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Acoustic Monitoring Reveals Patterns of Insectivorous Bat Diversity and Activity in South and North Nandi Forests, Kenya

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Abstract

Understanding how habitat degradation affects insectivorous bats is essential for guiding tropical forest conservation. This study employed passive acoustic monitoring to investigate patterns of insectivorous bat diversity and activity across three habitat types: matrix, edge, and interior in South and North Nandi Forests, western Kenya. Recordings were collected between June 2019 and July 2020 using ultrasonic detectors, and call sequences were manually verified using Kaleidoscope Pro to the species level. A total of 24 species representing 8 families and three foraging guilds were identified from over 60,000 validated bat passes. Overall, bat activity and species richness were highest in forest interiors and lowest in matrices, indicating sensitivity to habitat simplification and anthropogenic disturbance. Edge- and open-space foragers such as Mops pumilus and Tadarida spp. dominated the degraded habitats, whereas clutter-adapted species, including Nycteris spp., Myotis tricolor, and Kerivoula spp., were confined to forest interiors. Canonical Correspondence Analysis revealed that tree density, along with indicators of disturbance such as cut stumps and footpaths, significantly influenced bat assemblage composition. These findings demonstrate that structurally complex habitats support higher acoustic activity and greater species diversity, underscoring the importance of conserving interior forest habitats within fragmented landscapes. The study provides a valuable reference for using acoustic monitoring in long-term biodiversity assessments and highlights the potential of insectivorous bats as sensitive indicators of forest ecosystem integrity across tropical forests.

***Keywords:** Insectivorous bats; Acoustic monitoring; Habitat degradation; Forest fragmentation; Nandi Forests*

Introduction

Bats play a crucial role in controlling nocturnal insects, contributing to ecosystem balance and pest regulation (Russo & Jones, 2015; Kingston, 2016). About 1,500 species are recognized globally, reflecting remarkable diversification and ongoing taxonomic refinement (Torrent et al., 2025). Due to their trophic position and sensitivity to environmental change, insectivorous bats are widely used as bioindicators of habitat quality in tropical ecosystems (Trevelin et al., 2022). Assessing spatial and temporal patterns in bat diversity and activity provides insights into forest integrity and the ecological consequences of habitat disturbance (Yoh et al., 2023).

Across tropical Africa, forest conversion to agriculture and settlements has accelerated habitat loss, fragmentation, and degradation, putting pressure on insectivorous bats (Malonza et al., 2021; Uusitalo et al., 2024). Degradation alters vegetation structure, microclimate, prey abundance, and roost availability, strongly affecting bat foraging and acoustic detectability (Hayes et al., 2019; Rocha et al., 2017). Structural attributes such as canopy cover, tree density, and understorey shape the acoustic environment, influencing call propagation and guild partitioning (Geipel et al., 2013). Habitat simplification and edge effects favor open- and edge-foraging generalists while disadvantaging clutter-adapted specialists, producing community homogenization in degraded landscapes.

Passive acoustic monitoring is a non-invasive method for documenting nocturnal bat activity across habitat gradients (Fenton, 2011; Parker, 2022). Compared with mist-netting or harp trapping, ultrasonic detectors record calls from elusive species, generating continuous data that reveal fine-scale temporal and spatial variation (Rojo Cruz et al., 2019). Automated call classification with manual verification improves identification accuracy, making acoustic surveys suitable for cryptic or high-flying insectivores and assessing community responses to land-use change (Brinkley et al., 2021; Guerrero et al., 2023).

Despite growing acoustic applications globally, studies targeting forest-dependent bats in East Africa remain limited (Webala et al., 2019). The Nandi Forest complex (South and North Nandi) is a remnant of the Guineo–

Congolian rainforest margin in western Kenya, ecologically linked to Kakamega Forest. These fragments face pressure from agriculture, logging, charcoal production, and settlement, causing fragmentation and edge effects that may alter bat distributions (Malonza et al., 2021). Detailed acoustic baselines are lacking, constraining evidence-based conservation planning.

This study used acoustic monitoring to quantify insectivorous bat diversity and activity across matrix, edge, and forest interior habitats in South and North Nandi Forests. Specifically, it aimed to (1) compare bat activity and species composition across a degradation gradient, (2) identify key habitat variables influencing bat distribution, and (3) contrast acoustic community structure between South and North Nandi. The study provides new acoustic evidence supporting bats as indicators of forest integrity in Kenyan tropical forests.

Methodology

Study Area

This study was conducted in South (24,683 ha) and North (10,500 ha) Nandi Forests, which together form the Nandi Forest Complex in western Kenya (0°10′–0°25′ N, 35°00′–35°25′ E), lying between an elevation of 1700 m to 200 m above sea level. The region receives an average rainfall of about 1,700 mm annually (KFS 2018). Dominant canopy trees include *Prunus africana*, *Croton megalocarpus*, *Albizia gummifera*, and *Macaranga kilimandscharica*, with bamboo and fern understory in less disturbed areas (Malonza et al., 2021).

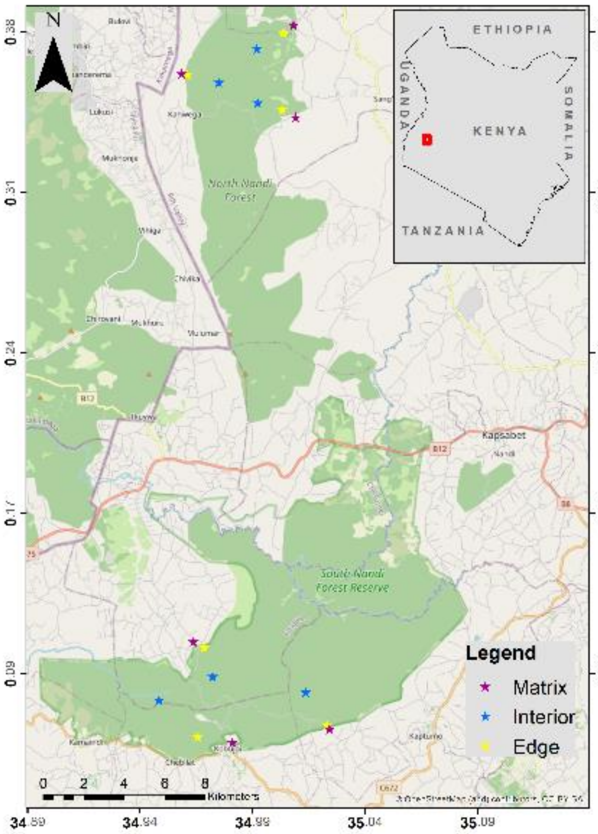

Figure 1: A map of the study area, North and South Nandi Forest, showing sampling locations (stars) and an inset map of Kenya indicating the study area

Data Collection

Data were collected from June 2019 to July 2020 across three habitat types: matrix, edge, and forest interior to capture habitat heterogeneity. The interior, about 200 m from the forest boundary, represented the least-disturbed core; the edge (200–500 m from adjacent farms or settlements) formed the transitional zone; and the matrix comprised agricultural fields, homesteads, roads, and pastures within 1 km of the forest border. Three replicated sites were established in each forest, named after the bordering villages. At each site, bat activity, relative abundance, and species richness were recorded across all habitat types. Habitat structure and disturbance were also assessed by measuring tree density (DBH ≥ 10 cm) within 20 × 20 m plots and recording indicators of degradation, such as cut stumps, saw pits, charcoal kilns, and footpaths.

Acoustic Bat Monitoring

Acoustic monitoring was conducted using three SM4 Bat Detectors (Wildlife Acoustics Inc., Massachusetts, USA), deployed simultaneously at the matrix, edge, and interior sites for two consecutive nights. Microphones were positioned 1.5 m above ground level and oriented toward small gaps or tracks to minimize signal attenuation by vegetation (Adams et al., 2009) (Fig.2). The detectors were configured to record ultrasonic calls at a maximum sampling rate of 384 kHz and 16-bit resolution, with a trigger level of 8 kHz and a minimum sound threshold of 12 dB (Parker, 2022). Recording sessions were programmed to start 30 minutes before sunset and continue until 30 minutes after sunrise. In total, 188 recording nights were completed: 94 nights in South Nandi Forest and 94 nights in North Nandi.

Figure 2: Researcher setting an SM4 Bat Detector (Wildlife Acoustics Inc., USA).

Bat activity was quantified as the number of passes, defined as two or more sequential echolocation calls from an individual (Krishna & Lee, 2025). Sequences exceeding five seconds were segmented in Kaleidoscope Pro (Wildlife Acoustics, USA). Activity data were aggregated by species and site. All recorded calls were manually verified by inspecting spectrograms and comparing them to a custom and regional Kenyan call library in Kaleidoscope Pro, using acoustic parameters such as frequency, duration, and call shape (Parker & Bernard, 2018; Brinkley et al., 2021; Guerrero et al., 2023).

Data Analysis

All acoustic data were processed to quantify bat activity, species richness, and community composition across habitats and forests. Recordings were screened in Kaleidoscope Pro to remove non-bat noise (e.g., insects, rain, mechanical sounds) and only verified bat sequences were retained. Bat activity (passes per night per site) was log-transformed [log (x + 1)] to reduce skewness; however, normality was not achieved even after transformation, justifying the use of non-parametric tests. Accordingly, Kruskal–Wallis tests were used to assess differences in bat activity among habitats and between forests, followed by Mann–Whitney U post hoc tests. Disturbance variables, including cut stumps, saw pits, charcoal kilns, and footpaths, were quantified as counts within each 20 × 20 m plot. Relationships between bat activity and environmental variables were examined using Canonical Correspondence Analysis (CCA) in CANOCO v.4.5 (Ter Braak & Šmilauer, 2002), with Monte Carlo permutation tests (n = 999, $P < 0.05$) and conditional forward selection identifying key predictors (Lepš & Šmilauer, 2003).

Bat Activity and Species Richness

A total of 99,479 bat passes were recorded across all sampling sites during the study period. Of these, 34,824 (35%) were filtered out as non-bat noise, leaving 64,655 passes identified as genuine bat echolocation calls belonging to eight echolocating families (Table 1). The family Vespertilionidae accounted for the highest proportion of recordings (41.48%), followed by Molossidae (33.70%), Miniopteridae (13.89%), Emballonuridae (5.90%), Rhinolophidae (3.92%), Nycteridae (0.94%), Hipposideridae (0.13%), and Megadermatidae (0.05%).

Within these families, 24 species were identified (Table 1). Four species, *Pipistrellus hesperidus*, *Afronycteris nana*, *Mops condylurus*, and *Miniopterus africana*, dominated the acoustic dataset. These species, primarily open-air and edge-space foragers, were largely associated with the Molossidae and Vespertilionidae families. In contrast, clutter-adapted foragers, including species of Rhinolophidae, Hipposideridae, and Nycteridae, were infrequently recorded and restricted mainly to forest interiors.

Across both forests combined, bat activity did not differ significantly among the three habitat types (matrix, edge, and interior) (H (2, n = 60) = 4.28, p = .118; Fig. 3). Rank totals were 630 for matrix, 633 for edge, and 448 for interior. However, pairwise comparison revealed a significant difference between matrix and interior (U = 97, p = .026), while comparisons between matrix–edge (U = 164, p = .49) and edge–interior (U = 161, p = .30) were not significant (Fig. 3).

Patterns varied between forest blocks. In South Nandi Forest, bat activity differed significantly among habitats (H (2, n = 49) = 9.42, p = .009), with rank totals of 457 (matrix), 510 (edge), and 258 (interior). Post hoc pairwise comparisons showed no significant difference between matrix and edge, but both habitats had significantly higher activity than the interior ($p < .05$; Fig. 3). Conversely, North Nandi Forest showed no significant differences in bat activity among the three habitats (H (2, n = 58) = 3.41, p = .182; $p > .05$ for all pairwise tests; Fig. 3). Despite this, species composition differed across habitats. Forest specialists such as *Nycteris* spp., *Kerivoula* spp., *Myotis tricolor*, and *Scotophilus nux* were recorded exclusively within forest interiors, whereas *Hipposideros ruber* occurred only in matrix habitats of South Nandi Forest.

Overall, the response of bat assemblages to varying levels of habitat degradation was distinct, particularly among forest specialist species. In contrast, edge- and matrix-adapted species showed weak or no clear associations with habitat quality gradients. Results of the Canonical Correspondence Analysis (CCA) indicated that tree density was the most influential environmental factor structuring bat assemblages across the study sites (F = 5.36, p = .005). This variable effectively separated sampling sites along a gradient of habitat degradation (Fig. 4).
Conversely, other disturbance-related variables—saw pits, charcoal kilns, footpaths, and cut tree stumps—did not significantly influence bat species distribution across either forest ($p > .05$; Fig. 4).

The CCA biplot (Fig. 4) showed that sites characterized by high tree density, corresponding to forest interiors, were strongly associated with narrow-space foraging species and forest-dependent specialists, including *Hipposideros ruber*, *Nycteris* spp., *Kerivoula* spp., and *Myotis tricolor*. In contrast, most edge and open-air foraging species occurred more evenly across degraded matrices and edges of both forests, suggesting a higher tolerance to habitat alteration.

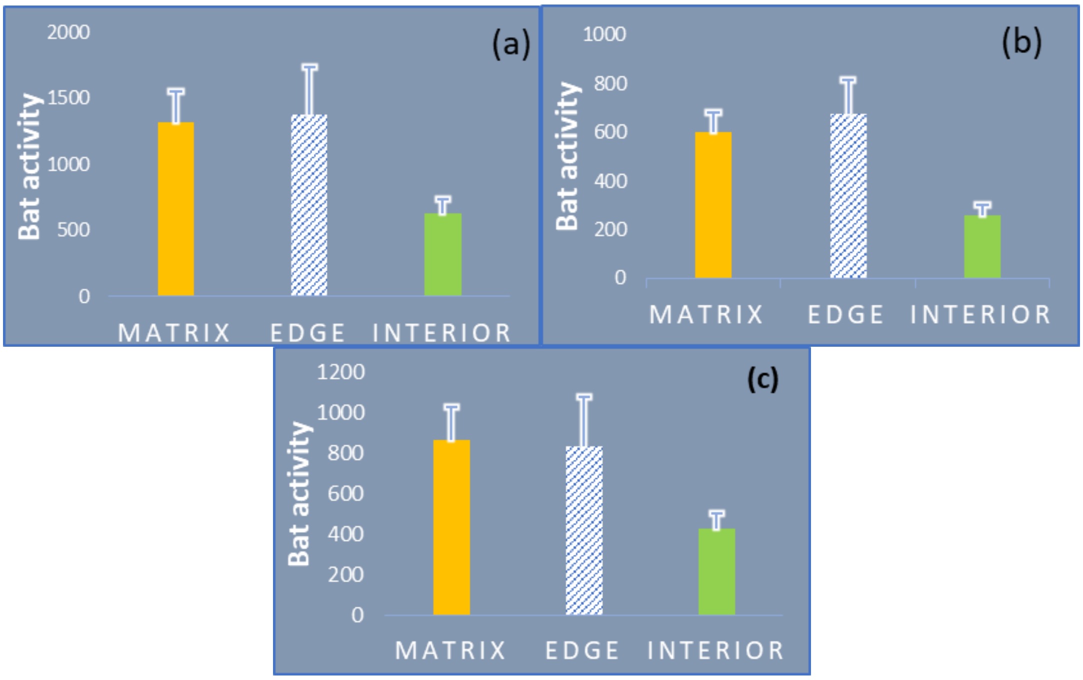

Figure 3 : Difference in bat activity responses to degradation among treatments: (a) Overall, b) South Nandi Forest, and (c) North Nandi Forest

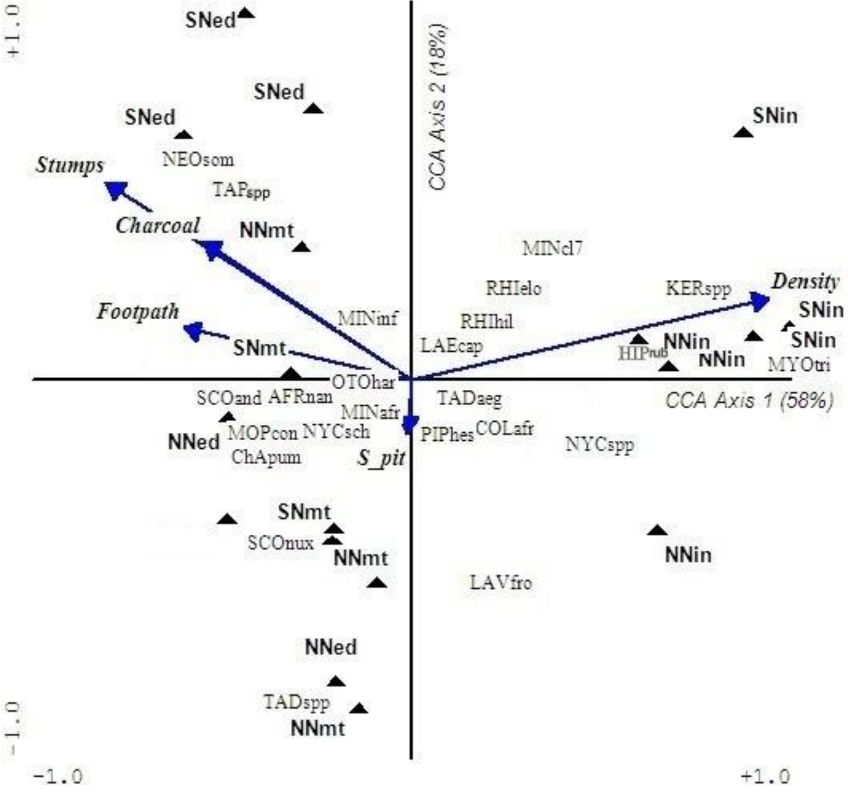

Figure 4 : A biplot of measured parameters (tree density, footpaths, charcoal kilns, cut-tree stumps, and saw pits) and their effects on bat assemblage

Table 1: Bat activity (i.e., number of bat passes) and species detected during acoustic surveys at South and North Nandi Forests

Family	**Species**	**South Nandi**			**North Nandi**			**Total**
		Matrix	**Edge**	**Interior**	**Matrix**	**Edge**	**Interior**	
Rhinolophidae	*Rhinolophus eloquens*	68	198	141	549	61	375	1392
	R. hildebranditi		64	108	225	650	95	1142
Hipposideridae	*Hipposideros ruber*	85						85
Megadermatidae	*Lavia frons*				15	6	9	30
Emballonuridae	*Coleura afra*					160	63	223
	Taphozous spp.	714	692	461	904	188	630	3589
Nycteridae	*Nycteris* spp.			117	58	132	298	605
Molosidae	*Mops pumilus*	696	1199		778	1642	329	4644
	M. condylurus	1108	755	67	2004	2512	392	6838
	Otomops harrisoni	671	740	369	1259	308	834	4181
	Tadarida aegyptiaca	270	1078	377	1701	432	960	4818
	Tadarida spp.	291	429		164	422		1306
Miniopteridae	*Miniopterus Africanus*	690	883	659	1785	1210	1058	6285
	Miniopterus clade 7		227	151		95	240	713
	Miniopterus inflatus	847	177	136	544	42	238	1984
Verspertilionidae	*Afronycteris nana*	659	2462	163	1035	3330	178	7827
	Kerivoula spp.			408			728	1136
	Laephotis Kirinyaga	725	520	391	840	554	501	3531
	Myotis tricolor			186			144	330
	Neoromicia somalica		361			166		527
	Nycticeinops schlieffeni	469	95	118	406	1270		2358
	Pipistrellus hesperidus	774	1148	342	2085	3892	605	8846
	Scotophilus andrewreborii	987	450		390	406		2233
	S. nux					32		32
Number of bat passes		**9, 054**	**11, 478**	**4, 194**	**14, 742**	**17, 510**	**7, 677**	**64, 655**
Species richness (*S*)		**15**	**17**	**16**	**17**	**21**	**18**	**24**

Discussions

Acoustic monitoring revealed clear differences in how insectivorous bat assemblages responded to habitat structure and degradation across South and North Nandi Forests. Overall, bat diversity and activity patterns were associated with vegetation complexity, especially tree density, which emerged as the strongest environmental variable influencing community composition. Forest interiors with high tree density supported greater bat richness, dominated by clutter-adapted, forest-dependent species such as *Hipposideros ruber*, *Nycteris* spp., *Kerivoula* spp., and *Myotis tricolor*. Similar patterns have been observed in other tropical forests where structural complexity enhances acoustic diversity by sustaining multiple frequency niches and reducing signal interference (Adams et al., 2020;Trevelin et al., 2022).

By contrast, open- and edge-adapted species showed greater tolerance to habitat disturbance. Edge and matrix habitats in both forests were dominated by high-intensity, broadband echolocators typical of open-space insectivores such as *Mops pumilus*, *Tadarida* spp., *Neoromicia somalica*, and *Scotophilus andrewreborii*. These bats exploit open foraging spaces and are acoustically efficient in detecting prey in uncluttered environments. Their frequent detections in degraded matrices suggest ecological flexibility and high mobility, enabling them to occupy disturbed areas (Frey-Ehrenbold et al., 2013; Rocha et al., 2017). However, their dominance in acoustically simplified habitats underscores the gradual functional replacement of forest specialists by generalists as degradation intensifies.

In contrast, forest specialists showed marked sensitivity to structural change. *Myotis tricolor* and *Kerivoula* spp. were acoustically restricted to forest interiors in both sites, while *Nycteris* spp. were recorded across all habitats in North Nandi but confined to interiors in South Nandi. *Scotophilus nux* was detected only in the interior of North Nandi. These species emit low-intensity, broadband calls adapted to cluttered spaces, which limit their detection range but allow precise prey localization within dense vegetation (Schnitzler & Kalko, 2001). The detection of *Hipposideros ruber* only within the matrix of South Nandi suggests a degree of tolerance to disturbance, possibly due to its flexible roosting behaviour. The absence of other forest specialists in South Nandi and the restricted distribution of *H. ruber* highlight the greater degradation of this forest, indicating a functional separation between the two fragments (Alroy, 2017; Vergara et al., 2021). Detection bias may have influenced observed diversity, as low-intensity callers like *Kerivoula spp.* and *Myotis tricolor* are harder to detect than loud, open-space species such as *Mops* and *Tadarida*. Nonetheless, their consistent presence in forest interiors supports a true habitat association rather than a detection artifact (Russo & Jones, 2015; López-Baucells et al., 2019).

Tree density exerted a major influence on bat community structure, shaping species distribution along the degradation gradient as visualized in the CCA biplot. Conversely, indicators of human disturbance, such as saw pits, charcoal kilns, footpaths, and cut stumps, had no significant statistical effect. Their limited influence likely reflects their localized or cumulative nature rather than direct acoustic impacts on bat assemblages. In tropical systems, such disturbances often result in lower call richness and reduced foraging activity among forest specialists, even when overall acoustic activity remains stable due to generalist dominance (Wordley et al., 2018). These relationships are clearly illustrated in Figure 4, where sites with higher tree density cluster with greater bat richness and activity, while degraded sites align with lower values along the disturbance gradient.

Differences between South and North Nandi Forests reflect variations in canopy continuity and disturbance intensity. North Nandi, characterized by denser canopy cover and lower edge exposure, exhibited a more balanced acoustic activity across habitats. In contrast, South Nandi showed reduced activity and lower call diversity in its interiors, a pattern indicative of structural degradation and edge intrusion. The dominance of open-space foragers in South Nandi's matrix and edges suggests ongoing fragmentation that limits the persistence of clutter-adapted species. These findings align with acoustic studies from Kakamega Forest and other East African sites, where degradation and edge effects similarly reduced forest specialist activity and altered community composition (Webala et al., 2019; Malonza et al., 2021).

Although this study primarily focused on spatial patterns, temporal variation was evident across sampling months. Bat activity tended to increase during wetter months, likely reflecting higher insect availability and favorable foraging conditions (Frey-Ehrenbold et al., 2013; Adams et al., 2020). Similar seasonal patterns have been reported in Kakamega and other tropical forests, where rainfall strongly influences prey abundance and consequently bat foraging intensity (Webala et al., 2019).

Generalist and edge-adapted bats were consistently detected across forests, but forest specialists' absence in South Nandi indicates ecological deterioration. Bats respond rapidly to habitat changes, and acoustic monitoring provides reliable signals of forest integrity (Kingston, 2016). Continued monitoring is critical for tracking community shifts and assessing restoration success.

Conclusions and Recommendations

This study shows that acoustic monitoring effectively reveals how habitat degradation shapes insectivorous bat assemblages in tropical forests. While overall activity was similar across habitats, species composition varied with forest integrity. Specialists like *Myotis tricolor*, *Kerivoula* spp., and *Nycteris* spp. were restricted to dense forest interiors, whereas edge- and open-space foragers (Molossidae, Vespertilionidae) dominated degraded areas. Tree density was the strongest predictor of bat distribution, emphasizing the role of canopy complexity for clutter-adapted species (Meyer et al., 2023; Rocha et al., 2024). Lower specialist presence in South Nandi indicates higher disturbance (Bernard & Fenton, 2023). To conserve these assemblages, management should maintain dense canopy cover, regulate disturbances such as logging and charcoal production, and enhance connectivity between forest fragments. Continuous acoustic monitoring is recommended, and bats should be included as bioindicators in biodiversity assessments to track forest health (Estrada-Villegas & Meyer, 2021).

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