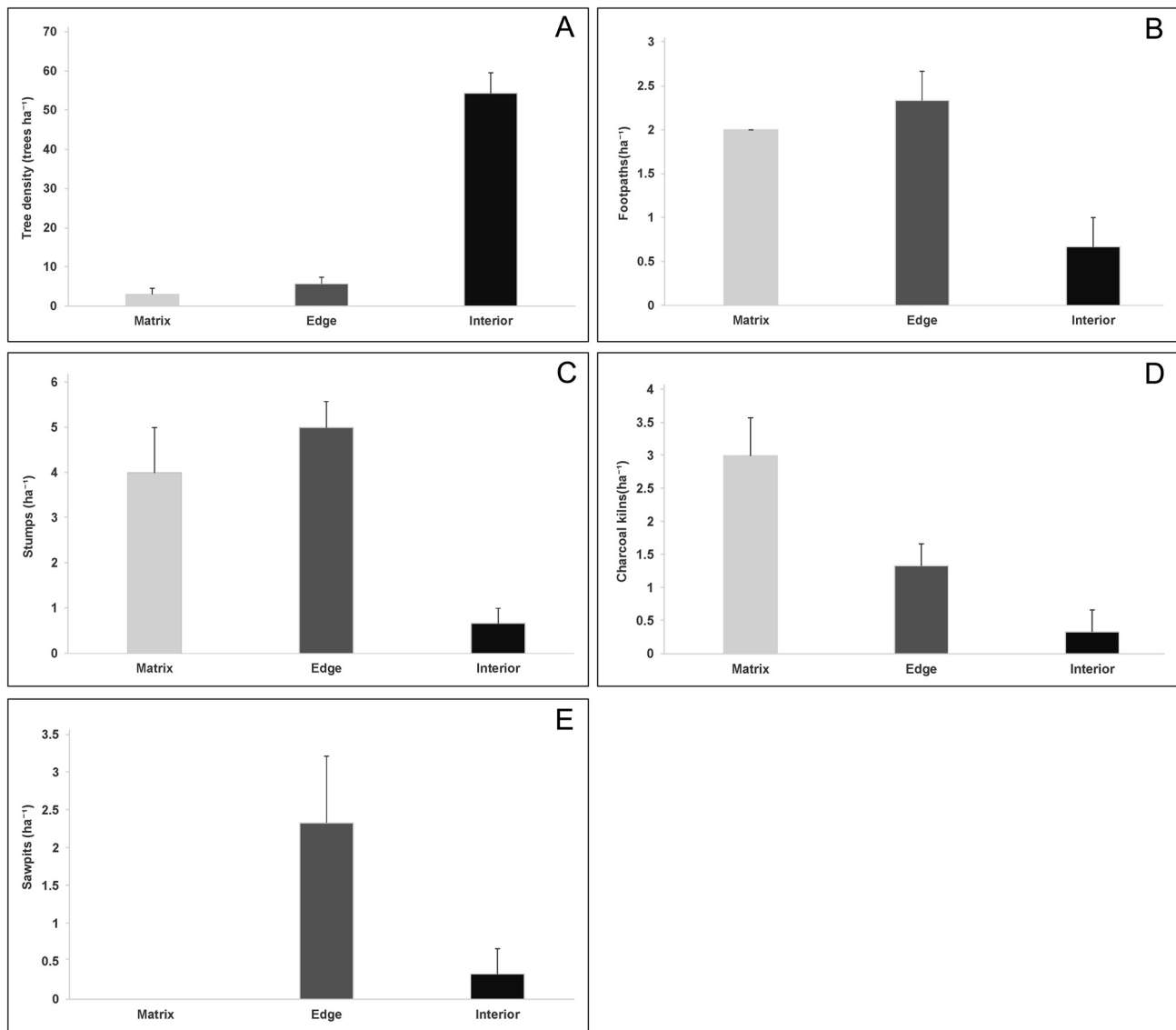


Figure 3. Differences in vegetation structure and human disturbance indicators across habitat types (matrix, edge, and interior) in South and North Nandi Forests, Kenya, sampled between July 2019 and June 2020. Shown are mean values (\pm SE) for (A) tree density (trees ha⁻¹), (B) footpaths, (C) cut stumps, (D) charcoal kilns, and (E) sawpits (all expressed as number per hectare, ha⁻¹). Values are standardized to per hectare (ha⁻¹) from 20 \times 20 m plots. Habitat categories are defined relative to the forest edge (0 m), with matrix sites located approximately 500–1000 m from the forest edge and interior sites located approximately 200–500 m within the forest.

Bat capture responses to degradation

A cumulative effort of 5,322 mist-net hours and 4,224 harp-trap hours resulted in the capture of 6,003 bats representing 21 species and seven families during the surveys conducted at South and North Nandi forests, western Kenya, from July 2019 to June 2020 (Appendix 1). Frugivores accounted for 60% of all captures, with *Epomophorus labiatus* ($n = 1,544$) and *E. wahlbergi* ($n = 1,413$) comprising 81% of frugivorous bats. Insectivores such as *Afronycteris nanus* ($n = 543$) and *Scotophilus andrewreborii* clade 2 ($n = 379$) were predominantly recorded at forest edges in both sites.

Analysis of pooled capture data from both forests indicated significant differences among treatments ($F_{2,42} = 6.88$, $p = 0.003$). Fewer bats were recorded in the forest interiors (26.1 ± 5.43) compared to the matrices

(189.9 ± 56.16) and the edges (205.0 ± 69.40), which did not show significant differences ($p > 0.05$). In South Nandi Forest, captures demonstrated significant differences ($F_{2,33} = 4.25$, $p = 0.023$), with interior habitats (17.3 ± 4.84) yielding fewer bats than matrix (92.2 ± 25.11) and edge (98.3 ± 44.78) habitats (Fig. 4). Similarly, at North Nandi Forest, captures also varied significantly across treatments ($F_{2,40} = 8.88$, $p = 0.001$), with interiors (14.8 ± 2.92) showing lower bat captures compared to matrix (116.3 ± 35.14) and edge (120.3 ± 38.08) habitats (Fig. 4).

Of the 21 detected species, eight were present in all three treatments (matrices, edges, and forest interiors), whereas three were restricted to matrices and edges. Forest specialists such as *Stenonycteris lanosa*, *Nycteris* spp., *Myotis tricolor* 1, and *Scotophilus nux* were confined to forest interiors. *Rhinolophus eloquens* clades 1 + 4 + 8,

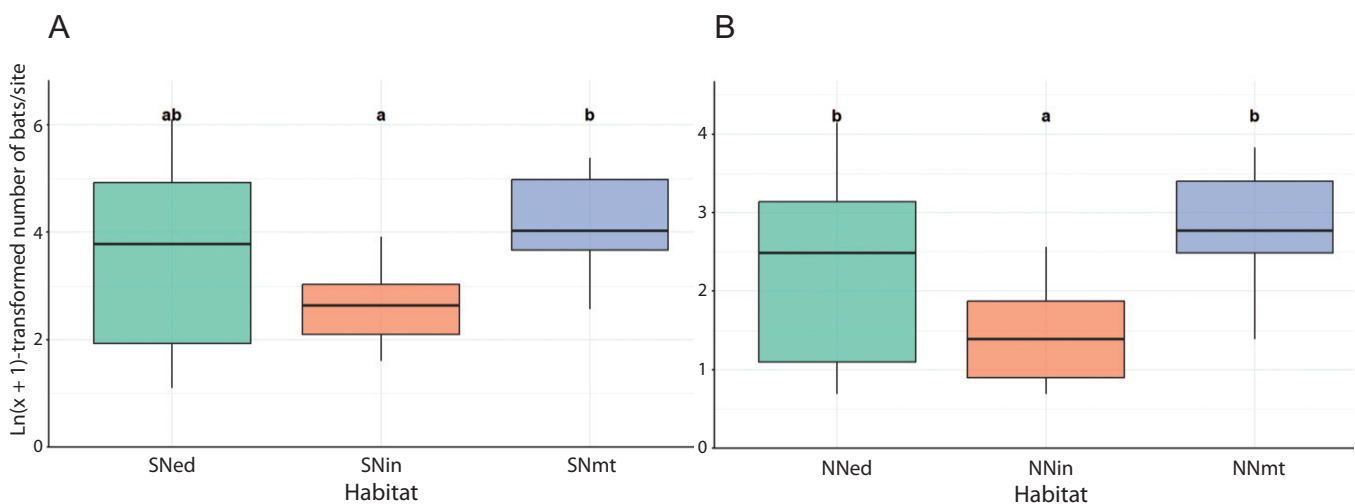


Figure 4. Differences in bat abundance, expressed as the $\ln(x + 1)$ -transformed number of individuals captured per site, among habitat types/treatments (matrix, edge, and interior) in (A) South Nandi and (B) North Nandi Forests, Kenya, sampled between July 2019 and June 2020. Boxplots show the median, interquartile range, and range. Differences among habitats were statistically significant (ANOVA, $p < 0.05$), with pairwise comparisons conducted using Tukey's HSD test at a 95% family-wise confidence level. Different letters above boxplots indicate significant differences among habitat types. Codes indicate forest and habitat type: SN = South Nandi; NN = North Nandi; mt = matrix; ed = edge; in = interior.

R. hildebrandtii, and *Hipposideros ruber* 2 were primarily associated with the forest interiors were sporadically observed in the matrices. In contrast, generalist species were widely distributed across treatments but were more frequently captured at the edges and matrices.

Bat species richness and diversity patterns were inconsistent with treatment-capture associations. Across both forests, rarefaction and extrapolation curves indicated richness between 12 and 17 species ($q = 0$). Diversity was highest in the forest interiors (Chao1 = 17 ± 1.59 ; $H' = 12.19 \pm 0.36$), intermediate at the edges (Chao1 = 16 ± 0.36 ; $H' = 8.02 \pm 0.14$), and lowest in the matrices (Chao1 = 12 ± 0.00 ; $H' = 7.52 \pm 0.12$ — Fig. 4). In North Nandi Forest, species richness ranged from 12 to 16 species, with forest interiors (Chao1 = 16 ± 2.03 ; $H' = 12.31 \pm 0.50$) supporting the greatest diversity,

followed by the edges (Chao1 = 15 ± 0.48 ; $H' = 8.50 \pm 0.18$) and the matrices (Chao1 = 12 ± 0.00 ; $H' = 7.61 \pm 0.17$). In South Nandi Forest, species richness ranged from nine to 15 species. Edges supported the highest species richness (Chao1 = 15 ± 0.56), whereas forest interiors showed greater diversity ($H' = 9.15 \pm 0.44$) despite lower richness (Chao1 = 12 ± 0.22); matrices again had the lowest values (Chao1 = 9 ± 0.00 ; $H' = 6.89 \pm 0.15$).

Species accumulation curves approached asymptotes for both forests, suggesting inventory completeness. Curves for matrices and edges levelled off, indicating adequate sampling, whereas those for forest interiors continued to rise with broader confidence intervals, consistent with higher diversity and the likelihood of detecting additional forest specialists (Fig. 5).

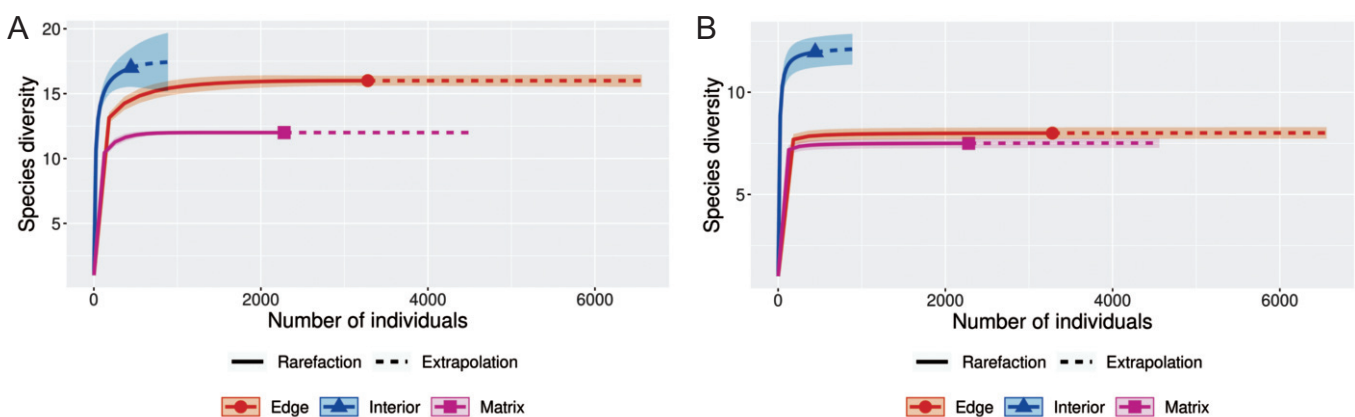


Figure 5. Rarefaction and extrapolation curves comparing bat diversity across three habitat types (matrix, edge, and forest interior) in South and North Nandi Forests, Kenya, sampled between July 2019 and June 2020. (A) Species richness ($q = 0$) and (B) species diversity ($q = 1$; exponential of Shannon entropy). The x-axis represents the cumulative number of individual bats captured (pooled across both forests), while the y-axis shows diversity estimates. Solid lines indicate rarefaction and dashed lines indicate extrapolation; shaded areas represent 95% confidence intervals.

Influence of habitat degradation on bat species assemblages

Permutation analyses of the Canonical Correspondence Analysis (CCA) indicated that bat species assemblages, derived from capture data, were significantly affected by tree density ($F = 13.08$, $p = 0.005$). Human-disturbance variables had minimal impact on assemblages, as evidenced by footpaths ($F = 1.38$, $p = 0.245$), saw-pits ($F = 1.06$, $p = 0.370$), cut stumps ($F = 0.77$, $p = 0.550$), and charcoal kilns ($F = 0.40$, $p = 0.910$; in all cases $d.f. = 2$ and 8). The CCA biplot categorises bat species according to their habitat use (Fig. 6). The less-disturbed forest interior hosted a specific bat species assemblage, comprising one frugivore, *Stenonycteris lanosa*, and several insectivores, including *Rhinolophus eloquens* 1 + 4 + 8, *R. hildebrandtii*, *Hipposideros ruber* 2, *Nycteris* spp., *Miniopterus* sp., *Myotis tricolor* 1, and *Scotophilus nux*, demonstrating a strong association with this treatment. The second bat species assemblage includes frugivores (*Eidolon helvum*, *Epomophorus labiatus*, *E. wahlbergi*, *Myonycteris angolensis*, and *Rousettus aegyptiacus*) and edge- and open-space insectivores (*Mops condylurus*, *M. pumilus*, *Miniopterus africanus* (clade 8), *Afronycteris*

nanus, *Laephotis kirinyaga*, *Pipistrellus hesperidus*, and *Scotophilus andrewreborii* (clade 2)). This assemblage was associated with the moderately to highly disturbed edges and matrices at both Forests (Fig. 6).

DISCUSSION

This is the inaugural study to investigate the impacts of habitat degradation on bats at the South and North Nandi forests of western Kenya. The study reveals that habitat degradation has a detrimental effect on bat abundance and species richness, which is in accordance with findings of other studies (e.g., Zipkin *et al.* 2009; de Oliveira *et al.* 2017; Webala *et al.* 2019; Froidevaux *et al.* 2021; Vergara *et al.* 2021). Generalist frugivores and the edge- and open-space insectivores dominated the more degraded edges and matrices, while specialist species and the overall bat species richness was highest in less disturbed forest interiors. Narrow-space foraging insectivorous species reliant on forest interiors exhibited heightened sensitivity to human activities, highlighting their susceptibility to habitat degradation (Cosson *et al.* 1999; Meyer *et al.* 2016).

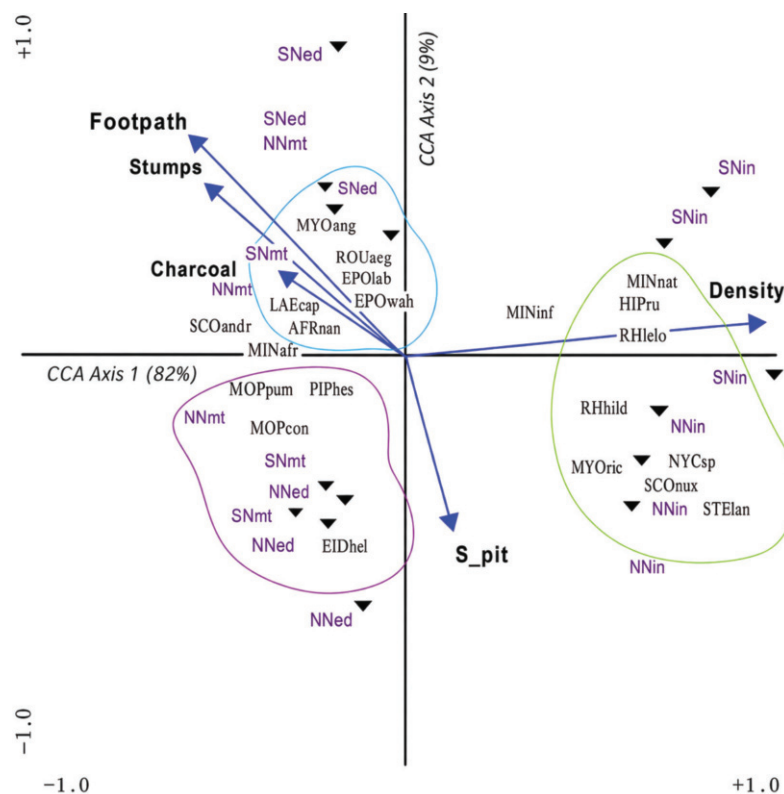


Figure 6. A biplot depicting bat assemblages in relation to habitat degradation in South and North Nandi forests, Kenya, sampled between June 2019 and July 2020. The first four CCA axes explained the significant relationship between bats and forest quality ($p = 0.005$). Three major bat groups are ordinated along the degradation gradient and circled for clarity: forest-interior specialists (green), forest-edge insectivores and specialist frugivores (purple), and generalist frugivores and open-space insectivores (blue). Arrows represent measured degradation features, and filled triangles are sampling sites, with the first two letters representing forest: SN = South Nandi; NN = North Nandi, whereas the next two letters represent sampled habitat: mt = matrix; ed = edge; in = interior. The abbreviated six-letter labels show bat taxa, with the first three uppercase letters standing for genera and the next three lowercase letters for species (e.g., EIDhel: *Eidolon helvum*). Some symbols overlap due to clustering of observations.

Table 1. Bat captures, species richness, evenness, and diversity at South and North Nandi forests of western Kenya. For ensembles: F, frugivore; FI, forest interior; FE, forest edge; OS, open space.

Family	Species	Ensemble	South Nandi			North Nandi			Total
			Matrix	Edge	Interior	Matrix	Edge	Interior	
Pteropodidae	<i>Eidolon helvum</i> (Kerr, 1792)	F	0	0	0	0	76	0	76
	<i>Epomophorus wahlbergi</i> (Sundevall, 1847)	F	216	375	49	379	514	11	1,544
	<i>E. labiatus</i> (Temminck, 1837)	F	189	446	45	316	387	30	1,413
	<i>Myonycteris angolensis</i> (Bocage, 1898)	F	12	56	8	33	64	15	188
	<i>Rousettus aegyptiacus</i> (Geoffroy, 1810)	F	0	153	5	0	211	20	389
Rhinolophidae	<i>Stenonycteris lanosa</i> (Thomas 1906)	F	0	0	0	0	0	1	1
	<i>Rhinolophus eloquens</i> Andersen, 1905 (Clades 1+4+8)	FI	0	5	22	0	1	42	70
	<i>R. hildebrandtii</i> (Peters, 1878)	FI	0	2	15	0	9	21	47
	<i>Hipposideros ruber</i> 2 (Noack, 1893)	FI	0	3	9	0	0	23	35
	<i>Nycteris</i> spp.	FI	0	0	0	0	0	7	7
Molossidae	<i>Mops condylurus</i> (A. Smith, 1833)	OS	143	7	0	107	21	0	278
	<i>M. pumilus</i> (Cretzschmar, 1830)	OS	145	17	0	140	37	0	339
Miniopteridae	<i>Miniopterus africanus</i> Sanborn, 1936	FE	49	43	5	64	62	2	225
	<i>M. inflatus</i> clade Thomas, 1903 (Clade 10)	FE	0	4	13	11	8	7	43
	<i>Miniopterus</i> spp.	FE	0	0	19	9	0	12	40
Vespertilionidae	<i>Afronycteris nanus</i> (Peters, 1852)	FE	55	127	13	189	149	10	543
	<i>Laephotis kirinyaga</i> (Monadjem, Patterson, Webala & Demos, 2020)	FE	0	24	4	19	54	0	101
	<i>Myotis tricolor</i> 1 (Temminck, 1852)	FI	0	0	0	0	0	28	28
	<i>Pipistrellus hesperidus</i> (Temminck, 1840)	FE	38	66	0	42	103	6	255
	<i>Scotophilus andrewreborii</i> Brooks & Bickham, 2014 (Clade 2)	FE	37	147	0	86	109	0	379
	<i>S. nux</i> Thomas, 1904	FI	0	0	0	0	0	2	2
Bat captures (N)			884	1,475	207	1,395	1,805	237	6,003
Species richness (S)			9	15	12	12	15	16	21
Shannon index (H')			1.92	1.95	2.19	2.03	2.14	2.48	
Evenness (J)			0.56	0.21	0.66	0.47	0.23	0.72	

To ensure that these observed patterns were not artefacts of sampling effort, a combination of mist nets and harp traps were used, resulting in the capture of 21 bat species across the two forests. Rarefaction curves approached asymptotes for edge and matrix habitats (Fig. 5), indicating that sampling was adequate, while the absence of an asymptote in forest interiors likely reflects sampling bias and the inherent limitations of ground-level trapping in structurally complex habitats (Meyer *et al.* 2016). Nevertheless, the sampling effort provided a robust representation of bat assemblages in both forests, offering a reliable basis for assessing the effects of habitat degradation on species richness and community composition.

Influence of forest degradation on relative bat abundance and species richness

Our study demonstrated clear differences in bat responses to treatments that varied in levels of human-induced habitat degradation, with the highest species richness found in the less-degraded forest interiors. Higher tree density and fewer signs of human disturbance, such as charcoal kilns, footpaths, sawpits, and cut stumps, characterise these habitats (Fig. 2). Forest interiors, characterised by mature indigenous trees, support forest-dependent, specialist bat species, which rely on tree cavities, foliage, and bark for roosting, and are typically associated with older, heterogeneous stands (Lacki *et al.* 2007; Silvis *et al.* 2015; Novella-Fernandez *et al.* 2022; Vázquez-Rueda *et al.* 2023). Although we did not quantify tree species composition within our plots, previous studies in Nandi Forest have documented high plant diversity and structurally heterogeneous vegetation, including a wide range of indigenous tree species such as *Croton macrostachyus*, *Celtis africana*, *Strombosia scheffleri*, and *Syzygium guineense* (Lung and Schaab 2010; Melly *et al.* 2020). These mature forest conditions provide a diversity of potential roosting substrates and microhabitats that are important for forest-specialist bats.

In contrast to species richness, bat captures, or relative bat abundance, were highest at the more degraded edges and matrices, which were characterised by lower tree density and increased human-use indicators such as charcoal kilns, footpaths, sawpits, and stumps (Fig. 2). Human disturbance in tropical forests is closely linked to accessibility via trails, paths, and roads, which facilitate extractive activities and increase habitat modification beyond the immediate footprint of these features (Laurance *et al.* 2009; Peres *et al.* 2010). These linear clearings reduce vegetation complexity and create edge-like conditions that differentially affect bat guilds, with edge and open-space foragers showing increased activity, while forest-dependent specialists exhibit reduced activity or altered behavior (Meyer *et al.* 2016; Ramalho and Aguiar 2020; Kusch *et al.* 2021; Rocha *et al.* 2023). Disturbance effects can extend into the adjacent forest, constraining the movement of narrow-space foraging bats and limiting access to suitable resources (Bhardwaj *et al.*

2021). Consequently, these disturbed habitats were dominated by widespread generalists, particularly *Epomophorus labiatus* and *E. wahlbergi*, resulting in reduced species richness compared to forest interiors. Similar trends have been observed elsewhere, where less disturbed forests sustain higher species richness (Struebig *et al.* 2011; Cosset *et al.* 2019), while disturbed habitats often support greater abundances of common or generalist species but lower species richness (Ferreira *et al.* 2017; Brändel *et al.* 2020).

In addition to the dominance of common and disturbance-tolerant frugivorous bats (e.g., Cunto and Bernard 2012), the greater abundance of bats at forest edges compared to interiors may be explained by habitat diversity, species-specific morphological traits, foraging strategies, and echolocation abilities (Denzinger and Schnitzler 2013). Many open- and edge-space insectivorous bat species, including representatives of the genera *Pipistrellus* and *Miniopterus*, exhibit plasticity in their echolocation call design, enabling them to switch call structure across different environmental contexts and thereby cope with varying levels of habitat clutter (e.g., Denzinger and Schnitzler 2013; Montauban *et al.* 2021), thereby overcoming perceptual challenges in structurally heterogeneous habitats. By contrast, forest-dependent specialists possess broader wings and frequency-modulated calls that facilitate navigation within dense vegetation, but limit their capacity to exploit open spaces or edge habitats (Schnitzler *et al.* 2003).

Habitat characteristics significantly affect bat abundance (Meyer *et al.* 2016; Laforge *et al.* 2021). In this study, bat captures were highest at forest edges and in the surrounding matrix, likely reflecting the influence of habitat heterogeneity on resource use and movement. Although we did not quantify fruit availability (e.g., fruiting tree abundance or diversity) across habitats, previous studies have shown that frugivorous bat abundance is strongly associated with the distribution of food resources (Meyer *et al.* 2016). It is therefore possible that edge and matrix habitats in our study area supported greater or more accessible fruit resources. Alternatively, the lower capture rates in forest interiors may be influenced by structural complexity, which can constrain the movement of larger-bodied frugivorous bats. Forest structure, composition, and landscape attributes, such as forest cover, are known to shape bat assemblages and activity patterns (Muylaert *et al.* 2016; López-Baucells *et al.* 2022), and differences between forest interiors, edges, and adjacent non-forested habitats may facilitate bat movement and foraging (Laforge *et al.* 2021). Our findings indicated that 99% of frugivorous bat captures occurred at edges and in the matrices, except for *Stenonycteris lanosa*, which was restricted to forest interiors. These patterns should be interpreted cautiously, as they may reflect variation in resource distribution and habitat structure rather than an inherent tolerance of frugivorous bats to disturbance.

The negative impacts of habitat degradation on bat species richness, as evidenced by our capture data, align with the findings of Webala *et al.* (2019) in the adjacent

Kakamega tropical rainforest, located less than 5 km south of the Nandi forests. The growing human population and the expansion of agricultural lands near forests in western Kenya have heightened environmental adversity for bats relative to undisturbed habitats. Habitat loss and degradation jeopardise forest interior specialists, chiefly through fragmentation, which diminishes core forest area and amplifies edge effects (Furey *et al.* 2010; Brasileiro *et al.* 2022). Consequently, species mobility is restricted, access to vital resources is curtailed, and the quality and integrity of the remaining interior habitats are compromised (Kingston 2013; Meyer *et al.* 2016; Rocha *et al.* 2023).

While this study focused on habitat degradation within existing forest areas, broader landscape processes such as habitat loss and fragmentation also influence bat communities in the Nandi Forests. Tropical ecosystems hold immense social, economic, and environmental importance for human well-being (Koech 2018; Maua *et al.* 2018). The separation of the forest into northern and southern blocks reflects historical forest clearing, largely driven by agricultural expansion, human settlement growth, and resource extraction. These processes not only reduce total forest cover but also increase edge effects and isolate interior habitats, potentially restricting the movement of forest specialists. Consequently, declining habitat suitability likely results from the combined effects of local habitat degradation and larger-scale fragmentation linked to socioeconomic pressures surrounding the forests (Kamugisha *et al.* 2023; Prakash and Verma 2022).

Influence of habitat degradation on individual bat species

Structurally complex vegetation supports a more diverse assemblage of gleaning insectivorous bats than simpler habitats, as it offers a greater diversity of foraging niches and prey resources (Geipel *et al.* 2013; Allegrini *et al.* 2022). Although human-induced habitat disturbance and degradation may impact bat habitat use, bat species and ensembles exhibit varying degrees of sensitivity to such perturbations as a result of differences in foraging behavior and roosting ecology. Rather than directly determining their sensitivity, wing morphology influences the manner in which species exploit and navigate various habitat structures (Duco *et al.* 2023; DeAnglis *et al.* 2024). In our study, frugivores and edge- or open-space insectivores dominated edge and matrix habitats at both forests. The disturbance-tolerant frugivores *Epomophorus labiatus* and *E. wahlbergi* occurred across all habitat types, aligning with their known ecological plasticity (Cunto and Bernard 2012; Ferreira *et al.* 2017; Alurralde and Díaz 2021; Rocha *et al.* 2023). Conversely, the forest-dependent *Stenonycteris lanosa* was restricted to the interior of North Nandi Forest, reflecting its sensitivity to human disturbance and strong dependence on interior forest conditions, likely influencing its foraging activity and habitat use, a pattern consistent with findings that specialist bat species

are more vulnerable to habitat degradation (Valle *et al.* 2021).

Forest specialist insectivores, such as *Nycteris* spp., *Myotis tricolor* 1, and *Scotophilus nux*, were only found in the interiors of North Nandi. These narrow-space foragers have morphological adaptations suited for cluttered environments, which limit their ability to utilise open or degraded habitats. High-duty-cycle (HDC) bats, such as rhinolophids and hipposiderids, are particularly well-adapted to these habitats, utilizing constant-frequency echolocation calls and Doppler-shift compensation to detect fluttering insects and navigate dense vegetation (Li *et al.* 2022; Pan *et al.* 2024). *Hipposideros ruber* 2, another forest specialist, was observed in the North Nandi interior and, to a lesser extent, at the edges of South Nandi, indicating a higher tolerance for disturbance. The absence of other specialists in South Nandi underscores its high level of degradation and highlights the functional separation between the two forest fragments (Zipkin *et al.* 2009; Alroy 2017; Vergara *et al.* 2021).

Overall, these findings underscore the vulnerability of forest specialist bat species, particularly narrow-space foraging insectivorous species, are more frequently associated with forest interior habitat than with edge or matrix environments. This pattern may reflect a combination of factors, including reduced disturbance, greater structural complexity, and increased distance from the forest edge, rather than the effects of disturbance alone. Indeed, edge effects are known to influence bat assemblages in complex and species-specific ways, often interacting with vegetation structure and matrix composition (Yoh *et al.* 2022). In addition, niche partitioning and species-specific ecological requirements may further explain the restriction of forest-dependent species to interior habitats, independent of disturbance gradients, as trait-environment relationships strongly shape bat assemblage structure in heterogeneous landscapes (Margarido *et al.* 2024). While some specialist species were recorded exclusively in less disturbed interiors, the present study does not explicitly disentangle the relative influence of habitat degradation from edge effects or intrinsic ecological preferences, as comparisons between disturbed and undisturbed interior forest conditions were not conducted. In contrast, generalist and edge-adapted species were more widely distributed across habitats, indicating greater tolerance to modified environments and contributing to differences in community composition. These findings indicate the urgent need to conserve structurally complex forest interiors while also recognising the multiple ecological processes, including edge effects, habitat configuration, and species-specific traits, that jointly shape bat assemblages in highly degraded and fragmented tropical landscapes.

Complementarity of capture methods

This study used two capture methods to assess the effects of habitat degradation on bats at the South and North Nandi forests, western Kenya. Ground-level mist

nets effectively captured frugivores and the less-maneuvrable insectivorous species, while harp traps were better suited for slower-flying, highly manoeuvrable echolocating insectivorous bats in the clutter of the dense vegetation (Pech-Canche *et al.* 2011; Kingston 2013). Harp traps address the limitations of mist nets by effectively capturing slower flying, highly manoeuvrable, and sophisticated echolocating bats that are adept at detecting and avoiding nets. They are particularly useful in constrained settings, such as dense vegetation (Kingston 2013; Tanshi *et al.* 2021). The methods facilitated a straightforward identification of *Myotis* species, which could be challenging to differentiate using ultrasonic recordings. However, trapping at ground level, without the use of canopy-level mist nets, may have overlooked certain high-flying species (Simmons and Voss 1998). Lastly, a combination of capture and acoustic methods would complement each other, enabling the detection of species that display poor response to either approach (Kunz and Parsons 2009).

AUTHOR CONTRIBUTIONS

SK: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; MJB: data analysis and interpretation, and critical revision of the article; JK: research concept and design, data analysis and interpretation, and critical revision of the article; DW: critical revision, and final approval of the article; PW: research concept and design, data analysis and interpretation, writing, critical revision, and final approval of the article.

COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose.

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