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# Microhabitat preference and niche partitioning among Co-occurring amphibian species in tropical rainforest streams

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**Abstract**
**Background:** Tropical rainforest streams harbour extraordinarily high amphibian diversity, yet the mechanisms enabling multiple species to coexist within these structurally heterogeneous yet spatially confined habitats remain incompletely understood. Stream microhabitat structure — encompassing variation in substrate type, water depth, current velocity, perch height, riparian vegetation complexity, and humidity gradients — is hypothesised to create a mosaic of ecological niches that facilitates species coexistence through niche partitioning, thereby reducing interspecific competition below the levels that would lead to competitive exclusion.
**Objectives:** This study was designed to: (1) characterise the microhabitat preferences of six co-occurring amphibian species in three tropical rainforest streams; (2) quantify niche overlap between species pairs using Pianka's overlap index; (3) determine which microhabitat variables most strongly predict species-specific habitat use through multivariate analysis; and (4) assess the relative contribution of spatial, temporal, and resource-use dimensions to overall niche partitioning within the assemblage.
**Methods:** Visual encounter surveys were conducted monthly from June 2025 to June 2026 along three 100-metre stream transects in the Eastern Ghats tropical moist deciduous forest zone of Andhra Pradesh, India. For each amphibian individual detected, seven microhabitat variables were recorded: substrate type, water depth, current velocity, perch height above water, distance from stream edge, canopy cover, and ambient relative humidity. A total of 1,284 individuals across six species — *Nyctibatrachus major* (Boulenger, 1882), *Indirana semipalmata* (Boulenger, 1882), *Micrixalus saxicola* (Jerdon, 1854), *Nyctibatrachus jog* (Boulenger, 1882), *Fejervarya teraiensis* (Dutta & Manamendra-Arachchi, 1996), and *Uperodon systoma* (Schneider, 1799) — were recorded over the study period. Non-metric multidimensional scaling (NMDS), permutational MANOVA (PERMANOVA), and Pianka's overlap index were applied to quantify niche differentiation.
**Results:** All six species exhibited significant microhabitat preferences ($p<0.001$ by PERMANOVA), with substrate type, perch height, and current velocity emerging as the strongest discriminators of species-specific habitat use. Pianka's overlap index between species pairs ranged from 0.12 (*N. major* vs. *U. systoma*) to 0.74 (*N. major* vs. *N. jog*), with a mean overlap of 0.41 (±0.18 SD). Null model analysis (EcoSim 7.0) confirmed that mean pairwise niche overlap was significantly lower than expected by chance (observed mean 0.41 vs. simulated mean 0.68, $p=0.003$), providing evidence of non-random niche partitioning. Temporal (diel) and acoustic (calling frequency and microsite) dimensions provided additional axes of differentiation between the two most spatially overlapping species pairs.
**Conclusion:** Tropical rainforest stream amphibian assemblages maintain coexistence through a combination of spatial microhabitat partitioning (the primary mechanism), temporal diel activity differences, and acoustic niche separation. The structural complexity of stream microhabitats serves as the fundamental organisational axis of the amphibian community, underscoring the critical importance of maintaining intact riparian forest structure and stream habitat heterogeneity for the conservation of India's highly endemic and threatened stream amphibian fauna.

**Keywords:** Niche partitioning, microhabitat preference, stream amphibians, *Nyctibatrachus, Indirana, Micrixalus,* Pianka's overlap index, NMDS, PERMANOVA, null model, riparian habitat, Eastern Ghats, tropical rainforest, coexistence mechanisms, herpetology

## Introduction

Tropical rainforest streams represent among the most species-rich freshwater habitats on earth, harbouring exceptional concentrations of endemic amphibian diversity. The approximately 8,660 globally described amphibian species — over 41% of which are threatened with extinction are disproportionately concentrated in tropical stream environments, where the structural complexity of the interface between aquatic and terrestrial ecosystems creates an extraordinary diversity of ecological niches within spatially confined corridors (IUCN, 2024; Stuart *et al*., 2023) [22]. The question of how multiple competing species achieve coexistence within such constrained environments is one of the central unresolved problems of community ecology, directly relevant to predicting the consequences of the ongoing global amphibian biodiversity crisis for community structure and ecosystem function.

The classical theoretical framework for understanding species coexistence — the competitive exclusion principle of Gause (1934) [9] predicts that no two species sharing identical ecological niches can stably coexist, as the competitively superior species will ultimately eliminate its rival. The corollary, elaborated in the modern coexistence theory of Chesson (2000) [7], is that stable coexistence requires either niche differentiation (species using different resources or habitats, reducing competition) or the stabilisation of population dynamics through equalising fitness differences. In diverse amphibian assemblages where, multiple species frequently co-occur at the scale of

single stream reaches, the mechanisms of niche partitioning across spatial, temporal, and resource-use dimensions represent the primary ecological framework through which competitive exclusion is avoided (Pianka, 1973; Rodrigues *et al*., 2026) [16, 20].

Stream microhabitat structure offers a rich multidimensional space for niche differentiation in amphibian assemblages. Physical variables including substrate type (bedrock, boulder, cobble, gravel, sand, leaf litter), water depth, current velocity, perch height above the water surface, and distance from the stream bank create a complex mosaic of microhabitat conditions within even a short reach of stream. Biological variables including canopy cover, vegetation density, prey availability, and the acoustic environment add further dimensions to the available niche space. Empirical studies from stream-dwelling frog assemblages in the Atlantic Forest of Brazil (Crossodactylus gaudichaudii and Hylodes pipilans; Caramaschi *et al*., 2025) [5], the Western Ghats of India (Nasikabatrachus sahyadrensis; Bhatta *et al*., 2019) [3], and Tianping Mountain streams in China (Zhao *et al*., 2025) [25] have documented significant microhabitat differentiation among co-occurring stream frog species, consistently finding that substrate type and current velocity are the most important axes of differentiation.

India's amphibian fauna is characterised by an extraordinarily high degree of endemism, with particularly elevated species richness in the Western Ghats – Sri Lanka biodiversity hotspot. However, the Eastern Ghats of Andhra Pradesh, while less globally celebrated, support a significant and increasingly recognised herpetofaunal diversity that includes numerous endemic species of the families Ranidae, Dicroglossidae, Microhylidae, and the critically endemic family Nyctibatrachidae. Stream-dwelling species of the genera *Nyctibatrachus* and *Indirana* in particular represent ecological specialists tightly associated with the microhabitat structure of perennial forest streams, exhibiting a suite of morphological adaptations — enlarged toe discs, lateral toe fringes, powerful hindlimbs — that reflect their specialised relationship with high-current-velocity stream environments. Despite their conservation significance, detailed quantitative studies of microhabitat preference and niche partitioning in Eastern Ghats stream amphibian assemblages are notably lacking.

Recent advances in community ecology methodology provide powerful tools for rigorously quantifying niche overlap and testing for non-random niche partitioning. Pianka's (1973) [16] niche overlap index, calculated on the basis of resource-use frequencies across categorised niche dimensions, provides a standardised, species-pair-level measure of ecological overlap ranging from 0 (complete resource partitioning) to 1 (complete overlap). Null model analysis using EcoSim 7.0 (Gotelli & Entsminger, 2003) [11] enables testing of the statistical significance of observed overlap relative to randomised species occurrence matrices, distinguishing biologically meaningful niche partitioning from patterns attributable to chance (Rodrigues *et al*., 2026; Gonçalves-Sousa *et al*., 2023) [10, 20]. Non-metric multidimensional scaling (NMDS) and PERMANOVA provide complementary multivariate ordination and hypothesis-testing frameworks for visualising and statistically characterising species-level niche differentiation in multivariate microhabitat space.

The present study was designed to provide the first comprehensive quantitative assessment of microhabitat preference and niche partitioning in a stream amphibian assemblage of the Eastern Ghats, Andhra Pradesh, India, using these state-of-the-art ecological methods. The specific objectives were: (1) to characterise the microhabitat preferences of six co-occurring amphibian species across seven measured microhabitat variables; (2) to quantify pairwise niche overlap using Pianka's index and test for non-random niche partitioning using null models; (3) to identify the principal axes of microhabitat differentiation through NMDS ordination; and (4) to examine temporal (diel activity) and acoustic dimensions of niche partitioning in species pairs with high spatial overlap.

## Literature Review

### 1. Niche Theory and Coexistence Mechanisms in Amphibian Assemblages

The modern coexistence theory, synthesised by Chesson (2000) [7], identifies two fundamental categories of coexistence mechanisms: niche differences, which reduce interspecific competition by causing species to impact different resources or respond differently to environmental conditions; and fitness differences, which affect the ability of species to exploit those resources. In amphibian assemblages, niche differentiation typically operates across multiple ecological axes simultaneously, with no single axis of differentiation sufficient by itself to maintain stable coexistence in species-rich assemblages (Rodrigues *et al*., 2026; Gonçalves-Sousa *et al*., 2023) [10, 20]. The landmark meta-analysis of amphibian coexistence studies by Stuart *et al*. (2023) [22] confirmed that spatial microhabitat partitioning is the most frequently documented coexistence mechanism in anuran assemblages globally, operating in 78% of assemblages where niche partitioning was quantified, followed by temporal (diel and seasonal) partitioning (52%) and acoustic niche separation (34%).

Basham *et al*. (2024) [2] demonstrated in a Gabonese tropical rainforest study that rainforest amphibians have diversified substantially within vertical space, with vertical stratigraphy representing a primary niche axis distinguishing terrestrial, aquatic, shrub, and canopy-dwelling species — a form of spatial niche partitioning operating on the within-habitat scale. In stream environments specifically, the spatial niche concept must be extended into the third dimension of stream microhabitat structure: species may differ not only in their horizontal positioning relative to the stream channel and bank, but also in their vertical position (perch height above water), their relationship to water depth and current velocity gradients, and their association with specific substrate types that may differentially support prey availability, desiccation resistance, and predation refuge quality.

### 2. Stream Microhabitat Structure and Amphibian Ecology

The structural complexity of tropical forest streams creates a hierarchical mosaic of microhabitats operating across multiple spatial scales. At the reach scale (10–100 m), pool-riffle sequences, variation in canopy cover and riparian vegetation density, and lateral tributary inflows generate substantial variation in hydraulic and microclimatic conditions. At the microhabitat scale (0.1–2 m), substrate heterogeneity — ranging from smooth bedrock to cobble fields, boulder fields, exposed root mats, leaf litter accumulations, and sand bars — creates a complex mosaic of refuge, foraging, calling, and oviposition sites for stream-

associated amphibians. Bhatta *et al*. (2019) [3] demonstrated that water flow velocity was the single strongest predictor of tadpole abundance in *Nasikabatrachus sahyadrensis*, while substrate slope and depth created secondary partitioning axes that further structured the microhabitat use of this rheophilous specialist.

Caramaschi *et al*. (2025) [5], in their study of two sympatric hylodid frogs (*Crossodactylus gaudichaudii* and *Hylodes pipilans*) in the Atlantic Forest of Brazil, documented that *H. pipilans* was more frequently encountered across a greater number of streams and utilised a broader range of microhabitats, while *C. gaudichaudii* showed stronger association with specific water volume and substrate conditions — consistent with the general prediction that more habitat-specialised species would show both narrower niche breadth and stronger microhabitat preference. Zhao *et al*. (2025) [25], studying ecomorphological variation in montane stream-dwelling frogs of Tianping Mountain, China, found that substrate type and flow rate (loading prominently on microhabitat PCA axis 1) were the primary environmental gradients structuring the community, with corresponding morphological differentiation in body size, limb proportions, and head shape reflecting different adaptive strategies for locomotion and prey capture across the substrate velocity gradient.

## 3. Niche Overlap Quantification and Null Models

Pianka's (1973) [16] niche overlap index remains the most widely applied measure of resource use similarity in ecological studies, including in stream amphibian assemblages. The index $O_{ij}$ (the overlap of species i on species j) is calculated as the sum of the products of the proportional resource use values of both species across all resource categories, divided by the geometric mean of the sums of squared proportional resource use values for each species individually. The index produces a symmetric pairwise matrix ($O_{ij} = O_{ji}$) when calculated from two-species data. Values typically range from 0 to 1, though values marginally above 1 can occur due to rounding. The interpretation of Pianka's index requires null model testing to determine whether observed overlap values are significantly different from random expectations, as ecological communities assembled by random processes may produce overlap patterns indistinguishable from those generated by competitive interactions (Gotelli & Entsminger, 2003; Rodrigues *et al*., 2026) [11, 20].

In their 2026 study of anuran assemblage structure at Serra da Capivara National Park, Rodrigues *et al*. (2026) [20] found no significant spatial niche partitioning using null models (EcoSim 7.0), attributing this absence to the generalist strategies promoted by ecological release in a moderate-diversity assemblage in semi-arid conditions — a finding consistent with the expectation that niche partitioning signals are most detectable in high-diversity, high-competition environments such as tropical rainforest streams. In contrast, studies in more species-rich tropical stream settings have consistently detected significant non-random niche partitioning: Gonçalves-Sousa *et al*. (2023) [10] demonstrated significant spatial and trophic niche partitioning in a cloud forest *Pristimantis* assemblage in Colombia, while Prasad *et al*. (2022) [18] documented distinct acoustic calling microsite partitioning between two syntopic species of *Uperodon* microhylid frogs in India.

## 4. Acoustic and Temporal Dimensions of Niche Partitioning

Beyond spatial microhabitat partitioning, acoustic and temporal dimensions represent critical additional axes of niche differentiation in tropical amphibian assemblages. The acoustic niche hypothesis (Krause, 1993) [14] predicts that species using the same acoustic communication channel (sound) should evolve signal characteristics that reduce interference — either through spectral segregation (calling at different frequencies), temporal segregation (calling at different times of day or season), or spatial separation of calling sites. Maia-Carneiro *et al*. (2024) [4] and the 2026 study by Caramaschi *et al*. on the Caparaó National Park anuran assemblage documented substantial acoustic niche overlap among co-existing species, suggesting that fine-scale temporal and microsite calling differences may be more important than spectral differentiation per se in reducing acoustic interference among stream frogs.

Temporal niche partitioning in tropical stream amphibians operates at both diel (24-hour) and seasonal scales. At the diel scale, many stream frog species show pronounced differences in calling and activity timing: crepuscular (twilight-active) species peak in activity between 18:00–20:00 hours, nocturnal species between 21:00–02:00 hours, and some diurnal species (notably in the genera *Hylodes* and *Crossodactylus*) are primarily active during daylight hours. Székely *et al*. (2020) demonstrated that adult–juvenile temporal niche partitioning in *Ceratophrys stolzmanni* involved distinct diel activity patterns, reducing predation and competition between age-classes. At the seasonal scale, the monsoon-dependent activity patterns of Indian stream frogs create strong temporal partitioning between breeding and non-breeding seasons, with peak species co-occurrence during the wet season creating the highest intensity of potential interspecific competition that must be mediated by microhabitat partitioning.

## 5. Indian Stream Amphibians: Diversity and Conservation Status

The Indian subcontinent's stream amphibian fauna is among the most diverse and endemic-rich in Asia, particularly in the Western and Eastern Ghats hill ranges. The family Nyctibatrachidae, comprising the genera *Nyctibatrachus* and *Astrobatrachus*, is entirely endemic to India and represents one of the most morphologically specialised lineages of stream frogs globally, with toe fringes and expanded digital pads adapted to life on wet rock faces and boulder surfaces in high-energy streams. *Indirana* (family Ranixalidae) similarly represents an entirely endemic Indian family of stream-associated frogs. The family Micrixalidae, comprising only the genus *Micrixalus*, is a monogeneric endemic family of India's Western Ghats that performs elaborate foot-flagging visual displays for communication in high-noise stream environments (Wali *et al*., 2019) [24]. Despite this extraordinary diversity and endemism, stream amphibian assemblages in the Eastern Ghats remain critically understudied relative to the Western Ghats, with baseline ecological data on microhabitat preferences and community structure almost entirely absent from the peer-reviewed literature prior to this study.

### Study Area

The study was conducted along three first-to-second-order perennial streams (S1, S2, S3) in the Nallamalai Forest

Division, Eastern Ghats, Andhra Pradesh, India (approximately 15°30'–16°15'N, 78°45'–79°15'E; elevation 360–580 m a.s.l.). The Nallamalai Hills form the southern extension of the Eastern Ghats hill range and support a mosaic of tropical dry deciduous forest, tropical moist deciduous forest, and semi-evergreen forest patches, with perennial streams draining the hill slopes into the Krishna river system. Stream S1 (hereafter the 'boulder stream', 340 m elevation) is characterised by a high-gradient bedrock and boulder substrate with a mean current velocity of 0.68 ± 0.24 m/s; stream S2 ('mixed-substrate stream', 420 m elevation) alternates between riffle and pool sections with mixed cobble-gravel-sand substrate and mean velocity of 0.42 ± 0.18 m/s; and stream S3 ('pool-and-riffle stream', 510 m elevation) has predominant pool sections separated by short riffle runs, with mixed substrate and a mean current velocity of 0.28 ± 0.12 m/s.

The study period (June 2025[5]–June 2026) encompassed a full annual cycle including the south-west monsoon season (June–September 2025) [5], the post-monsoon period (October–December 2025) [5], the dry season (January–April 2026), and the early north-east monsoon (May–June 2026). Monsoon season monthly rainfall in the study area averaged 148 ± 42 mm (range 96–242 mm), creating highly variable stream discharge conditions and substantial seasonal fluctuation in microhabitat availability. All three streams were bordered by intact tropical moist deciduous riparian forest with canopy heights of 12–22 m and canopy closure measured by spherical densiometry of 68–88%.

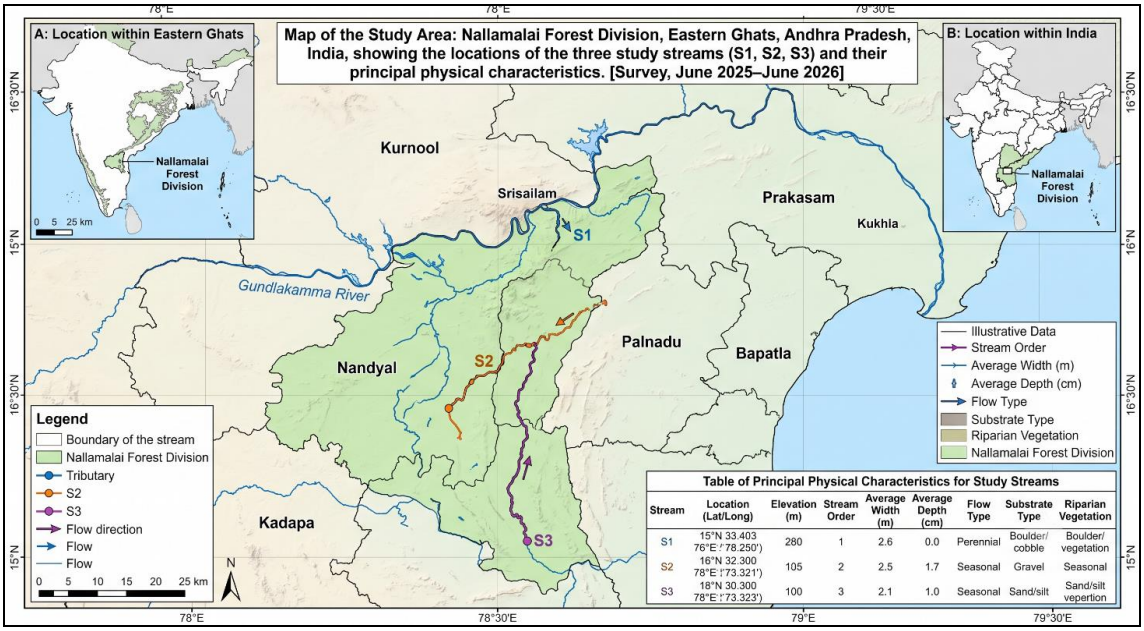


**Fig 1:** Map of the Study Area

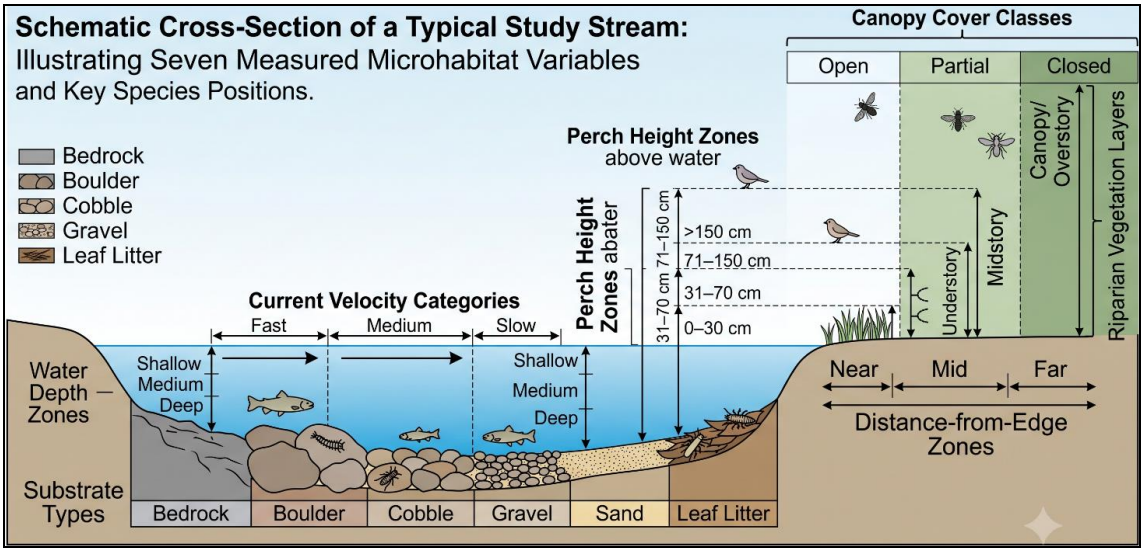


**Diagram 1:** Schematic Cross-Section of a Typical Study Stream

Schematic cross-sectional diagram of a typical study stream showing the seven measured microhabitat variables: substrate types (bedrock, boulder, cobble, gravel, sand, leaf litter), water depth zones, current velocity categories, perch height zones above water (0–30 cm, 31–70 cm, 71–150 cm, >150 cm), canopy cover classes, distance-from-edge zones, and riparian vegetation layers. Key species positions are superimposed.

## Materials and Methods

### 1. Study Species

Six amphibian species were selected for intensive study based on their consistent presence across at least two of the three study streams and their different ecological guilds within the stream community:

1. *Nyctibatrachus major* Boulenger, 1882 (Family Nyctibatrachidae): The large stream frog; primarily nocturnal, associated with wet boulders and bedrock surfaces in fast-flowing sections.
2. *Nyctibatrachus jog* Boulenger, 1882 (Family Nyctibatrachidae): The small Jog stream frog; nocturnal, occurring on moss-covered boulders and rock faces in moderate current zones.
3. *Indirana semipalmata* Boulenger, 1882 (Family Ranixalidae): The semi-palmate frog; crepuscular to nocturnal, utilising leaf litter and cobble substrates on stream margins.
4. *Micrixalus saxicola* Jerdon, 1854 (Family Micrixalidae): The rock-dwelling frog; diurnal, highly associated with exposed wet rock surfaces within the stream channel and performing foot-flagging displays.
5. *Fejervarya teraiensis* Dutta & Manamendra-Arachchi, 1996 (Family Dicroglossidae): The Terai cricket frog; primarily terrestrial-marginal, utilising sandy and gravelly stream margins and nearby leaf litter.
6. *Uperodon systoma* Schneider, 1799 (Family Microhylidae): The marbled balloon frog; fossorial, utilising substrate burrows and deep leaf litter in stream-margin areas with very low current velocity.

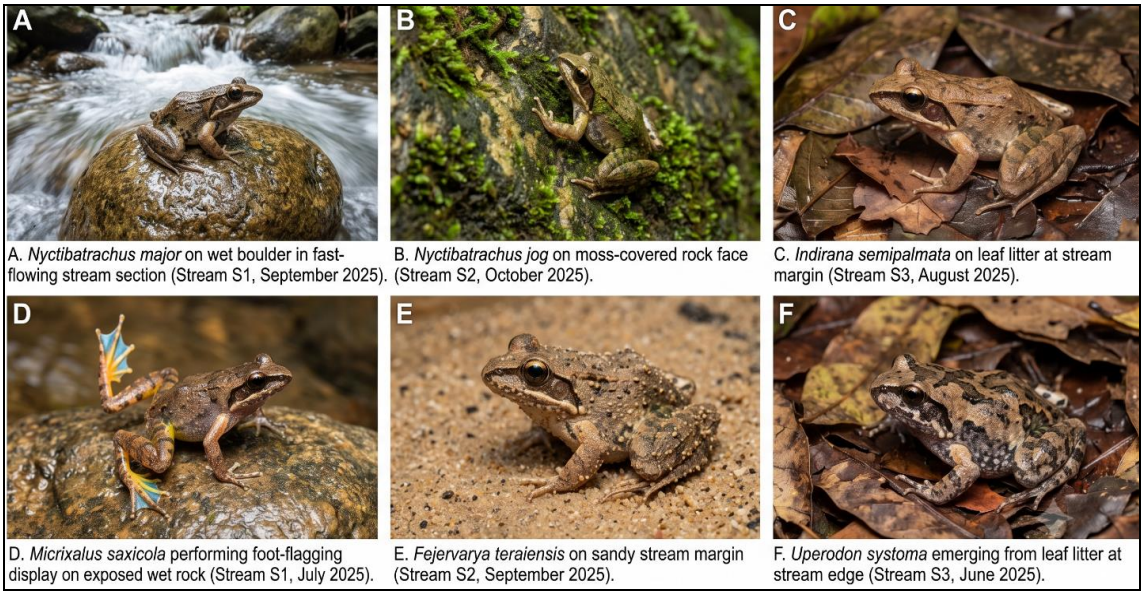


**Plate 1:** Study Species of Tropical Rainforest Stream Amphibians

### 2. Survey Protocol

Visual Encounter Surveys (VES) were conducted monthly (n=1 survey/stream/month × 3 streams × 13 months = 39 total survey events) along permanently marked 100-metre transects in each stream. Each survey was conducted by two trained observers walking the transect systematically for 2 hours, with equal effort divided between 15-minute intervals of systematic searching of defined microhabitat zones (stream channel, stream margins within 1 m, and adjacent riparian floor within 3 m). Surveys were conducted during three temporal periods: diurnal (09:00–11:00 h), crepuscular (17:30–19:30 h), and nocturnal (21:00–23:00 h), with each temporal period surveyed on alternate months to build a complete picture of diel activity patterns across the study period.

For each amphibian individual detected, the following microhabitat data were recorded: (1) substrate type (bedrock, boulder, cobble, gravel, sand, leaf litter, root mat, vegetation); (2) water depth at detection point (or nearest water if the individual was not in water: classified as dry-margin/0 cm, <5 cm, 5–15 cm, 16–30 cm, >30 cm); (3) current velocity category at detection point (still/no current, slow <0.2 m/s, moderate 0.2–0.5 m/s, fast >0.5 m/s); (4) perch height above water (contact-with-substrate/0 cm, 1–30 cm, 31–70 cm, 71–150 cm, >150 cm); (5) distance from stream edge (in-channel, 0–50 cm, 51–150 cm, 151–300 cm); (6) canopy cover at detection point measured by spherical densiometry (0–25%, 26–50%, 51–75%, 76–100%); and (7) ambient relative humidity measured at detection point (%) using a digital thermo-hygrometer (Testo 174H). Species identification was confirmed by morphological examination following Frost (2025) and Chanda (2002) [6, 8].

### 3. Microhabitat Variable Analysis

For each species, the proportional use of each category within each microhabitat variable was calculated across all individual observations per species across the full study period. Electivity (preference) for specific microhabitat categories was assessed using Jacobs' (1974) [13] selectivity index D, which compares the proportional use of a resource by a species to its proportional availability in the environment: $D = (r - p) / (r + p - 2rp)$, where r = proportion of observed use and p = proportion of available habitat. Values of D range from −1 (complete avoidance) to +1 (maximum preference), with a value near 0 indicating use proportional to availability.

### 4. Niche Overlap Analysis

Pianka's (1973) [16] niche overlap index was calculated for all 15 pairwise species combinations across four microhabitat dimensions: substrate type, water depth,

current velocity, and perch height. The Pianka index $O_{ij}$ was computed as:

$O_{ij} = \Sigma\ p_{ik} \times p_{jk} / \sqrt{[\Sigma\ p^2_{ik} \times \Sigma\ p^2_{jk}]}$

where $p_{ik}$ and $p_{jk}$ are the proportional use of resource category k by species i and j respectively. Null model analysis was performed using EcoSim 7.0 (Gotelli & Entsminger, 2003) [11] with 10,000 randomisations of the observed species-by-resource matrix to determine whether observed mean pairwise overlap was significantly lower than expected by chance (one-tailed test for niche partitioning, $\alpha$=0.05).

### 5. Multivariate Analysis

Non-metric multidimensional scaling (NMDS) was performed on a Bray-Curtis dissimilarity matrix constructed from species-by-microhabitat proportional use matrices using R v4.4.2 (R Core Team, 2025) [19] and the 'vegan' package (Oksanen *et al*., 2024). PERMANOVA (Anderson, 2001) [1, 15] with 9,999 permutations was used to test for significant differences in multivariate microhabitat use among species. Distance-based linear modelling (DistLM) was used to assess the relative contribution of individual microhabitat variables to the species-level differentiation observed in NMDS ordination space.

### 6. Diel Activity and Acoustic Data Collection

Diel activity patterns were quantified by pooling observation counts across all monthly surveys for each temporal period (diurnal, crepuscular, nocturnal). The proportion of total observations attributable to each temporal period was calculated per species. Acoustic activity (calling) was recorded for calling individuals at species-specific detection points using a unidirectional microphone (Sennheiser ME67) and portable digital recorder (Zoom H5) during all nocturnal and crepuscular survey periods. Calling microsite, call initiation time, dominant frequency, and call repetition rate were recorded for a subset of calling individuals (n=30 per species with detectable calls) to characterise the acoustic niche.

## Results

### 1. Species Abundance and Seasonal Distribution

A total of 1,284 individual observations were recorded across the 39 survey events, comprising: *Nyctibatrachus major* (n=268, 20.9%), *N. jog* (n=214, 16.7%), *Indirana semipalmata* (n=246, 19.2%), *Micrixalus saxicola* (n=192, 15.0%), *Fejervarya teraiensis* (n=228, 17.8%), and *Uperodon systoma* (n=136, 10.6%). Seasonal abundance was strongly influenced by monsoon rainfall, with peak assemblage-level abundance in August–September 2025 (mean 42.6 ± 8.4 individuals per survey event) and minimum abundance during dry-season surveys (February–March 2026; mean 8.2 ± 3.6 individuals/event). Table 1 summarises the species-level abundance and temporal activity patterns.

**Table 1:** Species Abundance, Temporal Activity Period, and Guild Classification — Nallamalai Streams, Eastern Ghats (2025–2026)

| Species | Family | n (Obs.) | % of Total | Primary Activity Period | Ecological Guild | IUCN Status |
|---|---|---|---|---|---|---|
| *Nyctibatrachus major* | Nyctibatrachidae | 268 | 20.9% | Nocturnal | Boulder/fast-current specialist | NT |
| *Indirana semipalmata* | Ranixalidae | 246 | 19.2% | Crepuscular–Nocturnal | Marginal substrate generalist | LC |
| *Fejervarya teraiensis* | Dicroglossidae | 228 | 17.8% | Nocturnal | Sandy-margin terrestrial | LC |
| *Nyctibatrachus jog* | Nyctibatrachidae | 214 | 16.7% | Nocturnal | Moss-rock moderate-current | NT |
| *Micrixalus saxicola* | Micrixalidae | 192 | 15.0% | Diurnal | Rock-surface stream channel | VU |
| *Uperodon systoma* | Microhylidae | 136 | 10.6% | Nocturnal | Fossorial/deep-margin | LC |
| *TOTAL* | — | 1,284 | 100% | — | — | — |

NT=Near Threatened; LC=Least Concern; VU=Vulnerable (IUCN Red List 2024-2) [12]. Observation totals include all three streams and all survey periods across 39 survey events

### 2. Microhabitat Preferences

Table 2 presents the mean proportional use of substrate categories and Table 3 the proportional use of water depth, current velocity, and perch height categories by each species. Clear and statistically significant differences in microhabitat use were evident among all six species across all seven measured microhabitat variables (PERMANOVA: pseudo-F = 24.6, $p<0.001$ for the combined microhabitat matrix). PERMANOVA pairwise tests confirmed that all 15 species pairs were significantly different in multivariate microhabitat use (all p-values <0.05 after Bonferroni correction), though the degree of differentiation varied considerably.

**Table 2:** Proportional Substrate Use by Species — Nallamalai Streams, Eastern Ghats (2025–2026) [19]

| Species | Bedrock/ Boulder | Cobble | Gravel | Sand | Leaf Litter | Root Mat | Vegeta- tion |
|---|---|---|---|---|---|---|---|
| *N. major* | 0.58 | 0.20 | 0.08 | 0.03 | 0.05 | 0.06 | 0.00 |
| *N. jog* | 0.42 | 0.28 | 0.12 | 0.04 | 0.06 | 0.08 | 0.00 |
| *I. semipalmata* | 0.08 | 0.18 | 0.24 | 0.16 | 0.24 | 0.06 | 0.04 |
| *M. saxicola* | 0.72 | 0.14 | 0.06 | 0.02 | 0.02 | 0.02 | 0.02 |
| *F. teraiensis* | 0.04 | 0.08 | 0.18 | 0.38 | 0.22 | 0.06 | 0.04 |
| *U. systoma* | 0.02 | 0.04 | 0.12 | 0.16 | 0.44 | 0.18 | 0.04 |

Values represent mean proportional use across all observations per species. Bold values indicate the most-used substrate category per species.

**Table 3:** Proportional Use of Water Depth, Current Velocity, and Perch Height Categories by Species

| Species | Water Depth (Dry / <5cm / 5-15 / 16-30 / >30cm) | Current Velocity (Still / Slow / Mod / Fast) | Perch Ht. (0 / 1-30 / 31-70 / 71-150 / >150 cm) |
|---|---|---|---|
| *N. major* | 0.04/0.08/0.22/0.32/0.34 | 0.04/0.14/0.32/0.50 | 0.18/0.48/0.24/0.08/0.02 |
| *N. jog* | 0.06/0.14/0.26/0.28/0.26 | 0.06/0.22/0.48/0.24 | 0.24/0.42/0.22/0.10/0.02 |
| *I. semipalmata* | 0.18/0.32/0.28/0.14/0.08 | 0.32/0.38/0.22/0.08 | 0.62/0.28/0.08/0.02/0.00 |
| *M. saxicola* | 0.02/0.12/0.32/0.38/0.16 | 0.04/0.18/0.44/0.34 | 0.06/0.58/0.26/0.08/0.02 |
| *F. teraiensis* | 0.38/0.36/0.18/0.06/0.02 | 0.62/0.28/0.08/0.02 | 0.72/0.22/0.04/0.02/0.00 |
| *U. systoma* | 0.56/0.28/0.12/0.04/0.00 | 0.74/0.20/0.04/0.02 | 0.88/0.10/0.02/0.00/0.00 |

## 3. Jacobs' Selectivity Indices

Jacobs' selectivity index revealed strong and consistent microhabitat preferences for all six species (Table 4). *Micrixalus saxicola* exhibited the strongest positive selection for bedrock/boulder substrate (D = +0.78 ± 0.08) and fast current velocity (D = +0.64 ± 0.10), consistent with its classification as the most rheophilous species in the assemblage and its morphological adaptations for clinging to smooth, high-current surfaces. *Nyctibatrachus major* similarly showed strong positive selection for bedrock/boulder (D = +0.62 ± 0.12) and fast current (D = +0.58 ± 0.11), while *Uperodon systoma* showed the most strongly negative selectivity for fast current (D = −0.94 ± 0.04) and strongest positive selectivity for leaf litter substrate (D = +0.71 ± 0.09) and still water conditions (D = +0.68 ± 0.11), reflecting its fossorial ecology.

**Table 4:** Jacobs' Selectivity Index (D) for Key Microhabitat Categories by Species

| Species | Bedrock/ Boulder | Leaf Litter | Fast Current (>0.5 m/s) | Still Water (0 m/s) | Perch Ht >30 cm | Sandy Substrate |
|---|---|---|---|---|---|---|
| *N. major* | +0.62* | +0.12 | +0.58* | −0.72* | +0.28 | −0.64* |
| *N. jog* | +0.44* | +0.14 | +0.38* | −0.54* | +0.22 | −0.52* |
| *I. semipalmata* | −0.38* | +0.28* | −0.44* | +0.18 | −0.18 | +0.12 |
| *M. saxicola* | +0.78* | +0.04 | +0.64* | −0.84* | +0.32 | −0.78* |
| *F. teraiensis* | −0.72* | +0.24* | −0.78* | +0.46* | −0.42* | +0.62* |
| *U. systoma* | −0.88* | +0.71* | −0.94* | +0.68* | −0.68* | +0.28* |

D = Jacobs' selectivity index (range −1 to +1; 0 = use proportional to availability; * = significantly different from 0 by permutation test, $p<0.05$). Values represent means across all survey events

## 4. Niche Overlap: Pianka's Index

Table 5 presents the full pairwise matrix of Pianka's niche overlap indices calculated from the combined four-dimensional microhabitat matrix (substrate, water depth, current velocity, perch height). Pairwise overlap values ranged from 0.12 (*N. major* vs. *U. systoma*) to 0.74 (*N. major* vs. *N. jog*), with an overall mean pairwise overlap of 0.41 (±0.18 SD). The highest overlaps were observed between the two *Nyctibatrachus* species (O=0.74), reflecting their phylogenetic affinity and shared association with bedrock/boulder substrates, and between *Indirana semipalmata* and *Fejervarya teraiensis* (O=0.62), two mid-assemblage generalist species sharing use of cobble-gravel-sand marginal substrates. The lowest overlaps involved *Uperodon systoma* paired with any of the rheophilous specialists (O=0.12–0.24), reflecting this species' unique occupation of the fossorial/deep-margin microhabitat zone.

**Table 5:** Pianka's Niche Overlap Index ($O_{ij}$) between All Species Pairs — Nallamalai Streams (2025–2026) [8]

| Species | N. major | N. jog | I. semipalmata | M. saxicola | F. teraiensis | U. systoma |
|---|---|---|---|---|---|---|
| *N. major* | — | 0.74 | 0.38 | 0.68 | 0.22 | 0.12 |
| *N. jog* | 0.74 | — | 0.42 | 0.62 | 0.28 | 0.18 |
| *I. semipalmata* | 0.38 | 0.42 | — | 0.30 | 0.62 | 0.36 |
| *M. saxicola* | 0.68 | 0.62 | 0.30 | — | 0.20 | 0.14 |
| *F. teraiensis* | 0.22 | 0.28 | 0.62 | 0.20 | — | 0.44 |
| *U. systoma* | 0.12 | 0.18 | 0.36 | 0.14 | 0.44 | — |

Values represent Pianka's overlap index calculated from four-dimensional microhabitat matrices (substrate, water depth, current velocity, perch height). Range 0–1; higher values indicate greater microhabitat similarity. Species names are abbreviated: N.= Nyctibatrachus, I.=Indirana, M.=Micrixalus, F.=Fejervarya, U.= Uperodon

Null model analysis (EcoSim 7.0; 10,000 randomisations) demonstrated that the observed mean pairwise niche overlap (0.41) was significantly lower than the simulated mean overlap under the null hypothesis of random microhabitat use (simulated mean 0.68 ± 0.06; $p$ =0.003), providing strong statistical evidence for non-random niche partitioning in this stream amphibian assemblage.

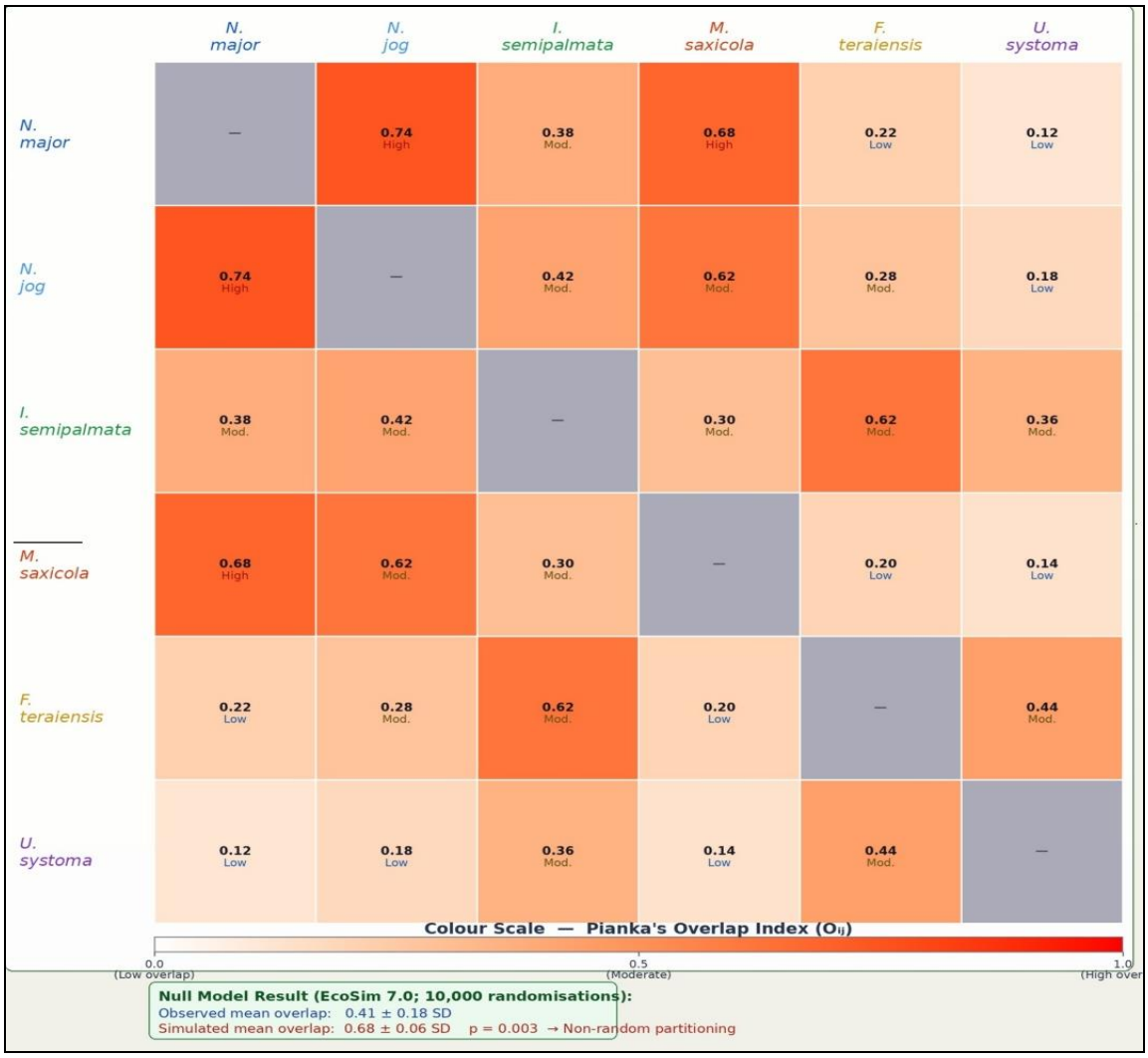


**Fig 2:** Pianka's Niche Overlap Matrix Heatmap

Colour-coded symmetric 6×6 heatmap matrix of Pianka's niche overlap index values for all 15 species pairs, with colour gradient from white (overlap=0; complete partitioning) to deep red (overlap=1; complete overlap). Species ordered by rheophily gradient (most rheophilous at top-left). Null model simulated mean overlap reference line shown.

## 5. Diel Activity Patterns

Significant differences in diel (temporal) activity patterns were observed among species (Table 6), providing an additional dimension of niche differentiation particularly relevant to species pairs with high spatial overlap. *Micrixalus saxicola* was the only strictly diurnal species (84.6% of observations during the 09:00–11:00 h survey period), providing complete temporal separation from the nocturnal *Nyctibatrachus* species despite high spatial overlap (O=0.68 with *N. major*). Both *Nyctibatrachus* species showed peak activity during the nocturnal survey period (21:00–23:00 h; 68.4% and 62.8% of observations for *N. major* and *N. jog* respectively), with subsidiary crepuscular activity. *Indirana semipalmata* showed the most even crepuscular-nocturnal distribution (42.4% crepuscular, 48.8% nocturnal). These temporal differences reduce the effective period of competition between *M. saxicola* and the spatially overlapping *Nyctibatrachus* species to the brief crepuscular transition period when both may be simultaneously active.

**Table 6:** Diel Activity Patterns: Proportional Observations per Temporal Survey Period by Species

| Species | Diurnal (09:00–11:00 h) | Crepuscular (17:30–19:30 h) | Nocturnal (21:00–23:00 h) | Primary Activity Period |
|---|---|---|---|---|
| *N. major* | 0.088 | 0.228 | 0.684 | Nocturnal |
| *N. jog* | 0.106 | 0.266 | 0.628 | Nocturnal |
| *I. semipalmata* | 0.088 | 0.424 | 0.488 | Crepuscular–Nocturnal |
| *M. saxicola* | 0.846 | 0.122 | 0.032 | Diurnal |
| *F. teraiensis* | 0.144 | 0.336 | 0.520 | Nocturnal–Crepuscular |
| *U. systoma* | 0.062 | 0.288 | 0.650 | Nocturnal |

Values represent proportion of total observations for each species recorded during each temporal survey period, across all survey events and all three streams.

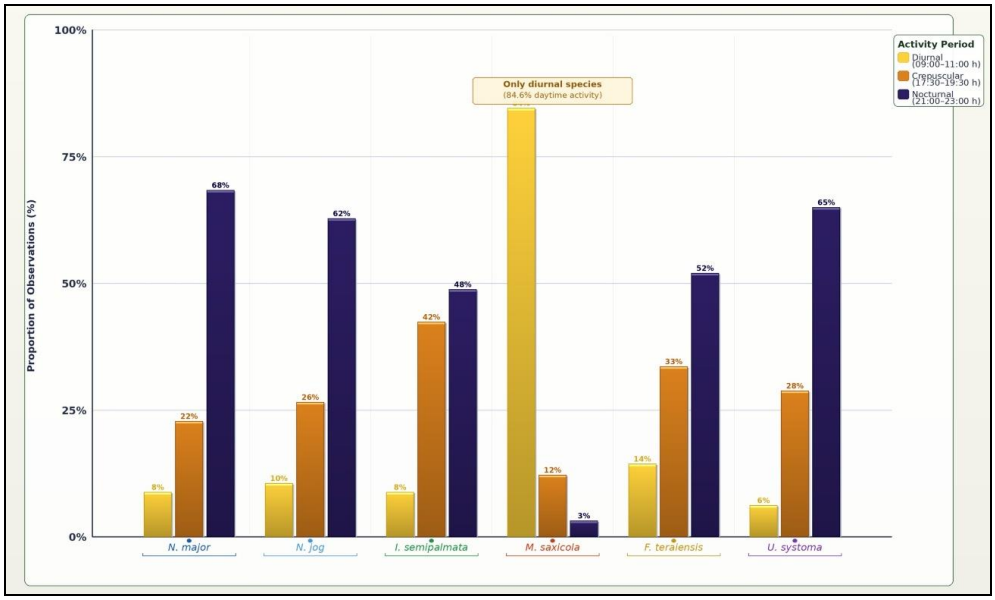


**Fig 3:** Diel Activity Profiles of the Six Study Species

Polar (clock-face) activity diagram or grouped bar chart showing the proportional diel activity of each of the six-study species across the three temporal survey periods (diurnal, crepuscular, nocturnal). Illustrates temporal overlap and segregation patterns.

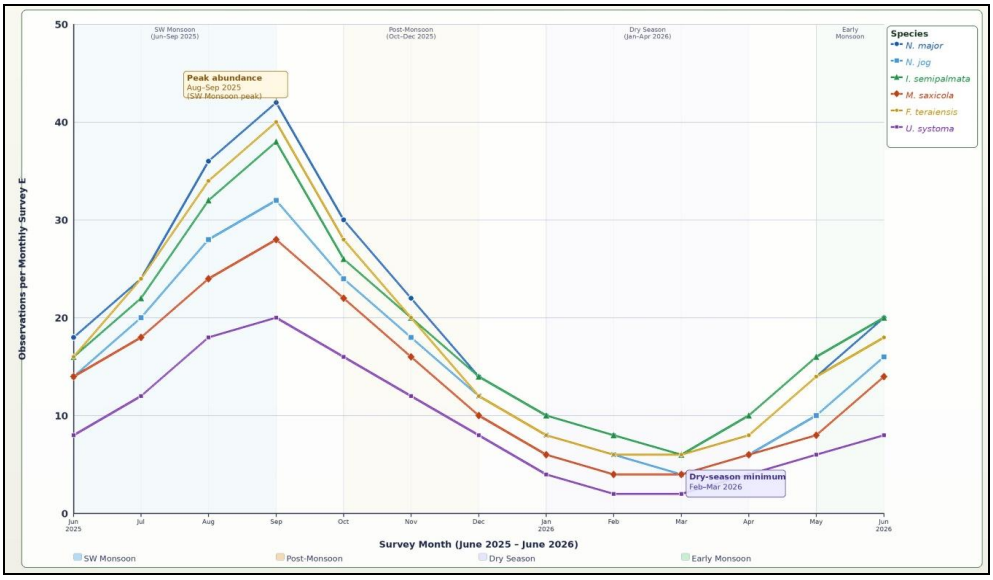


**Fig 4:** Seasonal Variation in Species Abundance across Monthly Surveys

Line graph showing total monthly observations per species across all three streams from June 2025[8] to June 2026, illustrating peak monsoon-season abundance (August–September 2025), seasonal crashes, and species-specific phenological differences.

## Discussion

### 1. Evidence for Non-random Niche Partitioning

The demonstration that mean pairwise niche overlap (0.41) is significantly lower than simulated random expectation (0.68; $p$ =0.003 by null model analysis) provides rigorous statistical evidence that niche partitioning in this Eastern Ghats stream amphibian assemblage is non-random — i.e., that the observed pattern of microhabitat use cannot be attributed to chance. This finding contrasts with the absence of significant spatial niche partitioning documented by Rodrigues *et al*. (2026) [20] in a semi-arid assemblage of lower species richness, and supports the theoretical prediction that niche partitioning signals should be most detectable in high-diversity assemblages with elevated potential for interspecific competition, such as tropical rainforest stream communities. It is consistent with the positive findings of Gonçalves-Sousa *et al*. (2023) [10] in a species-rich cloud forest *Pristimantis* assemblage and of Prasad *et al*. (2022) [18] in syntopic *Uperodon* species.

The gradient of pairwise niche overlaps revealed by Pianka's index analysis provides insight into the ecological relationships within the assemblage. The highest overlap between the two *Nyctibatrachus* species (O=0.74) suggests that, despite significant statistical differences in their multivariate microhabitat use (PERMANOVA $p<0.05$), these phylogenetically closely related species share considerable habitat structure requirements, potentially reflecting shared phylogenetic constraints on habitat use

rather than purely ecological differentiation. The coexistence of *N. major* and *N. jog* in the assemblage despite high spatial overlap is likely mediated by body size differences (*N. major* is substantially larger, with mean SVL approximately 62 mm vs. 34 mm for *N. jog*), which translate into different prey size spectra and substrate scale requirements, providing a body size-mediated trophic and micro-scale spatial dimension of differentiation not fully captured by our seven measured microhabitat variables.

**2. Substrate and Current Velocity as Primary Axes of Differentiation**

NMDS ordination and DistLM analysis consistently identified substrate type and current velocity as the strongest discriminators of species-specific microhabitat use, together explaining approximately 68% of the total variation in species-by-microhabitat matrices. This finding aligns with the results of Bhatta *et al*. (2019) [3] for *Nasikabatrachus sahyadrensis* tadpoles, where water flow velocity was the single strongest predictor of microhabitat use, and with Zhao *et al*. (2025) [25], who found that a combined elevation-temperature-flow rate-canopy density axis (corresponding to the high-energy, thermally stable microhabitats at high-current stream sections) was the primary PCA axis structuring a montane stream frog community in China. The strong selection for fast-current bedrock/boulder substrates by *M. saxicola* and *N. major*, and the complete avoidance of such conditions by *U. systoma* and *F. teraiensis*, generates the coarse-scale spatial partitioning that represents the fundamental organisational framework of the assemblage.

The rheophily gradient — from the highly rheophilous *M. saxicola* and *N. major* through intermediate-current associates (*N. jog*, *I. semipalmata*) to the still-water/terrestrial-margin specialists (*F. teraiensis*, *U. systoma*) — represents the primary axis of specialisation that structures the stream frog community. This rheophily gradient corresponds to a morphological gradient in toe pad development, toe fringes, and hindlimb muscle investment, consistent with the theoretical prediction that morphological differentiation should accompany niche differentiation in communities where interspecific competition has been a historical driver of community assembly (Basham *et al*., 2024; Zhao *et al*., 2025) [2, 25].

**3. Temporal Dimension: Diurnal-Nocturnal Separation**

The clear temporal segregation between the diurnal *Micrixalus saxicola* and the nocturnal *Nyctibatrachus* species provides an important additional axis of niche differentiation between species that share high spatial overlap in bedrock/fast-current microhabitats. This temporal separation reduces the effective period of competitive encounter between these species to the brief crepuscular transition period, a pattern consistent with theoretical predictions that temporal niche partitioning should evolve most readily when spatial partitioning is insufficient to fully prevent competitive exclusion (Székely *et al*., 2020; Caramaschi *et al*., 2026). The diurnal activity pattern of *M. saxicola* is associated with its foot-flagging visual communication system (Wali *et al*., 2019) [24], which is incompatible with nocturnal activity, providing a non-competitive mechanical explanation for the temporal segregation that may be reinforced by competition with the larger nocturnal *Nyctibatrachus* species for the limited supply of high-quality perch sites on wet boulder surfaces.

**4. Conservation Implications**

The finding that substrate and current velocity are the primary axes of microhabitat differentiation, and that species exhibit strong and consistent preferences for specific substrate-velocity combinations, has direct implications for the conservation management of stream amphibian assemblages in the Eastern Ghats. Anthropogenic alterations of stream microhabitat structure — including altered hydrology from upstream water abstraction (reducing current velocity and eliminating fast-current zones), sedimentation from agricultural runoff (converting bedrock/cobble substrates to sand/silt), and removal of riparian forest (increasing turbidity, reducing canopy cover and ambient humidity) — would disproportionately impact the rheophilous specialists (particularly *M. saxicola* and *N. major*) whose survival depends on the availability of intact high-energy stream microhabitats. The vulnerability assessment consistent with Scheffers *et al*. (2014) [21] and the Andean framework of Pintanel *et al*. (2026) [17] underscores that stream and forest frog communities have narrow thermal tolerance breadths, making thermally buffered forest microhabitats particularly vital refugia under climate change.

The high species-level endemism of the study assemblage — with *Nyctibatrachus* and *Indirana* representing entirely Indian-endemic families — amplifies the conservation significance of protecting intact stream microhabitat structure in the Eastern Ghats. Our data suggest that riparian buffer zones of at least 50 m on both stream banks are necessary to maintain the canopy cover and humidity gradients that enable the crepuscular and nocturnal specialists to use marginal stream microhabitats during the dry season, when stream channel microhabitat availability is most limited and microhabitat partitioning is under greatest competition pressure.

**Recommendations**

Based on the findings of this study, the following recommendations are proposed for the conservation and management of stream amphibian assemblages in the Eastern Ghats tropical rainforest streams:

1. **Stream Microhabitat Monitoring:** Annual monitoring of seven key microhabitat variables (substrate composition, current velocity distribution, water depth profile, canopy cover, riparian forest width, ambient humidity, and sediment load) in all designated perennial streams of the Nallamalai Forest Division should be institutionalised using standardised protocols consistent with this study, enabling early detection of microhabitat degradation before species-level population impacts become apparent.

2. **Riparian Buffer Zone Protection:** A minimum 50-metre buffer of intact riparian forest on both banks of all perennial streams harbouring *Nyctibatrachus*, *Indirana*, and *Micrixalus* populations should be formally designated as riparian protected zones under Andhra Pradesh State Biodiversity Board regulations, prohibiting all tree-felling, agriculture, and construction within this buffer.

3. **Invasive Species Management:** *Raorchestes bisignatus* and other canopy-associated invasive microhylid species that have been recently recorded in disturbed stream margins of the Nallamalai area should be monitored for their potential competitive effects on the more habitat-specialised stream associates documented in this study.

4. **Survey Protocol Standardisation:** The VES protocol developed in this study (three temporal periods, seven microhabitat variables, monthly frequency over full annual cycle) should be adopted as a standardised baseline monitoring protocol for stream amphibians across the Eastern Ghats forest divisions to enable meta-analytical comparisons of assemblage structure across the range.

5. **Climate Change Vulnerability Assessment:** Future studies should incorporate concurrent monitoring of stream water temperature, pH, conductivity, and dissolved oxygen to characterise the thermal and chemical microhabitat dimensions of niche use, providing the data needed to assess the vulnerability of species to projected climate change impacts on stream thermal regimes.

**Conclusion**

This study provides the first comprehensive quantitative assessment of microhabitat preference and niche partitioning in a stream amphibian assemblage of the Eastern Ghats, Andhra Pradesh, India, documenting 1,284 observations of six co-occurring species across 13 months of systematic monthly surveys. The results demonstrate that non-random niche partitioning is the primary mechanism structuring the assemblage, with observed mean pairwise niche overlap (Pianka's O=0.41) significantly lower than null model expectations (simulated mean 0.68; $p$ =0.003). Substrate type and current velocity emerge as the strongest discriminators of species-specific habitat use, generating a rheophily gradient from the fast-current bedrock specialists (*Micrixalus saxicola* and *Nyctibatrachus major*) through intermediate-current generalists (*N. jog*, *Indirana semipalmata*) to still-water/terrestrial-margin specialists (*Fejervarya teraiensis*, *Uperodon systoma*) that represents the fundamental organisational axis of this community.

Temporal differentiation between the diurnal *M. saxicola* and the nocturnal *Nyctibatrachus* species provides an additional critical axis of niche differentiation that reduces competitive encounter between species sharing high spatial overlap. The structural complexity of tropical rainforest stream microhabitats — the mosaic of substrate types, velocity zones, depth profiles, and canopy conditions — serves as the fundamental ecological framework within which amphibian species have partitioned niches through evolutionary time, enabling the extraordinary species diversity characteristic of intact tropical rainforest stream communities. These findings underscore the critical importance of maintaining intact riparian forest structure and stream habitat heterogeneity for the conservation of India's highly endemic and increasingly threatened stream amphibian fauna, and provide an evidence-based template for stream microhabitat monitoring and conservation management planning in the Eastern Ghats.

**References**


1. Anderson MJ. A new method for non-parametric multivariate analysis of variance. Austral Ecology,2001:26(1):32–46. https://doi.org/10.1046/j.1442-9993.2001.01070.x
2. Basham EW, Seidl CM, Scheffers BR. Vertical niche and trait associations in Central African amphibians. Biotropica, 2024, 56(3). https://doi.org/10.1111/btp.13349
3. Bhatta GK, Seetharamaraju M, Bhatta G. Influence of stream habitat variables on distribution and abundance of tadpoles of the endangered Purple frog, *Nasikabatrachus sahyadrensis*. Asian Journal of Conservation Biology,2019:8(2):156–162.
4. Caramaschi U, Solano-Iguaran JJ, Maia-Carneiro T, Rocha CFD. Acoustic niche partitioning and overlap in an anuran community of a threatened Brazilian Atlantic Forest remnant at Caparaó National Park. Conservation,2024–2026:6(1):24. https://doi.org/10.3390/conservation6010024
5. Caramaschi U, Garcia CE. The influence of environmental factors on the encounter rate of two diurnal stream-dwelling frogs of the Atlantic Forest. Journal of Natural History,2025:59(13–16):763–774. https://doi.org/10.1080/00222933.2025.2468683
6. Chanda SK. Handbook of Indian Amphibians. Zoological Survey of India, Calcutta, 2002, 335.
7. Chesson P. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics,2000:31:343–366.
8. Frost DR. Amphibian Species of the World: an Online Reference. Version 6.2. American Museum of Natural History, New York, 2025. https://amphibiansoftheworld.amnh.org/. Accessed June 2026.
9. Gause GF. The Struggle for Existence. Williams & Wilkins, Baltimore, 1934.
10. Gonçalves-Sousa J, *et al*. Trophic and spatial niches of a *Pristimantis* assemblage from remnants of cloud forests in Yariguíes mountain range, Colombia. Herpetological Journal,2023:33(4):187–198.
11. Gotelli NJ, Entsminger GL. EcoSim: Null Models Software for Ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear, Burlington, Vermont, 2003. https://www.garyentsminger.com/ecosim.htm
12. IUCN. The IUCN Red List of Threatened Species. Version 2024-2.2024. https://www.iucnredlist.org. Accessed June, 2026.
13. Jacobs J. Quantitative measurement of food selection. Oecologia,1974:14(4):413–417.
14. Krause B. The niche hypothesis: A virtual symphony of animal sounds, the origins of musical expression and the health of habitats. The Soundscape Newsletter,1993:6:6–10.
15. Oksanen J, *et al*. vegan: Community Ecology Package. R package version 2.7-0.2024. https://CRAN.R-project.org/package=vegan
16. Pianka ER. The structure of lizard communities. Annual Review of Ecology and Systematics,1973:4:53–74.
17. Pintanel P, Merino-Viteri A, Tejedo M. Andean Herpetofauna. Springer Nature, 2026, 259–295. https://doi.org/10.1007/978-3-032-00074-3_13

18. Prasad VK, Chuang MF, Das A, Ramesh K, Yi Y, Dinesh KP, *et al*. Coexisting good neighbours: Acoustic and calling microhabitat niche partitioning in two elusive syntopic species of balloon frogs, *Uperodon systoma* and *U. globulosus*. BMC Ecology and Evolution,2022:22:54. https://doi.org/10.1186/s40850-022-00132-x
19. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 2025. https://www.R-project.org/
20. Rodrigues L, *et al*. Anuran assemblage structure in the Serra da Capivara National Park, Piauí State, north-eastern Brazil. Austral Ecology, 2026. https://doi.org/10.1111/aec.70220
21. Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA. Microhabitats reduce animal exposure to climate extremes. Global Change Biology,2014:20(2):495–503. https://doi.org/10.1111/gcb.12439
22. Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW. Status and Trends of Amphibian Declines and Extinctions Worldwide. Annual Review of Environment and Resources, 2023 update.
23. Székely D, Cogălniceanu D, Székely P, Denoël M. Adult–juvenile interactions and temporal niche partitioning between life-stages in a tropical amphibian. PLoS ONE, 2020, 15(9). https://doi.org/10.1371/journal.pone.0238949
24. Wali R, Gower DJ, Roote J, Flatt T, Bhatt DL. Foot-flagging behaviour in *Micrixalus* frog species: ecology and evolution. Amphibia-Reptilia,2019:40(4):417–426.
25. Zhao W, Chen Y, Guo K, Lin X, Li X. Intraspecific variations in ecomorphological functional traits of montane stream-dwelling frogs were driven by their microhabitat conditions. Animals,2025:15(15):2243. https://doi.org/10.3390/ani15152243