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Research Paper

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MOTH COMMUNITY RESPONSES TO VEGETATION COMPLEXITY AND MICROCLIMATE IN NYARIBUNGAN, MAHAKAM ULU, EAST KALIMANTAN

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ARTICLE HIGHLIGHTS

- Moth communities differed across three tropical forest habitats.
- Natural forest supported the richest moth community.
- Plant richness and canopy cover were linked to higher moth diversity.
- Higher night temperature was linked to lower moth abundance.
- Vegetation complexity is important for sustaining moth diversity.

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ABSTRACT

Vegetation complexity and local microclimatic conditions are important factors shaping moth communities in tropical forest landscapes. This study examined differences in moth community structure and composition among habitat types and evaluated the relationships of moth abundance and species richness with vegetation richness and local environmental variables in Nyaribungan Village, Mahakam Ulu, East Kalimantan, Indonesia. Moths were sampled using light traps in 12 plots distributed across three habitat types: natural forest, disturbed forest, and riparian buffer, with four plots in each habitat. Woody plants were recorded within a ±50 m radius and vascular understory plants within a 5 m radius from each trap point. Environmental variables included canopy cover, nighttime temperature, nighttime relative humidity, distance to river, and elevation. A total of 1,149 moth individuals representing 196 species from 18 families were recorded. Natural forest supported the highest abundance, species richness, and Shannon diversity, whereas disturbed forest had the lowest values and riparian buffer was intermediate. Moth community composition differed significantly among habitat types at the global level. Bivariate negative binomial models showed that woody plant richness, vascular plant richness, and canopy cover were positively associated with moth abundance and species richness, whereas night temperature was negatively associated with both metrics. These findings indicate that vegetation-rich, closed-canopy habitats were associated with more abundant and species-rich moth communities, highlighting the importance of natural forest remnants and riparian habitats for maintaining moth diversity in disturbed tropical forest landscapes.

Keywords: canopy cover, microclimate, moth communities, riparian buffer, vegetation richness

INTRODUCTION

Moths are among the most diverse and ecologically important insect groups in terrestrial ecosystems. They function as herbivores, pollinators, and prey for higher trophic levels, and their communities often respond sensitively to habitat change and environmental stress. Because of these characteristics, moths have long been used as indicators of habitat quality and ecological condition in forest landscapes (Willott 1999; Kitching *et al.* 2000; Intachat *et al.* 2001; Beck *et al.* 2002; New 2004; Axmacher *et al.* 2009; Tyler 2020). Their ecological value is particularly relevant in biodiversity monitoring because local moth assemblages can reflect site-specific habitat characteristics and are useful for conservation assessment.

In forest ecosystems, moth abundance, species richness, and community composition are influenced by vegetation structure, host-plant availability, and local abiotic conditions. More structurally complex habitats generally provide a wider range of larval resources, resting substrates, and sheltered microhabitats, whereas habitat opening may alter canopy buffering and expose insects to warmer and less stable near-ground conditions. Previous studies have shown that moth communities vary across forest-to-farmland gradients, respond to forest disturbance, and track changes in vegetation and microclimate (Beck *et al.* 2002; Schulze & Fiedler 2003; Axmacher *et al.* 2004; Axmacher *et al.* 2009; Beck *et al.* 2011; Root *et al.* 2017; Tyler 2020; La Cava *et al.* 2024; Wildermuth *et al.* 2024). Tyler (2020) further reported that moth abundance was positively related to local vascular plant diversity and that species richness increased with woody plant diversity in the surrounding vegetation, reinforcing the importance of local habitat structure for moth assemblages.

These relationships are especially relevant in Borneo, where tropical forest landscapes have undergone extensive change through logging, degradation, and fragmentation, but still retain exceptionally high biodiversity. Earlier work from Borneo showed that moth assemblages differ across habitat gradients and forest conditions, and that disturbance and spatial turnover can shape community structure (Willott 1999; Beck *et al.* 2002; Schulze & Fiedler 2003; Kitching *et al.* 2013). Riparian habitats are also important in modified tropical landscapes because they can retain forest-associated biota and function as movement corridors or microclimatic refugia (Gray *et al.* 2019; Luke *et al.* 2019; Williamson *et al.* 2021). Recent studies have further emphasized that canopy structure, land-use intensity, weather, elevation, and landscape context can contribute to moth community patterns (Milodowski *et al.* 2021; Achury *et al.* 2025; Neff *et al.* 2025).

Mahakam Ulu, located in the upper Mahakam region of East Kalimantan, represents an ecologically important but still understudied tropical forest landscape. The regency lies within the Heart of Borneo landscape and the upstream part of the Mahakam River system, where forest cover, hilly terrain, and river corridors form a heterogeneous forest mosaic (WWF-Indonesia 2013). Nyaribungan Village, located in Laham District, contains a local habitat mosaic consisting of natural forest remnants, disturbed forest patches, and riparian buffers along river margins. Previous vegetation research in logged-over forests of Mahakam Ulu also showed that the region retains high plant diversity, indicating that disturbed forest landscapes in this area may still support important ecological functions (Setiawan *et al.* 2021).

Despite these advances, important knowledge gaps remain for upland tropical forest landscapes in East Kalimantan. Previous studies in Borneo have shown that moth assemblages respond to forest disturbance, habitat gradients, and spatial turnover, but plot-scale evidence integrating moth communities with vegetation richness, canopy cover, nighttime microclimate, riparian proximity, and elevation remains limited, particularly from the upper Mahakam region. Moreover, ecological information from Nyaribungan is still scarce, although this area represents a relevant habitat mosaic consisting of natural forest, disturbed forest, and riparian buffer within the same landscape. The novelty of this study lies in providing plot-scale evidence from an understudied upper Mahakam forest landscape by simultaneously evaluating moth community responses in relation to woody plant richness, vascular plant richness, canopy cover, nighttime temperature, relative humidity, distance to river, and elevation across three contrasting habitat types.

MATERIALS AND METHODS

Study Area

This study was conducted in Nyaribungan Village, Laham District, Mahakam Ulu Regency, East Kalimantan, Indonesia, within the upper Mahakam tropical forest landscape. Research activities were carried out from February to October 2025, including preparation, plot establishment, vegetation and environmental measurements, specimen identification, and data processing. Moth sampling was conducted only in April and May 2025 across three habitat types: natural forest, disturbed forest, and riparian buffer. A total of 12 sampling plots were established, with four plots in each habitat type, at coordinates ranging from 0.104167° S to 0.045277° N and 115.052167° E to 115.128171° E. These habitat types represented a gradient of vegetation complexity and microclimatic conditions within the study area.

Study Design and Moth Sampling

Moths were sampled in 12 plots using a standardized light-trap setup placed at the center of each plot. Each plot was sampled once for one night, resulting in 12 trap-nights in total. Sampling was conducted from 19:00 to 23:00 WITA, and the same trapping duration and light-trap configuration were applied across all plots to ensure comparability among habitat types. Sampling was not repeated across seasons; therefore, the results represent plot-level moth assemblages during the April – May 2025 sampling campaign rather than seasonal variation in moth communities. To reduce short-term variation in trapping effectiveness, sampling was avoided during rainfall and the full-moon phase (McGeachie 1989; Yela & Holyoak 1997; Jonason *et al.* 2014). The sampling sequence among plots was arranged according to field accessibility, safety, and weather conditions, while ensuring that natural forest, disturbed forest, and riparian buffer plots were sampled using the same protocol.

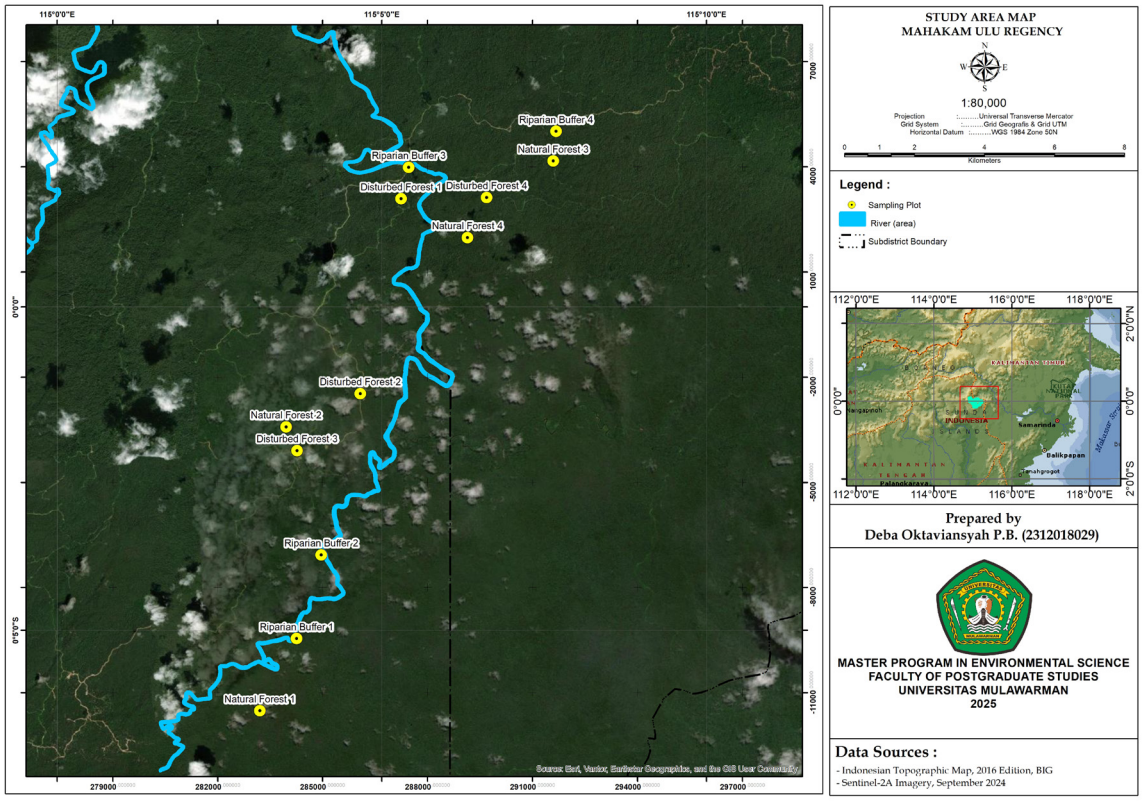


Figure 1 Map of the forested landscape surrounding Nyaribungan Village, Laham District, Mahakam Ulu Regency, East Kalimantan, Indonesia, showing the distribution of sampling plots in natural forest, disturbed forest, and riparian buffer habitats

The trap consisted of a Philips TrueForce Essential LED bulb (45 W, E27, 6500 K) and a Megaman YTT140Z2 LED bulb (50 W, 6500 K), supported by six 1-m iron rods and a 2 × 1 m white cloth. Although UV and actinic lights are commonly used in moth surveys, cool-white LED lamps were used because they provided a stable, energy-efficient, portable, and suitable light source for remote forest sampling (Brehm 2017; Niermann & Brehm 2022). The same LED configuration, trap design, and sampling duration were applied across all plots; therefore, lamp-related selectivity was kept constant among habitat types. The recorded assemblage should therefore be interpreted as the moth assemblage attracted to this specific LED light-trap configuration rather than a complete inventory of all nocturnal Lepidoptera.

Arriving moths were observed, photographed, and recorded in each plot. Specimen documentation and field conditions were photographed using a Nikon D500 camera with a Nikon AF-S 60 mm f/2.8G ED Micro lens and an XKZ diffuser. Species identification was based on field observations and laboratory verification using primary taxonomic references from The Moths of Borneo series (Holloway 1983, 1985, 1986, 1989, 1993, 1996, 1997, 2005, 2011), with the online Moths of Borneo database (Holloway n.d.) and iNaturalist (iNaturalist n.d.) used only as supplementary resources for photographic comparison and taxonomic cross-checking.

Vegetation and Environmental Measurements

Vegetation was recorded at two spatial scales around each light-trap point following an approach adapted from Tyler (2020). Each sampling plot was defined as a trap-centered survey area, with vascular understory plants recorded within a 5 m radius and woody plants within a ±50 m radius from the light-trap point. All observed plant species were recorded and documented, and vegetation richness was calculated as the total number of woody and vascular plant species in each plot.

Environmental variables included canopy cover (%), nighttime temperature (°C), nighttime relative humidity (%), distance to river (m), and elevation (m). Plot coordinates and elevation were recorded using a GPS. Canopy cover was measured using a spherical densiometer at standardized points around the trap, and the plot value was calculated as the mean of all readings. Nighttime temperature and relative humidity were measured during moth sampling, whereas distance to river was derived from maps as the shortest distance from each light-trap point to the nearest river channel.

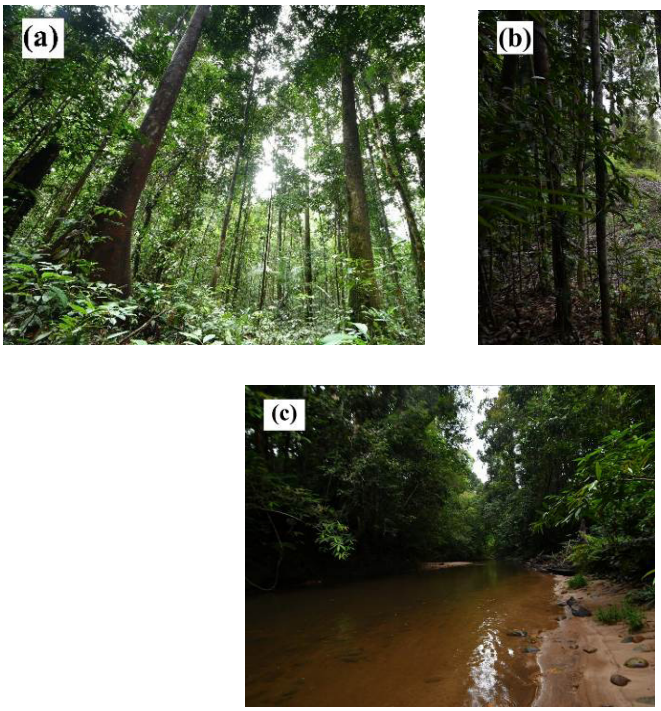


Figure 2 Representative habitat conditions of the three study habitat types in Nyaribungan Village, East Kalimantan, Indonesia

Notes: (a) natural forest, (b) disturbed forest, and (c) riparian buffer.

Data Analysis

All analyses were conducted at the plot level. Moth community structure was quantified using abundance (N), species richness (S), Shannon diversity (H'), and Pielou's evenness (E) (Magurran 2004).

Shannon diversity (H') was calculated as:

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

where:

p_i = n_i/N
n_i = number of individuals of species i
N = total number of individuals in the plot.

Thus, p_i represents the proportional abundance of species i in the assemblage.

Pielou's evenness (E) was calculated as:

$$E = \frac{H'}{\ln(S)}$$

where:

H' = Shannon diversity index
S = total number of species in the plot.

This index ranges from 0 to 1, with values closer to 1 indicating a more even distribution of individuals among species (Magurran 2004).

Differences in community metrics among habitat types were tested using one-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) test for pairwise comparisons (Fisher 1925; Tukey 1949). Differences in moth community composition were evaluated using PERMANOVA based on Bray–Curtis dissimilarity with 9,999 permutations (Anderson 2001), and PERMDISP was used to assess whether compositional differences were influenced by within-habitat dispersion (Anderson 2006). Habitat-associated species were identified using Indicator Value (IndVal) analysis (Dufrêne & Legendre 1997). Relationships between moth abundance or species richness and vegetation or environmental covariates were assessed using bivariate negative binomial models, with results expressed as incidence rate ratios (IRR) and 95% confidence intervals (Hilbe 2011). The explanatory variables included woody plant richness, vascular plant richness, canopy cover, nighttime temperature, nighttime relative humidity, distance to river, and elevation. To account for multiple testing, p-values were adjusted using the false discovery rate (FDR) procedure (Benjamini & Hochberg 1995). All analyses were performed in R 4.5.0, and graphs were generated using GraphPad Prism 10.0.

RESULTS AND DISCUSSION

Across all sampling plots, 1,149 moth individuals representing 196 species from 18 families were recorded, providing the basis for comparisons among the three habitat types.

Habitat Characteristics Across the Three Habitat Types

The three habitat types differed significantly in most vegetation and microclimatic characteristics (Table 1). Woody plant richness was significantly higher in natural forest and riparian buffer than in disturbed forest, whereas vascular plant richness and canopy cover differed significantly among all three habitats, with the highest values recorded in natural forest, intermediate values in riparian buffer, and the lowest values in disturbed forest.

Night temperature also differed among habitats, with natural forest showing lower values than both riparian buffer and disturbed forest, while night relative humidity was significantly lower in disturbed forest than in the other two habitats. Distance to river was markedly lower in riparian buffer than in natural forest and disturbed forest, whereas elevation did not differ significantly among habitats. Overall, these results indicate a clear habitat gradient from the more structurally complex and cooler natural forest to the warmer, more open, and vegetation-poor disturbed forest, with riparian buffer occupying an intermediate position but retaining relatively high humidity due to its proximity to the river.

This gradient is ecologically important because moth assemblages are closely associated with both vegetation structure and local abiotic conditions. Higher woody and vascular plant richness, together with denser canopy cover, can increase structural heterogeneity, host-plant availability, and sheltered microhabitats for nocturnal insects, while also buffering near-ground temperature and humidity (Axmacher *et al.* 2009; Tyler 2020; Milodowski *et al.* 2021; Williamson *et al.* 2021; Wildermuth *et al.* 2024).

Table 1 Habitat characteristics across the three habitat types

Variable	Habitat type		
	Natural forest Mean ± SD	Riparian buffer Mean ± SD	Disturbed forest Mean ± SD
Woody plant richness	31.00 ± 0.82[a]	30.00 ± 1.15[a]	20.75 ± 1.71[b]
Vascular plant richness	32.75 ± 1.71[a]	24.00 ± 0.82[b]	20.25 ± 1.89[c]
Canopy cover (%)	87.76 ± 4.20[a]	73.96 ± 1.70[b]	62.24 ± 6.15[c]
Night temperature (°C)	22.88 ± 0.35[b]	23.65 ± 0.09[a]	24.00 ± 0.49[a]
Night relative humidity (%)	90.26 ± 0.50[a]	91.81 ± 0.60[a]	85.98 ± 1.41[b]
Distance to river (m)	1416.00 ± 719.26[a]	95.00 ± 5.77[b]	1182.50 ± 555.60[a]
Elevation (m)	139.62 ± 7.25[a]	117.85 ± 16.06[a]	141.29 ± 14.94[a]

Notes: Values are presented as mean ± SD. Different superscript letters within a row indicate significant differences among habitat types based on Tukey's honestly significant difference (HSD) test at $P < 0.05$ after one-way ANOVA. Means followed by the same letter are not significantly different.

The lower temperature and relatively high humidity recorded in natural forest and riparian buffer therefore suggest more favorable local conditions for moth persistence and activity than those found in disturbed forest. The especially short distance of riparian buffer plots to the river, combined with their high humidity, supports the view that riparian habitats can partly maintain favorable microclimatic conditions even within modified tropical landscapes (Luke *et al.* 2019; Williamson *et al.* 2021).

In contrast, the lower vegetation richness, reduced canopy cover, and warmer night conditions in disturbed forest indicate a more exposed habitat setting that is likely less suitable for forest-associated moths. Together, these patterns provide an ecological basis for the differences in moth abundance, diversity, and community composition observed among habitats.

Moth Abundance, Species Richness, and Diversity Across Habitats

Moth community metrics differed clearly among the three habitat types (Table 2). Natural forest supported the highest moth abundance, with 546 individuals, followed by riparian buffer (316 individuals) and disturbed forest (287 individuals). A similar pattern was observed for species richness, with natural forest recording 177 species, compared with 125 species in riparian buffer and 108 species in disturbed forest. At the family level, Erebidae, Geometridae, and Crambidae were the most prominent groups across all habitats, and both their abundance and species richness were consistently greatest in natural forest.

The dominance of Erebidae, Geometridae, and Crambidae suggests that a relatively small number of families accounted for a substantial proportion of the moth assemblage across habitats. This pattern is ecologically plausible because these families are commonly prominent in tropical moth communities, and their diversity is often associated with plant diversity, vegetation structure, and below-canopy environmental conditions. The stronger representation of Erebidae and Geometridae in natural forest further supports the view that structurally complex, closed-canopy habitats provide a wider range of host plants, resting substrates, and microhabitats for forest-associated moth lineages (Axmacher *et al.* 2009; Hawes *et al.* 2009; La Cava *et al.* 2024).

Moth community structure differed clearly among the three habitat types (Fig. 3a–d). Natural forest showed the highest values for all four community metrics, with an abundance of 136.50 ± 15.59 individuals, species richness of 109.25 ± 5.38 species, Shannon diversity of 4.63 ± 0.05, and Pielou's evenness of 0.99 ± 0.00.

Riparian buffer showed intermediate values, with an abundance of 79.00 ± 6.27 individuals, species richness of 61.50 ± 4.65 species, Shannon diversity of 4.06 ± 0.08, and evenness of 0.98 ± 0.00, whereas the lowest values were recorded in disturbed forest, with an abundance of 71.75 ± 2.22 individuals, species richness of 47.75 ± 1.89 species, Shannon diversity of 3.80 ± 0.05, and evenness of 0.98 ± 0.00. These differences were significant for abundance (ANOVA: $F_{2,9} = 52.577$, $P < 0.001$), species richness ($F_{2,9} = 230.820$, $P < 0.001$), Shannon diversity ($F_{2,9} = 207.497$, $P < 0.001$), and Pielou's evenness ($F_{2,9} = 8.044$, $P = 0.0099$).

Table 2 Abundance and species richness of moth families in natural forest, disturbed forest, and riparian buffer

Family	Natural Forest		Disturbed Forest		Riparian Buffer	
	Species richness (S)	Individuals (n)	Species richness (S)	Individuals (n)	Species richness (S)	Individuals (n)
Bombycidae	1	4				
Cossidae	1	3				
Crambidae	30	118	31	115	28	77
Drepanidae	4	11	1	3	2	4
Erebidae	59	181	28	55	39	105
Euteliidae			1	2	1	3
Geometridae	43	127	24	52	31	79
Lacturidae	1	1				
Lasiocampidae	4	9	1	3	1	3
Noctuidae	4	13	2	4	3	8
Nolidae	5	14	3	6	3	7
Notodontidae	2	5	2	6	1	2
Pyralidae	6	11	4	12	5	7
Sphingidae	6	15	3	6	4	9
Thyrididae	4	11	1	2	1	2
Tineidae	1	2	1	3	1	2
Tortricidae	1	3	1	4	1	1
Uraniidae	5	18	5	14	4	7
Total	**177**	**546**	**108**	**287**	**125**	**316**

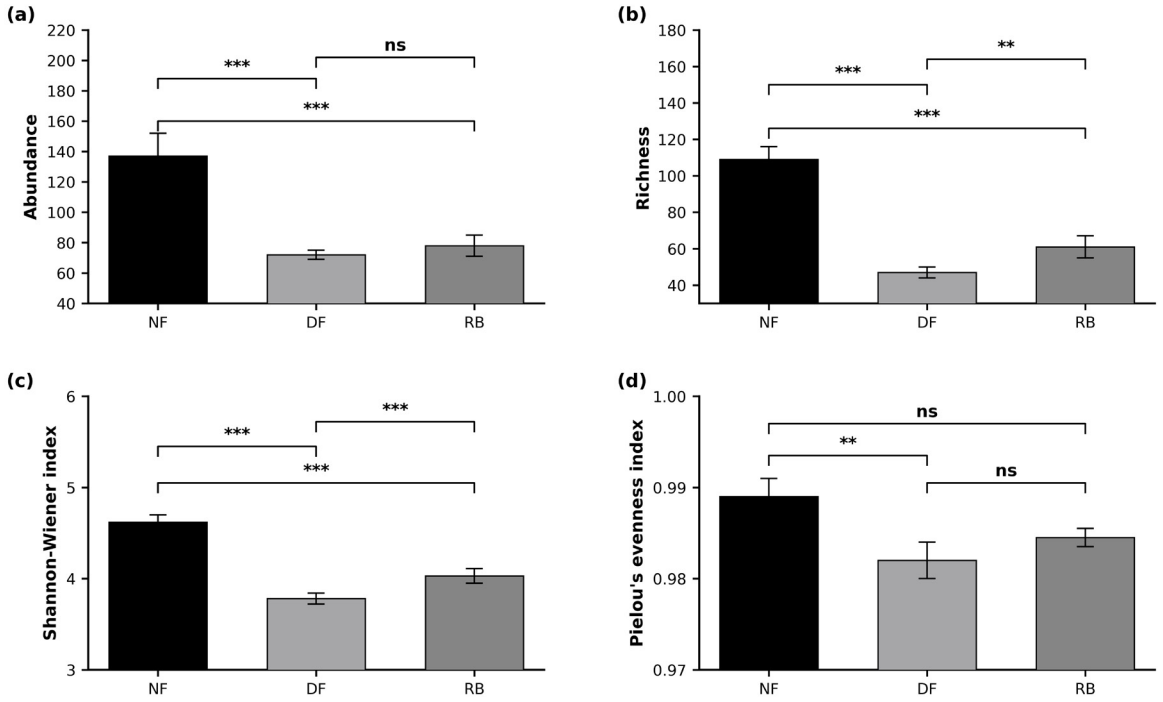


Figure 3 Mean (± SD) moth abundance, species richness, Shannon diversity, and evenness across three habitat types

Notes: NF = Natural Forest; DF = Disturbed Forest; RB = Riparian Buffer. Differences among habitats were tested using one-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) test for pairwise comparisons. Significance levels are indicated as *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns = not significant.

Riparian buffer showed intermediate values, with an abundance of 79.00 ± 6.27 individuals, species richness of 61.50 ± 4.65 species, Shannon diversity of 4.06 ± 0.08, and evenness of 0.98 ± 0.00, whereas the lowest values were recorded in disturbed forest, with an abundance of 71.75 ± 2.22 individuals, species richness of 47.75 ± 1.89 species, Shannon diversity of 3.80 ± 0.05, and evenness of 0.98 ± 0.00. These differences were significant for abundance (ANOVA: F2,9 = 52.577, P < 0.001), species richness ($F_{2,9}$ = 230.820, P < 0.001), Shannon diversity ($F_{2,9}$ = 207.497, P < 0.001), and Pielou's evenness ($F_{2,9}$ = 8.044, P = 0.0099).

The higher abundance, species richness, and Shannon diversity recorded in natural forest likely reflect the combined effects of greater vegetation complexity and more buffered microclimatic conditions. In this study, natural forest had the highest woody plant richness, vascular plant richness, and canopy cover, whereas disturbed forest showed the opposite pattern and riparian buffer remained intermediate. More structurally complex vegetation can increase the availability of larval host plants, pupation sites, resting substrates, nectar resources, and microhabitats, while closed canopies help stabilize near-ground thermal and moisture conditions. Similar positive relationships between moth communities and vegetation characteristics have been reported by Axmacher *et al.* (2009) and Tyler (2020), whereas more recent studies have emphasized that canopy structure and local microclimate are central mechanisms shaping arthropod communities in forest ecosystems, including structurally modified tropical forests (Milodowski *et al.* 2021; Williamson *et al.* 2021; La Cava *et al.* 2024; Wildermuth *et al.* 2024).

The lower abundance, richness, and diversity observed in disturbed forest suggest that habitat opening and structural simplification may be associated with reduced habitat suitability for many moth species. In contrast, the intermediate values recorded in the riparian buffer indicate that this habitat may still provide partial refuge conditions through relatively high humidity and remaining vegetation cover. However, riparian buffer habitat should be considered complementary to, rather than a substitute for, natural forest because its moth richness, diversity, and canopy condition remained lower than those of natural forest. Riparian habitats may also function as movement corridors for forest-associated moths in modified tropical landscapes, as shown by Gray *et al.* (2019). Recent work from modified landscapes has shown that habitat type and land-use intensity can shape moth community structure, while local environmental conditions such as weather and habitat context also contribute to moth community patterns (Achury *et al.* 2025; Neff *et al.* 2025). Taken together, these results indicate that natural forest was associated with more favorable habitat conditions for moth communities, whereas disturbed forest appeared to represent a less favorable habitat setting because of lower vegetation complexity and warmer night conditions.

Potential Indicator Species and Community Composition

Indicator Value (IndVal) analysis identified eight moth species as potential habitat indicator species (Table 3). Seven potential indicator species were associated with natural forest, namely *Hypomecis transcissa* (Walker, 1860), *Penicillifera apicalis* (Walker, 1862), *Strepsigonia quadripunctata* (Walker, 1862), *Sarbine cruciata* (Walker, 1862), *Agrioglypta excelsalis* (Walker, [1866]), *Nygmia fumosa* (Snellen, 1877), and *Albinospila floresaria* (Walker, 1866).

One species, *Xanthomelaena schematias* (Meyrick, 1894), was identified as a potential indicator species of riparian buffer habitat, whereas no potential indicator species were detected in disturbed forest. Because each habitat type was represented by only four plots, these species should be interpreted as potential indicator species rather than confirmed habitat specialists. This pattern suggests that natural forest may support more habitat-associated moth taxa than disturbed forest, while riparian buffer habitat may still retain some ecologically distinctive assemblage elements. The occurrence of one potential indicator species in riparian buffer habitat is ecologically plausible because humid riparian conditions can preserve favorable microhabitats for some forest-associated taxa. Overall, these findings suggest that habitat differences in the study area were associated not only with variation in overall moth diversity, but also with differences in taxonomic composition and habitat-association patterns of the assemblages (Hawes *et al.* 2009; Williamson *et al.* 2021; Achury *et al.* 2025).

Table 3 Potential indicator moth species associated with each habitat type based on Indicator Value (IndVal) analysis

Species	Family	Indicator habitat	IndVal	P-value
Hypomecis transcissa (Walker, 1860)	Geometridae	Natural forest	1	0.009
Penicillifera apicalis (Walker, 1862)	Bombycidae	Natural forest	1	0.009
Strepsigonia quadripunctata (Walker, 1862)	Drepanidae	Natural forest	1	0.009
Sarbine cruciata (Walker, 1862)	Erebidae	Natural forest	0.913	0.026
Agrioglypta excelsalis (Walker, [1866])	Crambidae	Natural forest	0.845	0.022
Nygmia fumosa (Snellen, 1877)	Erebidae	Natural forest	0.845	0.041
Albinospila floresaria (Walker, 1866)	Geometridae	Natural forest	0.707	0.037
Xanthomelaena schematias (Meyrick, 1894)	Crambidae	Riparian buffer	0.724	0.026

Notes: Only species with significant IndVal results are shown. Higher IndVal values indicate stronger potential association with a particular habitat type. Because each habitat type was represented by only four plots, these results should be interpreted as potential habitat associations rather than definitive evidence of habitat specialization.

Table 4 Results of global PERMANOVA and PERMDISP testing for differences in moth community composition among habitat types.

Analysis	Factor	df	Sum of squares	R^2	F	p-value
PERMANOVA	Habitat	2	0.593	0.267	1.641	0.0041
PERMDISP	Habitat	2	—	—	2.792	0.1075

Table 5 Pairwise PERMANOVA comparing moth community composition among habitat types

Comparison	df	Sum of squares	R^2	F	P-value	P-adj
NF vs DF	1	0.349	0.257	2.07	0.0307	0.0921
NF vs RB	1	0.268	0.221	1.698	0.0828	0.1242
DF vs RB	1	0.273	0.174	1.264	0.1966	0.1966

Notes: NF = Natural Forest; DF = Disturbed Forest; RB = Riparian Buffer. P-values were adjusted using the Benjamini–Hochberg false discovery rate procedure.

Differences in Moth Community Composition Among Habitats

Moth community composition differed significantly among habitat types based on the global PERMANOVA result ($F = 1.641$, $R^2 = 0.267$, $P = 0.0041$), indicating that habitat type explained 26.7% of the variation in community composition (Table 4). The global PERMDISP test was not significant ($F = 2.793$, $P = 0.1075$), indicating that within-habitat variation in community composition did not differ significantly among habitats.

Pairwise PERMANOVA showed that the largest unadjusted contrast occurred between natural forest and disturbed forest ($R^2 = 0.257$, $P = 0.0307$), whereas comparisons between natural forest and riparian buffer ($R^2 = 0.221$, $p = 0.0828$) and between disturbed forest and riparian buffer ($R^2 = 0.174$, $P = 0.1966$) were not significant (Table 5). However, after adjustment for multiple comparisons, none of the pairwise comparisons remained significant. Overall, these results support a significant global effect of habitat type on moth community composition, with the strongest unadjusted contrast occurring between natural forest and disturbed forest.

The significant global PERMANOVA result suggests that habitat differences were associated not only with variation in the number of individuals and species, but also with differences in the taxonomic composition of moth assemblages, a pattern widely reported in tropical moth communities across contrasting habitat conditions (Willott 1999; Hawes *et al.* 2009; Kitching *et al.* 2013). Because PERMDISP was not significant, this pattern is unlikely to have been driven primarily by differences in within-habitat dispersion. The stronger contrast between natural forest and disturbed forest is ecologically plausible because these habitats differed markedly in vegetation richness, canopy cover, and night temperature,

variables known to influence arthropod and moth assemblages through changes in structural complexity and microclimate (Milodowski *et al.* 2021; Wildermuth *et al.* 2024). Riparian habitats may retain part of the forest-associated fauna by buffering local environmental conditions, although this tendency should be interpreted cautiously in the present study because none of the pairwise comparisons remained significant after multiple-comparison adjustment (Luke *et al.* 2019; Williamson *et al.* 2021). More broadly, recent studies have shown that habitat type and land-use intensity can shape moth community structure across environmental gradients, supporting the interpretation that variation in vegetation structure and microclimate was associated with the compositional differences observed here (Achury *et al.* 2025). Overall, the results indicate a habitat-related shift in moth community composition, particularly between the most structurally distinct habitats.

Vegetation Richness, Canopy Cover, and Microclimate as Associated Factors

Bivariate negative binomial models showed consistent patterns for moth abundance and species richness (Table 6). For abundance, woody plant richness (IRR = 1.045, 95% CI = 1.016–1.073, P-adj = 0.003), vascular plant richness (IRR = 1.052, 95% CI = 1.039–1.065, P-adj < 0.001), and canopy cover (IRR = 1.025, 95% CI = 1.019–1.032, P-adj < 0.001) were positively associated with moth abundance, whereas night temperature was negatively associated with abundance (IRR = 0.648, 95% CI = 0.541–0.775, P-adj < 0.001). A similar pattern was observed for species richness, which increased with woody plant richness (IRR = 1.062, 95% CI = 1.032–1.092, P-adj < 0.001), vascular plant richness (IRR = 1.063, 95% CI = 1.051–1.076, P-adj < 0.001), and canopy cover (IRR = 1.031, 95% CI = 1.025–1.038, P-adj < 0.001), but declined with higher night temperature (IRR = 0.589, 95% CI = 0.481–0.720, P-adj < 0.001). By contrast, night relative humidity, distance to river, and elevation were not significantly associated with either response variable after FDR adjustment.

These results suggest that vegetation complexity was strongly associated with both moth abundance and species richness in the study area (Fig. 4). Higher woody and vascular plant richness likely increased the availability of larval host plants, nectar sources, resting substrates, and microhabitats, while denser canopy cover may have helped buffer understory thermal conditions (Axmacher *et al.* 2009; Tyler 2020). Similar links between moth communities and forest structural attributes have been reported in previous studies, including work emphasizing the importance of below-canopy structure, canopy architecture, and microhabitat conditions for arthropod and moth assemblages (Niermann & Brehm 2022; La Cava *et al.* 2024; Wildermuth *et al.* 2024). The negative association with night temperature further suggests that warmer and more exposed habitats may have offered less favorable conditions for many moth species, consistent with evidence that moth activity and detectability are sensitive to local weather and microclimatic variation (Fetnassi *et al.* 2022; Niermann & Brehm 2022; Neff *et al.* 2025). Overall, these findings indicate that vegetation-rich, closed-canopy habitats were associated with higher moth abundance and species richness in this disturbed tropical forest landscape.

Table 6 Results of bivariate negative binomial models for moth abundance and richness in relation to environmental covariates

Covariate	Moth abundance		Moth species richness	
	IRR (95% CI)	P-adj	IRR (95% CI)	P-adj
Woody plant richness (species)	1.045 (1.016–1.073)	0.003 **	1.062 (1.032–1.092)	7.57×10^{-5} ***
Vascular plant richness (species)	1.052 (1.039–1.065)	2.30×10^{-14} ***	1.063 (1.051–1.076)	5.66×10^{-23} ***
Canopy cover (%)	1.025 (1.019–1.032)	2.30×10^{-14} ***	1.031 (1.025–1.038)	3.98×10^{-22} ***
Night temperature (°C)	0.648 (0.541–0.775)	5.00×10^{-6} ***	0.589 (0.481–0.720)	6.27×10^{-7} ***
Night relative humidity (%)	1.047 (0.985–1.113)	0.17	1.076 (1.005–1.153)	0.051
Distance to river (m)	1.000 (0.9999–1.0004)	0.17	1.000 (0.9999–1.0004)	0.287
Elevation (m)	1.005 (0.995–1.016)	0.324	1.003 (0.991–1.016)	0.612

Note : IRR = incidence rate ratio; CI = confidence interval; P-adj = false discovery rate-adjusted P-value. IRR > 1 indicates a positive association, whereas IRR < 1 indicates a negative association; * P < 0.05;** P < 0.01; *** P < 0.001.

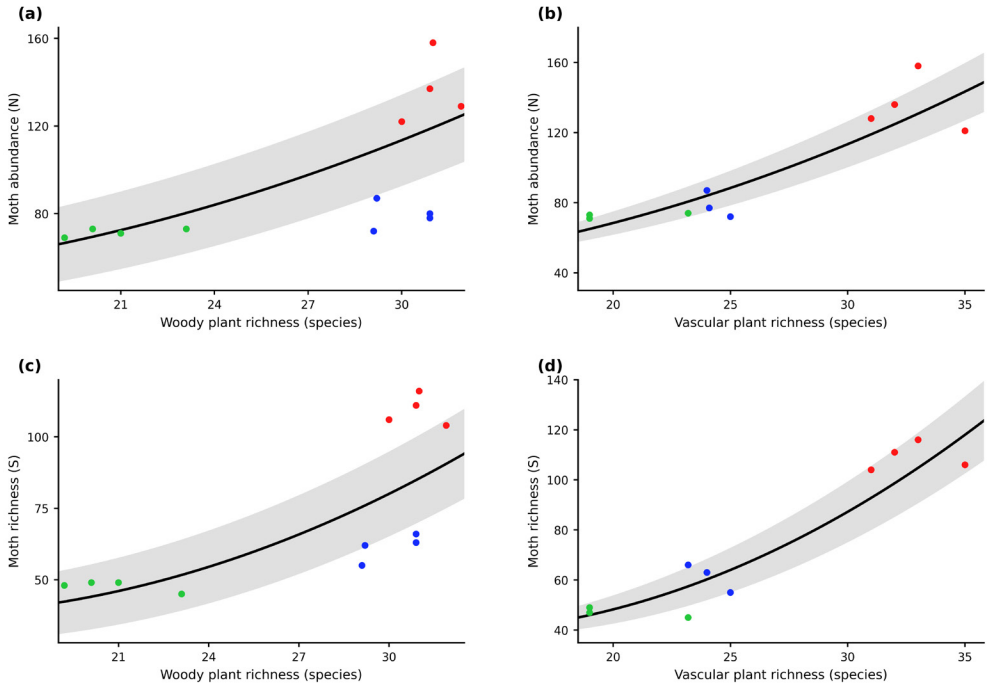


Figure 4 Relationships of moth abundance and species richness with woody and vascular plant richness across the three habitat types.

Notes: Panels show the relationships of moth abundance with woody plant richness (a) and vascular plant richness (b), and of moth species richness with woody plant richness (c) and vascular plant richness (d). Points represent sampling plots, with red indicating natural forest, green indicating disturbed forest, and blue indicating riparian buffer. Black lines indicate model predictions, and gray shaded areas represent 95% confidence intervals.

Limitations and Conservation Implications

This study has several limitations that should be considered when interpreting the findings. First, each habitat type was represented by four plots, and each plot was sampled once for one night; therefore, the results represent a plot-scale snapshot during the April – May 2025 sampling campaign rather than seasonal variation in moth communities. Because moth trapping was not repeated throughout the full February – October research period, phenological patterns could not be assessed in this study. Second, moths were sampled using a standardized cool-white LED light-trap configuration, so the recorded assemblage should be interpreted as the moth community attracted to this specific light source rather than a complete inventory of all nocturnal Lepidoptera in the landscape. Third, because this study was observational, the relationships between moth communities, vegetation richness, canopy cover, and microclimate should be interpreted as associations rather than direct causal effects. Despite these limitations, the findings support habitat management that prioritizes the protection of natural forest remnants, the maintenance of riparian buffer habitats, and the improvement of vegetation structure in disturbed forest areas to sustain moth diversity and community heterogeneity in Nyaribungan.

CONCLUSION

Natural forest supported the highest moth abundance, species richness, and diversity, followed by riparian buffer, whereas disturbed forest showed the lowest values. Moth community composition also differed significantly among habitat types at the global level. At the plot level, woody plant richness, vascular plant richness, and canopy cover were positively associated with moth abundance and species richness, whereas higher night temperature was negatively associated with both metrics. These findings indicate that vegetation-rich, closed-canopy habitats were associated with more favorable conditions for moth communities. This is likely because such habitats provide greater availability of larval host plants, pupation sites, resting substrates, and more buffered microclimatic conditions. In disturbed tropical forest landscapes, maintaining natural forest remnants and conserving riparian habitats may therefore play an important role in supporting moth diversity and community heterogeneity.

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