

## RESEARCH ARTICLE

# Charaxes Butterflies as Bioindicators of Forest Integrity: Conservation Priorities for Kenya's Threatened Nandi Forests

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## ABSTRACT

Fragmented tropical forests urgently need practical, cost-effective tools to assess ecosystem health and direct management resources where they matter most. Butterflies of the genus *Charaxes* are promising candidates: their larvae depend on specific woody host plants, and adults are readily sampled using fruit-baited traps, linking assemblage patterns directly to forest structure and quality. We assessed *Charaxes* diversity, disturbance responses and habitat associations across North Nandi Forest (~11,000 ha; 1700–2130 m a.s.l.) and South Nandi Forest (~15,000 ha; 1600–2000 m a.s.l.), two of Kenya's last Guineo-Congolian rainforest fragments. Six sites spanning a disturbance gradient were sampled monthly throughout 2023, with Van Someren-Rydon fruit-baited traps and visual censuses deployed concurrently at all sites to ensure comparability. A total of 1847 individual *Charaxes* belonging to 18 species were recorded. Both forests maintained high diversity (Shannon  $H' = 2.61$ – $2.64$ ; Pielou's  $J' > 0.91$ ) and log-normal rank-abundance distributions, confirming intact community structure. Species inventories were near-complete (Chao1: 90%–95%). Total *Charaxes* abundance declined by 61% from intact to heavily disturbed sites (Kruskal–Wallis  $H(2) = 14.32$ ,  $p = 0.001$ ,  $\eta^2 = 0.72$ ), with three forest specialists, *Charaxes cithaeron*, *C. violetta* and *C. zoolina*, declining by 72%–76% and showing strong fidelity to closed-canopy habitats (79%–84% of captures under shade). Canonical correspondence analysis explained 52.3% of species–environment variation ( $F_{(5,6)} = 3.14$ ,  $p = 0.002$ , 999 permutations), with *Prunus africana* density ( $r = 0.68$ ), canopy cover ( $r = 0.64$ ) and host plant richness ( $r = 0.61$ ) as the strongest predictors. Bioindicator evaluation using IndVal analysis identified four robust candidate species (IndVal 68.7–76.3,  $p < 0.005$ ), and significant compositional turnover between forest blocks ( $\beta\text{SIM} = 0.38$ ) confirmed that each contributes uniquely to regional diversity. Based on these findings, we recommend equal conservation investment in both forests, maintaining canopy cover above 70%, targeted protection and enrichment planting of *P. africana* and *Turraea stapfiana*, and a tiered monitoring protocol using the three specialist species as early-warning bioindicators of forest deterioration.

## 1 | Introduction

East Africa's montane forests are biological treasures shaped by millions of years of climatic oscillation and geographic isolation. Cooler, cloud-draped and layered with epiphytes, they support fauna and flora found nowhere else on Earth. Yet

they are also among the continent's most imperilled ecosystems, caught between expanding agriculture, selective logging and increasingly erratic rainfall (Burgess et al. 2007; Abera et al. 2024). Unlike the vast lowland forest blocks of Central Africa, highland fragments function as ecological islands: once species are lost from a patch, natural recolonisation is unlikely

without deliberate human effort (Newmark 1998). The pressures are ongoing; deforestation and forest degradation continue to erode both forest area and habitat quality across the region (Lung and Schaab 2006; Obonyo et al. 2023; Ojatre et al. 2023; Chisika and Yeom 2024). For those responsible for managing what remains, a fundamental challenge is knowing whether management interventions are actually working. Monitoring every taxon in every corner of a forest is neither financially realistic nor logistically feasible, yet without reliable measures of ecosystem condition, management decisions lack scientific grounding (Sánchez Herrera et al. 2024). The concept of bioindicators offers a practical route through this dilemma. Rather than surveying all biodiversity, ecologists focus on species or groups whose populations respond predictably to environmental change, thereby reflecting broader ecosystem conditions (McGeoch 1998; Siddig et al. 2016). When these criteria are met, indicator monitoring can detect habitat deterioration early and guide interventions before losses become irreversible (Kremen 1992; Chowdhury et al. 2023).

Butterflies are among the most widely used invertebrate bioindicators worldwide (Thomas 2005; Bonebrake et al. 2010; van Swaay et al. 2019). Their suitability rests on several practical strengths: their taxonomy is comparatively well resolved, their behaviour is conspicuous, their generation times are short and their populations respond sensitively to changes in vegetation structure, microclimate and disturbance (Habermann et al. 2025; Wenda et al. 2025). In tropical forests, fruit-feeding butterfly assemblages are particularly informative because standardised baited traps allow quantitative, repeatable sampling across sites and seasons (Nyafwono et al. 2014; Malinga et al. 2023). Studies across African montane forests, from Nyungwe in Rwanda to the Eastern Arc Mountains of Tanzania, confirm that butterfly communities reliably track gradients of canopy openness, floristic diversity and human disturbance (Uwizelimana et al. 2022; Saouli et al. 2022; Mwangi et al. 2025). Within the Nymphalidae, the genus *Charaxes* is especially well suited for bioindicator application in African montane forests. These large, morphologically distinctive butterflies are readily attracted to fermenting fruit, facilitating standardised capture and consistent identification (Larsen 2005; D'Abrera 2019; Landmann et al. 2023). Their larvae feed on specific woody plants across multiple families, creating a direct ecological link between butterfly assemblages and forest composition: when forests lose particular host trees or structural complexity, associated *Charaxes* species tend to decline in parallel, translating habitat change into a measurable biological signal (Crous et al. 2015). This tight dependency on forest structure makes *Charaxes* not merely a convenient sampling target, but a mechanistically grounded indicator of forest integrity.

The Nandi Forests of western Kenya provide an ideal setting in which to test this potential. North Nandi (~11,000 ha) and South Nandi (~15,000 ha) are among the last fragments of the Kakamega-Nandi Guineo-Congolian rainforest complex, recognised as Key Biodiversity Areas and Important Bird Areas (Nature Kenya 2024). Their elevations range from 1600 to 2130 m a.s.l., supporting diverse fauna including globally threatened taxa such as Chapin's Flycatcher (*Fraseria lendu*). Both forests face ongoing degradation from selective logging, agricultural encroachment, tea expansion and charcoal production, with South Nandi under particularly intensive pressure

(Barnes 1990; Ojatre et al. 2023; CIFOR-ICRAF 2024). Despite their conservation significance, systematic assessments of invertebrate biodiversity and responses to disturbance remain scarce. This study presents a year-long systematic survey of *Charaxes* butterflies across North and South Nandi Forests to address five interconnected questions: (1) What is the species richness, diversity and community structure of *Charaxes* assemblages in these forests, and how do these compare with other East African montane systems? (2) How do abundance, composition, and functional groups vary along a gradient of anthropogenic disturbance? (3) Which environmental variables most strongly influence *Charaxes* distributions, and can these variables be managed? (4) Which *Charaxes* species meet the criteria for reliable bioindicators of forest integrity? (5) Do the two forest blocks harbour sufficiently distinct assemblages to warrant equal and independent conservation investment?

## 2 | Materials and Methods

### 2.1 | Study Area

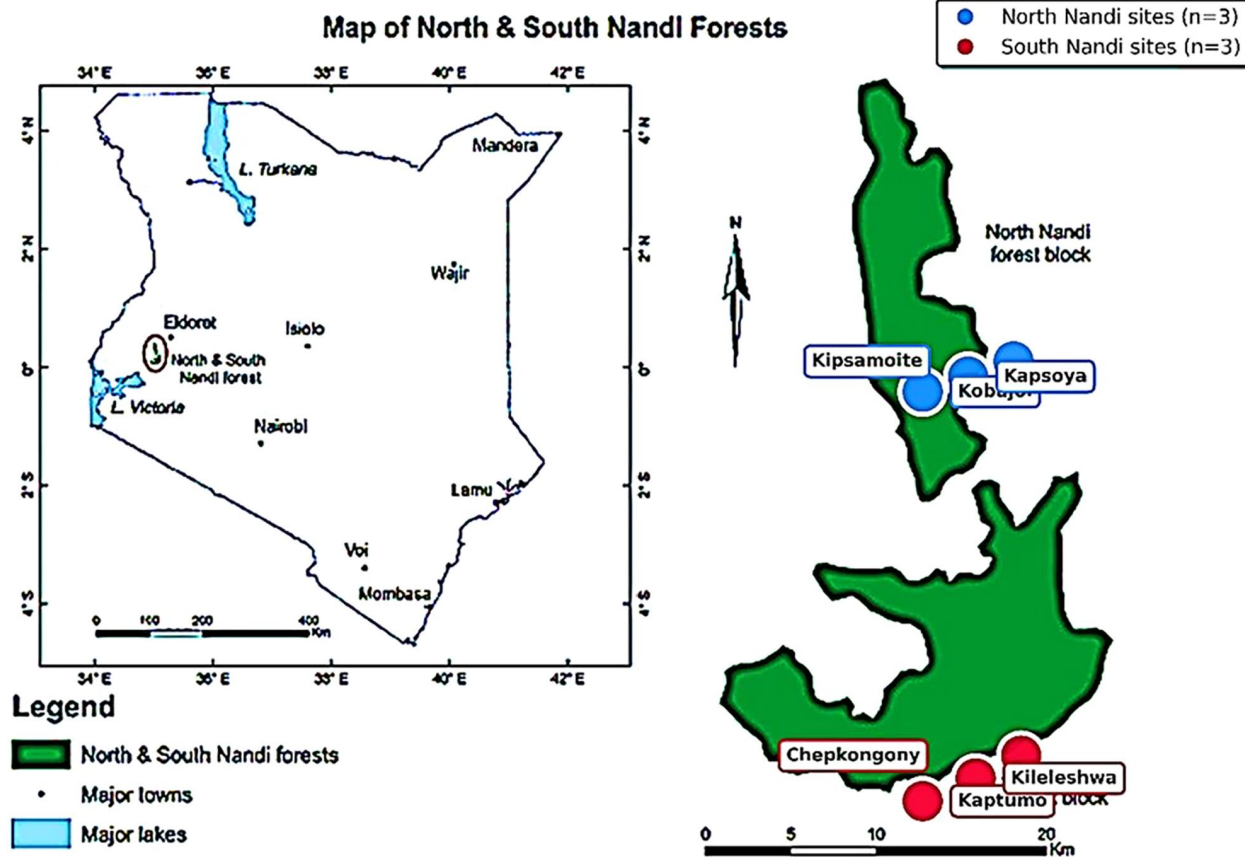
The study was conducted in North and South Nandi Forests, Nandi County, western Kenya (Figure 1). North Nandi Forest (0°06'N, 35°02' E) covers approximately 11,000 ha at elevations of 1700–2130 m a.s.l., while South Nandi Forest (0°03'N, 35°00' E) spans roughly 15,000 ha at 1600–2000 m a.s.l., giving a combined study landscape of approximately 26,000 ha (Figure 1). Together they form the eastern portion of the Kakamega-Nandi forest complex, one of Kenya's last Guineo-Congolian rainforest remnants (Lung and Schaab 2006). Vegetation ranges from closed-canopy moist tropical forest in undisturbed areas to secondary growth and forest-farmland mosaics near the margins (Melly et al. 2020). Both forests are gazetted reserves managed by the Kenya Forest Service, with Community Forest Associations participating in co-management. Dominant canopy species include *Prunus africana*, *Croton megalocarpus*, *Olea capensis*, *Tabernaemontana stapfiana* and *Funtumia africana*. The region experiences a bimodal rainfall pattern, with long rains from March to May and short rains from October to November, and annual precipitation of approximately 1200–2000 mm.

### 2.2 | Sampling Design

Six study sites were established, three in each forest block, to represent a gradient of anthropogenic disturbance. Site selection was based on prior reconnaissance of canopy cover, logging history and proximity to settlements. In North Nandi, the sites were Kobujoi (low disturbance), Kapsoya (moderate disturbance) and Kipsamoite (high disturbance); in South Nandi they were Chepkongony (low), Kileleshwa (moderate) and Kaptumo (high). Disturbance classifications were subsequently confirmed through quantitative measurements of canopy cover, tree density, stump counts and distance from the forest edge (Table 1).

### 2.3 | Independent and Dependent Variables

The independent variable was the level of anthropogenic disturbance, operationalised as a three-level categorical gradient (low,



**FIGURE 1** | Map of study area showing location of North and South Nandi Forests in western Kenya, with sampling sites indicated. Inset shows location within Kenya.

**TABLE 1** | Study site characteristics and environmental measurements for the six sampling sites in North and South Nandi Forests, 2023.

Forest block	Code	Site name	Elev. (m)	Dist. to edge (m)	Canopy cover (%)	Disturbance	Key host plants present
North Nandi	NN3-Interior	Kobujoi	1891	420	88	Low	<i>Olea capensis</i> , <i>Croton megalocarpus</i>
North Nandi	NN2-Mid	Kapsoya	1805	185	82	Moderate	<i>Prunus africana</i> , <i>Tabernaemontana stapfiana</i>
North Nandi	NN1-Edge	Kipsamoite	1742	45	67	High	<i>P. africana</i> , <i>C. megalocarpus</i>
South Nandi	SN3-Interior	Chepkongony	1956	485	91	Low	<i>P. africana</i> , <i>T. stapfiana</i>
South Nandi	SN2-Mid	Kileleshwa	1867	215	85	Moderate	<i>P. africana</i> , <i>T. stapfiana</i>
South Nandi	SN1-Edge	Kaptumo	1728	38	71	High	<i>P. africana</i> absent; <i>C. megalocarpus</i> present

moderate, high) based on a composite index of canopy cover, stump density, canopy gap frequency and distance from the forest edge, measured at each site. The dependent variables were *Charaxes* abundance (total individuals per site per sampling

period), species richness, Shannon diversity ( $H'$ ), Pielou's evenness ( $J'$ ) and community composition (species  $\times$  site abundance matrix). Environmental predictors, including *P. africana* density, host plant richness, native tree richness, canopy cover and

distance from forest edge, were treated as continuous covariates in multivariate analyses.

## 2.4 | Butterfly Sampling

*Charaxes* butterflies were sampled from January to December 2023, totalling 72 field visits across all six sites (12 monthly visits  $\times$  6 sites). Two complementary methods were used concurrently at all sites in each monthly sampling session, ensuring that data were fully comparable across the disturbance gradient. The primary method used Van Someren-Rydon fruit-baited traps—cylindrical mesh traps with baited platforms. Five traps per site were suspended 1.5 m above the ground along permanent transects at 50 m intervals. Traps were baited with fermented banana prepared by mashing ripe bananas and allowing fermentation for 48 h, a well-established attractant for fruit-feeding Nymphalidae including *Charaxes* (Larsen 2005). Each site was sampled for four consecutive days per month, with traps checked and refreshed each morning between 08:00 and 10:00 h. All captured butterflies were identified to species, sexed, measured (forewing length) and released within 30 min. Visual transect censuses complemented trap sampling. Observers walked the same permanent transects for 60 min per visit, recording all *Charaxes* within 5 m of the transect centreline and noting flight height and microhabitat (sun or shade; interior or edge). Concurrent sampling across all six sites in each monthly session controlled for seasonal and weather-related variation.

## 2.5 | Environmental Measurements

Environmental measurements were recorded monthly within five 20  $\times$  20 m plots centred on trap locations at each site. Variables measured included: canopy cover (%; using a spherical densiometer at five points per plot); tree species richness and density (all stems  $\geq$  10 cm DBH); host plant density (stems/ha of known *Charaxes* larval hosts); *P. africana* and *T. stapfiana* density; disturbance intensity (composite index of stump density, canopy gaps and evidence of logging); distance from forest edge;

elevation; and microhabitat characteristics (shade percentage, capture height).

## 2.6 | Data Analysis

Analyses were structured sequentially to address each research question. Species richness, Shannon diversity ( $H'$ ), Pielou's evenness ( $J'$ ) and effective number of species were calculated for each site and forest block. Per-block individual counts presented in figures and text reflect the direct sum of site-level captures (because sampling effort was equal across all six sites and each forest block contained three sites; no statistical weighting or reweighting was involved) rank-abundance distributions were plotted and tested against log-normal and geometric series models using chi-squared goodness-of-fit tests. Species accumulation curves were generated with the Specaccum function in R v4.3.2 (R Core Team 2023) package vegan, and Chao1 richness estimators were used to assess sampling completeness (Chao et al. 2023). Differences in total abundance and species richness across disturbance categories were tested with Kruskal–Wallis tests, followed by Dunn's post hoc comparisons for pairwise contrasts. Effect sizes for Kruskal–Wallis tests are reported as eta-squared ( $\eta^2$ ). Species–environment relationships were explored using canonical correspondence analysis (CCA) in CANOCO 5.0, with statistical significance assessed by Monte Carlo permutation tests (999 permutations). Pearson correlations between individual environmental predictors and *Charaxes* abundance and richness were calculated, with variables showing  $r > 0.30$  and  $p < 0.05$  treated as ecologically meaningful. Indicator species analysis (IndVal; Dufrene and Legendre 1997) was performed using the R package indicpecies to assess the fidelity and specificity of each species to forest block and disturbance category. Candidate bioindicators were evaluated against five criteria (Table 2). Compositional complementarity between the two forest blocks was quantified using the Sørensen dissimilarity index ( $\beta$ SIM), which captures the species turnover component of beta diversity independently of richness differences. The full CCA ordination output and

**TABLE 2** | Criteria used to evaluate *Charaxes* species as bioindicators of forest integrity.

Criterion	Definition/threshold	Species meeting criterion
Disturbance sensitivity	> 50% abundance decline from intact to disturbed sites ( $p < 0.05$ )	<i>Charaxes cithaeron</i> (72%), <i>C. violetta</i> (76%), <i>C. zoolina</i> (74%), <i>C. protoclea</i> (58%), <i>C. smaragdalis</i> (54%)
Habitat fidelity	> 70% of captures in specific habitat type	<i>C. cithaeron</i> (84%), <i>C. violetta</i> (81%), <i>C. zoolina</i> (79%)
Statistical indicator value	Significant IndVal $> 0.50$ , $p < 0.05$	<i>C. protoclea</i> (76.3), <i>C. smaragdalis</i> (68.7), <i>C. cithaeron</i> (69.8), <i>C. violetta</i> (significant; no block specificity)
Detectability	Annual captures $> 20$ individuals; detected in $> 50\%$ of sampling months	<i>C. cithaeron</i> ( $n = 107$ ), <i>C. protoclea</i> ( $n = 89$ ), <i>C. smaragdalis</i> ( $n = 74$ ), <i>C. violetta</i> ( $n = 51$ )
Identification reliability	Distinctive morphology enabling consistent field identification	All four strong-indicator species; confirmed against D'Abbrera (2019) and Larsen (2005)

biplot are available from the corresponding author upon request.

## 2.7 | Permits and Ethical Compliance

All fieldwork was conducted under permit NACOSTI/P/16/38430/9288 from the National Commission for Science, Technology and Innovation, with notification to the Kenya Forest Service. Sampling was entirely non-lethal and followed Kenya's Wildlife Conservation and Management Act (2013) and institutional guidelines at Moi University.

## 3 | Results

### 3.1 | Sampling Effort and Species Inventory

Over 432 trap-days spread across 72 monthly field visits, we recorded 1847 individual *Charaxes* butterflies belonging to 18 species. South Nandi yielded all 18 species ( $n=1018$ ), while North Nandi recorded 17 species ( $n=829$ ). Species accumulation curves for both blocks approached asymptotes by the end of sampling (Figure 2), and Chao1 estimators indicated that the surveys captured approximately 90% of estimated richness in North Nandi and 95% in South Nandi, confirming near-complete inventories for both.

### 3.2 | Diversity and Community Structure

Both forests maintained high species diversity throughout the study year. Shannon diversity indices were  $H' = 2.614$  for North Nandi and  $H' = 2.637$  for South Nandi, with Pielou's evenness exceeding 0.91 in both blocks—values at the upper end of ranges reported for *Charaxes* assemblages elsewhere in African

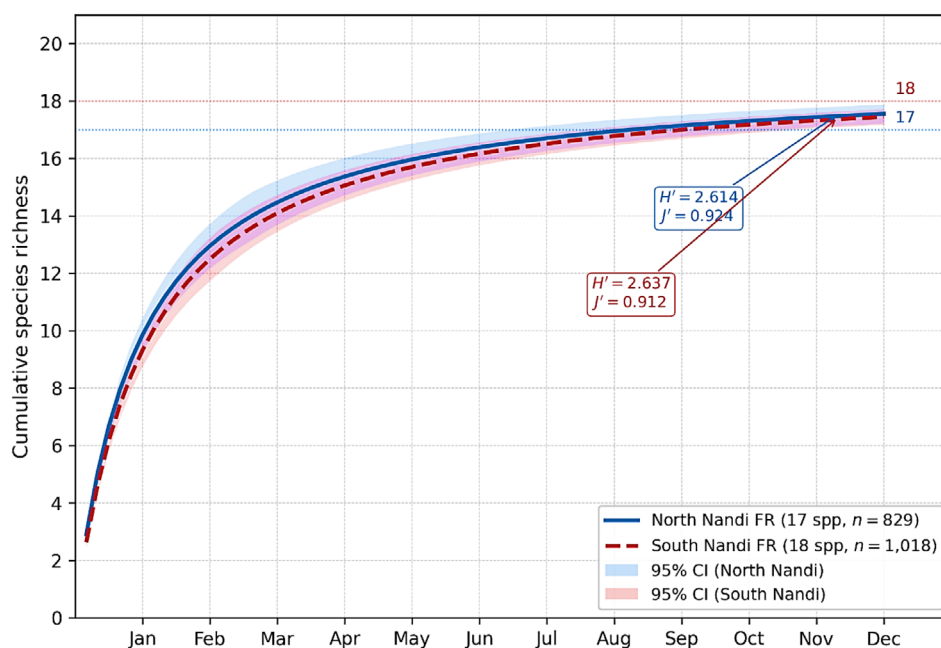
tropical forests. Rank-abundance distributions fitted log-normal models well (North:  $\chi^2 = 4.21$ ,  $p = 0.52$ ; South:  $\chi^2 = 3.87$ ,  $p = 0.57$ ; Figure 3), indicating assemblages with balanced species representation rather than the geometric-series pattern typical of degraded or disturbed communities.

### 3.3 | Responses to Disturbance

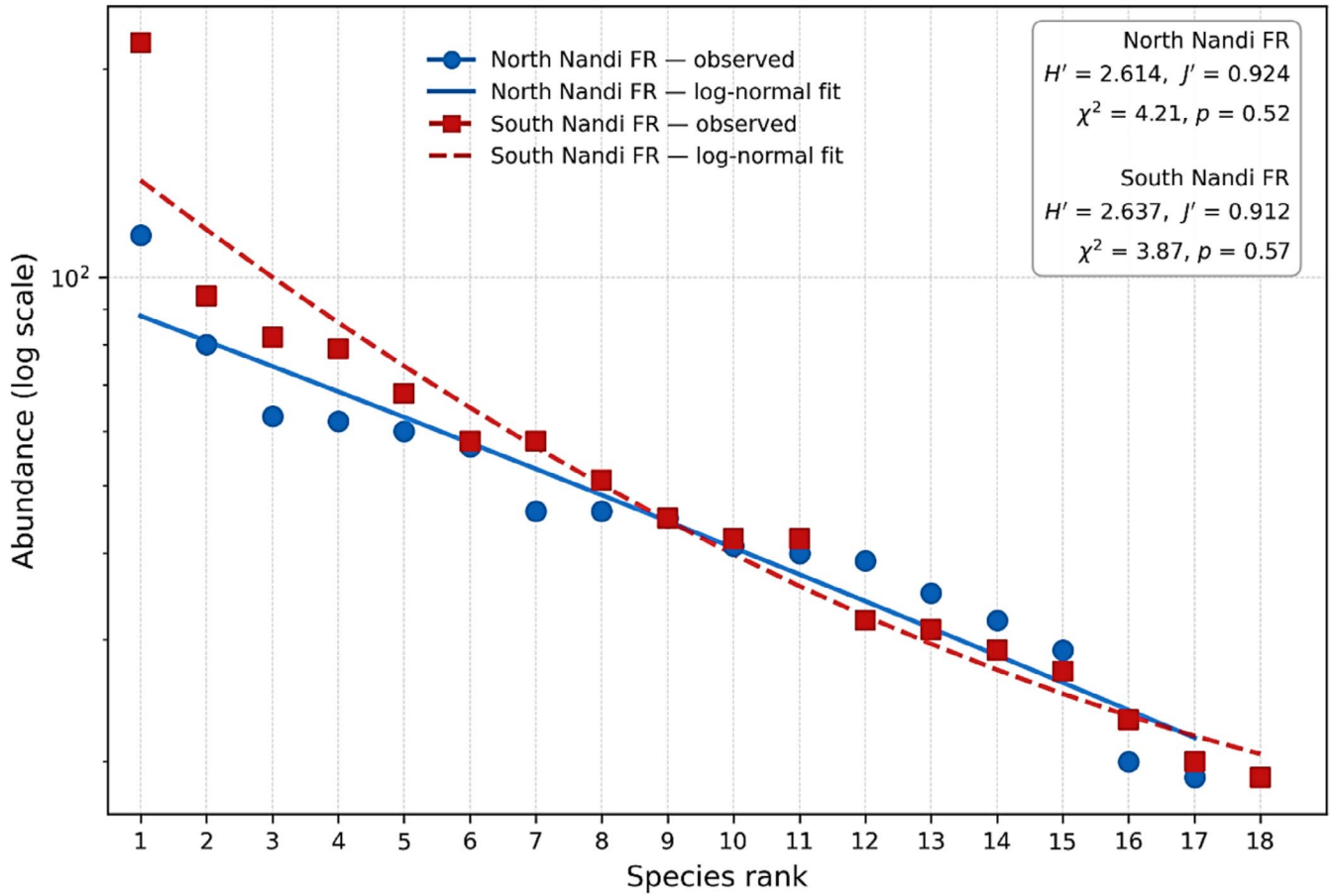
Total *Charaxes* abundance declined significantly along the disturbance gradient (Kruskal–Wallis  $H(2) = 14.32$ ,  $p = 0.001$ ,  $\eta^2 = 0.72$ ; Figure 4). Mean abundance fell from  $424.5 \pm 19.1$  SE individuals at low-disturbance sites to  $346.5 \pm 30.4$  SE at moderate sites and  $237.0 \pm 49.5$  SE at heavily disturbed sites—a 61% reduction from intact to degraded conditions. Species richness followed a parallel trend, declining from  $17.5 \pm 0.7$  SE species at low-disturbance sites to  $15.5 \pm 0.7$  SE and  $13.5 \pm 0.7$  SE at moderate and heavily disturbed sites, respectively (Kruskal–Wallis  $H(2) = 8.67$ ,  $p = 0.013$ ,  $\eta^2 = 0.43$ ). Forest specialist species were the most sensitive to disturbance (Figure 4B). *Charaxes cithaeron* declined by 72% from intact to heavily disturbed sites, with 84% of all captures recorded in closed-canopy shade. *C. violetta* showed the steepest decline at 76% (81% shade fidelity), while *C. zoolina* declined by 74% (79% shade fidelity). In contrast, generalist species proved considerably more resilient: *C. candiope* declined by only 45%, *C. etheocles* by 42% and *C. brutus* by 28%, with all three recorded across a wide range of microhabitats.

### 3.4 | Species–Environment Relationships

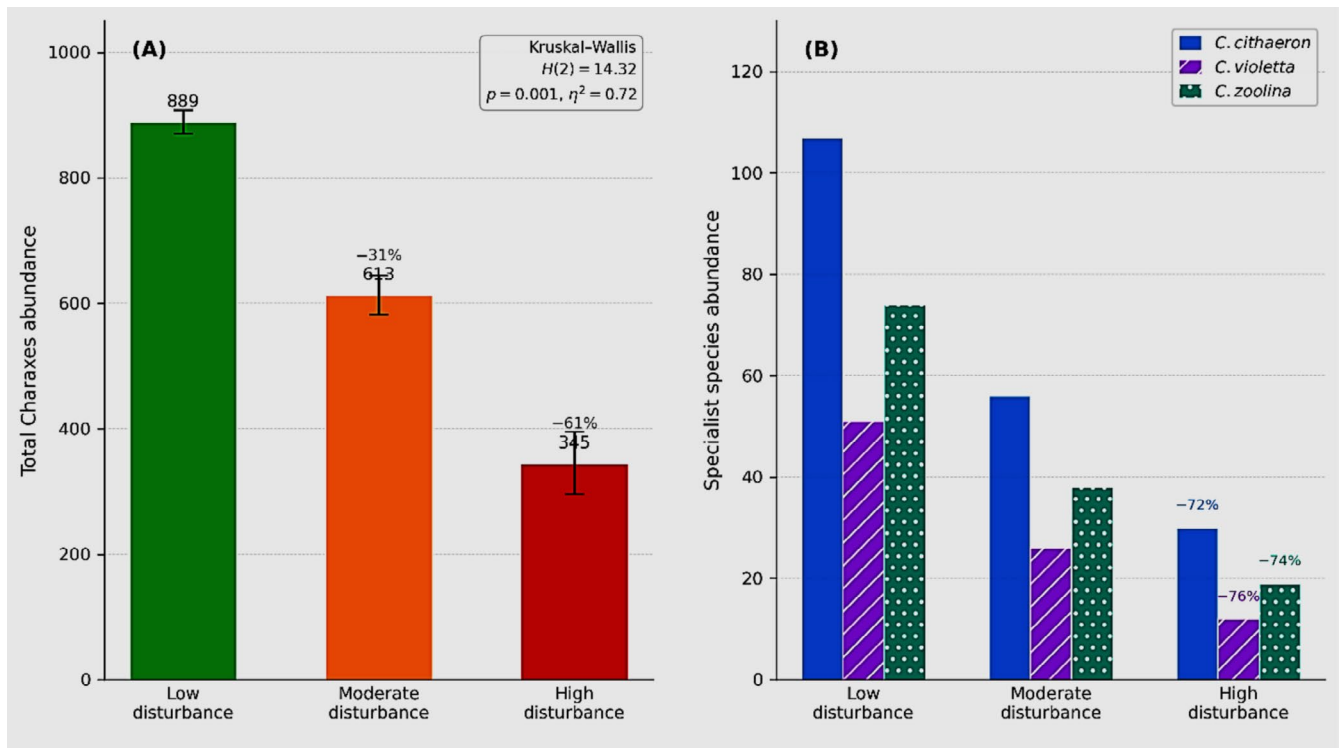
CCA explained 52.3% of species–environment variation on the first two axes (axis 1: 31.7%; axis 2: 20.6%; Monte Carlo permutation test:  $F_{(5,6)} = 3.14$ ,  $p = 0.002$ , 999 permutations). Among the environmental predictors, *P. africana* density showed the strongest correlation with *Charaxes* abundance ( $r = 0.68$ ,  $p < 0.001$ ),



**FIGURE 2** | Rarefaction curves with 95% confidence intervals for North Nandi ( $n = 829$ ) and South Nandi ( $n = 1018$ ) displaying  $H'$  and  $J'$  values for each block; sampling period January–December 2023.



**FIGURE 3** | Rank-abundance distributions on a log scale. Observed points (circles=North Nandi, squares=South Nandi) with fitted log-normal curves. The relatively shallow slope confirms the high evenness ( $J' > 0.91$ ). The statistics inset carries the  $H', J', \chi^2$  and  $p$  values for both forest blocks.



**FIGURE 4** | Two-panel disturbance figure. (A) Total abundance declining from 889 → 613 → 345 across the gradient with error bars and the Kruskal-Wallis statistics inset. (B) The three specialist species (*Charaxes cithaeron*, *C. violetta* and *C. zoolina*) as grouped bars with decline percentages (−72%, −76% and −74%) labelled above the high-disturbance bars. Hatching distinguishes the three species in black-and-white printing.

followed by canopy cover ( $r=0.64$ ,  $p<0.001$ ), host plant richness ( $r=0.61$ ,  $p<0.001$ ), *T. stapfiana* density ( $r=0.59$ ,  $p<0.001$ ) and native tree richness ( $r=0.58$ ,  $p=0.003$ ). Disturbance intensity was negatively associated with both abundance ( $\beta=-0.45$ ,  $p<0.001$ ) and species richness ( $\beta=-0.38$ ,  $p=0.006$ ). Distance from the forest edge ( $r=0.43$ ,  $p=0.032$ ) and elevation ( $r=0.31$ ,  $p=0.019$ ) showed weaker but statistically significant correlations.

### 3.5 | Indicator Species Evaluation

Of the 18 *Charaxes* species recorded, four were classified as strong bioindicators after evaluation against the five criteria in Table 2. *C. cithaeron* was the strongest indicator for North Nandi (IndVal=69.8,  $p=0.003$ ), combining a 72% abundance decline, 84% shade fidelity, high detectability ( $n=107$ ) and unambiguous field identification. *C. protoleia* (IndVal=76.3,  $p=0.001$ ) and *C. smaragdalis* (IndVal=68.7,  $p=0.004$ ) were strong indicators for South Nandi, each showing moderate abundance declines and high habitat fidelity. *C. violetta* was a strong overall indicator (76% decline, 81% shade fidelity,  $n=51$ ) but lacked significant block specificity. Three further species—*C. zoolina*, *C. candiope* and *C. etheocles*—were classified as moderate indicators, while the remaining species, including the abundant generalists *C. brutus* and *C. castor*, were weak indicators.

### 3.6 | Forest Block Complementarity

Beta diversity between North and South Nandi was substantial ( $\beta\text{SIM}=0.38$ ; this value represents the species turnover component of the Sørensen dissimilarity index and is therefore independent of any richness differences between blocks), indicating that a substantial proportion of each forest's species pool is not shared with the other. Seven species showed strong block-specific indicator values; *C. lucretius* (rarity score=0.83), for example, occurred almost exclusively in North Nandi. Applying the conservation priority scoring framework (Table 3), both

**TABLE 3** | Conservation priority scores for North and South Nandi Forests.

Conservation criterion	North Nandi (score 1–5)	South Nandi (score 1–5)
Alpha diversity (species richness, Shannon $H'$ , effective species)	5	5
Beta diversity contribution (compositional turnover)	4	4
Rarity-weighted richness (sum of species rarity scores)	5	4
Indicator species representation (no significant block-specific indicators)	4	4
Threat level and protection status	4	5
Total	22	22

blocks achieved identical total scores (North: 22; South: 22), confirming that each forest contributes equally to regional diversity and warrants equal conservation investment.

## 4 | Discussion

The 18 *Charaxes* species recorded in the Nandi Forests exceed richness reported from comparable East African montane systems, including Kakamega Forest (12 species; Larsen 1996), the Taita Hills (9 species) and Eastern Arc fragments (11–14 species; Mtui et al. 2022). When adjusted for area, however, richness falls within expectations for forests of approximately 26,000 ha in Central Africa (Ewers and Didham 2006), indicating that the assemblage is not anomalously rich but ecologically consistent with its size and biogeographic context. Diversity metrics reinforce this interpretation. Shannon diversity ( $H'=2.61$ – $2.64$ ) exceeds typical values reported for African tropical *Charaxes* communities (1.8–2.4; Larsen 2005), while evenness ( $>0.91$ ) is notably higher than the range commonly observed in tropical butterfly assemblages (0.65–0.85; Magurran 2004). The log-normal rank-abundance distributions observed here, together with clear deviation from geometric series expectations, indicate structurally complex communities with relatively balanced species representation rather than assemblages dominated by disturbance-tolerant generalists. Taken together, these patterns indicate that, despite sustained anthropogenic pressure, the Nandi Forests retain substantial conservation value.

The functional composition of the assemblage provides further insight into its condition. Forest specialists accounted for 44% of species and 38% of individuals, demonstrating that interior-dependent taxa persist in meaningful numbers. This is ecologically significant, as the loss of specialists often precedes broader community simplification (Koh and Wilcove 2008). The absence of several species recorded in Kakamega Forest is attributable primarily to widespread generalists rather than range-restricted specialists, suggesting that the conservation-relevant component of the community remains largely intact. However, the magnitude of specialist declines across disturbance gradients, exceeding 70% for multiple species, indicates that these systems are already undergoing measurable erosion. Without intervention, continued degradation is likely to shift assemblages towards generalist dominance, reducing both ecological function and conservation value.

Three lines of evidence support the use of *Charaxes* as bioindicators of forest condition in these montane systems. First, specialist abundance declined by 70%–76% across gradients of canopy loss and logging intensity, providing a strong and quantifiable biological signal. Second, the observed relationships between butterfly populations and habitat structure are mechanistically grounded. Canopy cover regulates microclimatic conditions, particularly light and temperature, which directly influence butterfly thermoregulation and activity (Landmann et al. 2023; Wenda et al. 2025; Mwinzi et al. 2025), while host plant availability, especially *P. africana* and *T. stapfiana*, constrains larval development and adult resource use (Crous et al. 2015). Third, indicator species analysis identifies a small subset of species that can be monitored efficiently, allowing for cost-effective assessment without the need for full assemblage surveys. These attributes make *Charaxes* a practical tool for operational forest

**TABLE 4** | Management thresholds, restoration priorities and monitoring triggers for maintaining *Charaxes* assemblage integrity in the Nandi Forests.

<b>Variable</b>	<b>Threshold/ indicator</b>	<b>Ecological basis</b>	<b>Management action</b>	<b>Priority sites</b>
Canopy cover	Maintain > 70% (intact); restore to $\geq$ 70% (degraded)	Strong positive relationship with specialist abundance; regulates microclimate (light, temperature) affecting butterfly activity and survival	Enforce control of illegal logging and charcoal production; implement native tree planting to restore canopy structure	Kipsamoite (North Nandi); Kaptumo (South Nandi); all degraded sites
Host plant density ( <i>Prunus africana</i> )	Increase density; prevent local extinction	Strongest predictor of <i>Charaxes</i> abundance ( $r = 0.68$ , $p < 0.001$ ); critical for larval development and adult resource use	Enrichment planting; strict protection from bark harvesting; integrate into community forestry programmes	Kaptumo (absent); other degraded sites
Host plant diversity (incl. <i>T. stapfiana</i> )	Maintain or enhance diversity	Supports specialist species and overall assemblage stability; linked to resource availability	Mixed-species enrichment planting; protect existing vegetation	Degraded and edge habitats
Specialist species abundance ( <i>C. cithaeron</i> , <i>C. violettia</i> , <i>C. zoolina</i> )	$\geq$ baseline levels; decline > 20% triggers concern	Sensitive to disturbance; early indicators of habitat degradation	Annual rapid monitoring using baited traps; initiate full survey if threshold exceeded	All monitoring sites
Forest disturbance (logging intensity, canopy loss)	Minimise further disturbance	Directly linked to > 70% decline in specialist species across gradient	Strengthen enforcement; regulate resource extraction; promote alternative livelihoods	All sites, especially degraded areas
Habitat connectivity	Maintain or restore corridors ( $\geq$ 50% canopy cover)	Facilitates dispersal and gene flow between forest blocks	Corridor restoration through native tree planting; landscape-level planning	Between North and South Nandi
Monitoring frequency	Annual rapid assessment; full survey every 5 years	Balances cost and detection of long-term trends	Implement tiered monitoring protocol; adapt management based	

monitoring. Nonetheless, important limitations remain. The 1-year sampling period does not capture interannual variability driven by climatic fluctuations or stochastic population dynamics, and baited traps may underrepresent species with low attraction to fermenting fruit. In addition, cross-taxon congruence is known to be inconsistent (Lawton et al. 1998; Ewers et al. 2015), and *Charaxes* should therefore be interpreted as indicators of forest structural integrity and associated plant communities rather than proxies for biodiversity as a whole.

The conservation status of the Nandi Forests is, therefore, best described as transitional. High diversity, even community structure and log-normal abundance distributions indicate that core ecological processes remain intact. At the same time, the marked decline of specialist species in disturbed sites demonstrates that degradation is already affecting sensitive components of the system. These patterns point to forests that are still functioning but increasingly vulnerable, with a narrowing window for effective intervention. Structural habitat attributes, particularly canopy cover and host plant diversity, emerge as the principal determinants of assemblage integrity, providing clear and actionable targets for management.

Differences between North and South Nandi further emphasise the need for integrated conservation planning. The observed compositional turnover ( $\beta\text{SIM} = 0.38$ ), together with the presence of block-specific indicator species, demonstrates that the two forest blocks are complementary rather than redundant components of the regional system. Protecting one in isolation would result in the loss of species unique to the other, a pattern consistent with established principles of systematic conservation planning (Margules and Pressey 2000). The identical conservation priority scores for the two blocks reinforce the conclusion that both warrant equal investment and coordinated management.

The species–environment relationships identified here translate directly into management priorities. Canopy cover is the most influential modifiable variable, with specialist species declining sharply below approximately 70%. Maintaining cover above this threshold in intact areas and restoring degraded sites to similar levels should therefore be a central objective. Host plant availability, particularly of *P. africana*, is equally critical. This species emerged as the strongest predictor of *Charaxes* abundance ( $r = 0.68$ ,  $p < 0.001$ ), and its absence at the most degraded site, Kaptumo, is likely a key driver of the reduced specialist populations observed there. Given its additional socio-economic importance and vulnerability to overexploitation, targeted protection and enrichment planting of *P. africana* and *T. stapfiana* would deliver both ecological and livelihood benefits (Vinceti et al. 2013; Oloya et al. 2021; Poorter et al. 2021). Restoration of the most degraded sites, including Kipsamoite and Kaptumo, should proceed in phases, beginning with threat reduction, followed by canopy restoration using native species and subsequently host plant enrichment and adaptive monitoring, in line with restoration frameworks shown to be effective in tropical systems (Rey Benayas et al. 2009; Malinga et al. 2023).

To operationalise these findings, management thresholds and restoration priorities are synthesised in Table 4 as a practical decision-support framework. By consolidating key variables, ecological thresholds and site-level interventions, the table provides

a structured basis for translating ecological evidence into management action while avoiding duplication within the text.

Monitoring strategies should similarly balance practicality and sensitivity. Annual rapid assessments based on a small number of indicator species (*C. cithaeron*, *C. violetta* and *C. zoolina*) can provide early warning of declining forest condition, with a reduction of more than 20% in combined specialist abundance serving as a trigger for more detailed investigation. Comprehensive assemblage surveys should be conducted at approximately five-year intervals, or sooner if rapid assessments indicate deterioration. This tiered approach offers a cost-effective means of maintaining surveillance while retaining the capacity to detect longer-term ecological change.

The present study provides a robust but temporally limited assessment. Extending monitoring over multiple years will be necessary to capture interannual variability and strengthen inference regarding trends. Expanding surveys to additional taxa would help determine the extent to which butterfly responses reflect broader ecosystem dynamics, while genetic analyses could clarify connectivity between the two forest blocks. Incorporating socio-economic research on land tenure, community engagement and institutional capacity would further support the development of co-management frameworks capable of sustaining restoration efforts over the long term.

Overall, the evidence indicates that the Nandi Forests retain high ecological value but are under increasing pressure. The drivers of change are identifiable and, importantly, manageable. Canopy structure, host plant availability and targeted monitoring provide a clear framework for intervention, while the demonstrated complementarity of the two forest blocks underscores the need for coordinated conservation strategies. The continued presence of diverse and structurally balanced *Charaxes* assemblages suggests that effective conservation outcomes remain achievable, provided that management actions are implemented before further degradation reduces the resilience of these systems.

#### Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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