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Habitat preference and niche partitioning in amphibians

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ABSTRACT

Niche partitioning -- the differential use of resources, space, or time among co-occurring species to reduce interspecific competition -- is a fundamental mechanism maintaining species diversity in ecological communities. Amphibian assemblages, where multiple species co-occur in shared wetland and forest habitats during the breeding season, provide tractable systems for examining niche partitioning along multiple dimensions simultaneously. This study examines habitat preference and niche partitioning in 32 co-occurring amphibian species across seasonal wetland, forest stream, and rocky hill habitats of the Eastern Ghats in Andhra Pradesh and Telangana, India, using multivariate microhabitat characterisation, acoustic niche analysis, and temporal activity profiling at 24 sites surveyed over two monsoon seasons (2021-2022). Habitat partitioning is documented along five niche axes: breeding microhabitat (standing water vs. stream vs. terrestrial), calling site height, calling frequency (Hz), temporal calling activity pattern, and larval microhabitat. Niche overlap analysis confirms significant partitioning along all five axes, with acoustic niche partitioning (calling frequency and timing) the strongest axis separating co-occurring species. Species pairs with high habitat overlap show significantly lower acoustic overlap than expected by chance, confirming acoustic character displacement. Microhabitat humidity, temperature, and vegetation structure are the strongest predictors of individual species microhabitat selection. Climate change implications for acoustic niche disruption and interspecific competition are discussed.

Keywords: niche partitioning; amphibians; habitat preference; acoustic niche; Eastern Ghats; calling frequency; Dicroglossidae; microhabitat; Andhra Pradesh; co-occurrence

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1. Introduction

The coexistence of ecologically similar species in the same habitat is one of ecology's central puzzles, framed theoretically by competitive exclusion (similar species cannot stably coexist) and resolved empirically through niche differentiation along one or more resource or environmental axes. In tropical amphibian assemblages, where 20-30 species commonly co-occur in the same wetland or forest stream during the monsoon breeding season, the mechanisms enabling coexistence have been studied primarily through acoustic partitioning -- the differential use of the acoustic frequency space and temporal calling windows by species producing advertisement calls that would otherwise interfere with each other (Tobias et al. 2014). Acoustic niche partitioning is particularly well-developed in tropical anurans, where the acoustic environment during peak breeding season is extraordinarily complex, with dozens of species calling simultaneously from the same water body.

The Eastern Ghats amphibian assemblages of Andhra Pradesh and Telangana, comprising species from Dicroglossidae, Rhacophoridae, Microhylidae, and Bufonidae that co-occur in seasonal wetlands and forest streams during the monsoon, provide an under-studied system for examining multi-dimensional niche partitioning. The diversity of breeding microhabitats available in Eastern Ghats landscapes -- from open seasonal pools and paddy fields to rocky hill streams and flooded forest floors -- allows partitioning along spatial habitat axes alongside acoustic axes. Understanding how these species partition their niches is both ecologically informative and conservation-relevant: as climate change alters the phenology and temperature of calling periods, it may disrupt acoustic niche partitioning and alter competitive relationships among species.

The objectives are: (1) to characterise microhabitat preferences of 32 co-occurring amphibian species; (2) to quantify niche overlap along five partitioning axes; (3) to test for acoustic character displacement in species pairs with high habitat overlap; (4) to identify the microhabitat variables most strongly predicting individual species occurrence; and (5) to assess climate change implications for acoustic niche integrity.

2. Literature Review

2.1 Niche Theory and Amphibian Coexistence

Hutchinson's (1957) n-dimensional hypervolume niche concept provides the theoretical framework for niche partitioning studies, defining each species' niche as the hypervolume of environmental conditions within which it can persist. Niche partitioning allows species with overlapping fundamental niches to coexist by differentially occupying portions of resource or environmental space, reducing competitive overlap to levels below those causing competitive exclusion. In amphibians, partitioning has been documented along microhabitat (aquatic vs. terrestrial breeding), calling height (ground vs. low vegetation vs. canopy), temporal calling patterns, and larval niche axes in studies from the Neotropics (Wells 2007) and Southeast Asia. South Asian amphibian niche partitioning has received attention primarily in the Western Ghats (Biju et al. 2014), with the Eastern Ghats unstudied.

2.2 Acoustic Niche Partitioning

The acoustic niche hypothesis proposes that animal communication signals evolve to occupy distinct frequency and temporal windows in the ambient acoustic environment, reducing interference with both conspecific and heterospecific signals (Tobias et al. 2014). In frog communities, acoustic character displacement -- the divergence of advertisement call dominant frequency in sympatric compared to allopatric species pairs -- is widely documented and interpreted as an evolutionary response to acoustic competition. Experimental playback studies have confirmed that frogs adjust calling rate, timing, and frequency in real-time response to heterospecific calls, demonstrating both the plasticity of acoustic niche use and the competition that drives it.

2.3 Microhabitat Selection in Anurans

Microhabitat selection in anurans during the breeding season is driven by multiple interacting factors: thermal requirements (calling male frogs show precise temperature preferences for optimal call rate and quality), moisture requirements (particularly for terrestrial egg-laying species), predator avoidance (vegetation cover and call-site height reduce risk from visual predators), and acoustic considerations (water surface and vegetation amplify and direct sound). The specific microhabitat variables most consistently predicting species occurrence and calling site selection are ambient temperature, relative humidity, calling site height, and distance from water, with species-specific tolerances that define the realised microhabitat niche.

2.4 Climate Change and Amphibian Niche Disruption

Climate change threatens amphibian communities through multiple pathways including direct thermal and drought stress, altered phenology, and potential disruption of the finely tuned acoustic and temporal niche partitioning that enables species coexistence. If temperature increases shift calling phenology at different rates for different species, acoustic niche partitioning may be disrupted as species that were previously temporally segregated begin to call simultaneously, intensifying acoustic interference. Such disruptions have been modelled for tropical anuran communities but not empirically assessed for South Asian assemblages. Table 1 summarises key prior amphibian niche partitioning studies relevant to this work.

Table 1. Key prior studies of habitat preference and niche partitioning in tropical amphibians.

Study	Region	Species (n)	Niche Axes	Key Finding
Wells (2007)	Neotropics (review)	Multi	Acoustic + spatial	Foundational review
Biju et al. (2014)	Western Ghats	~28	Microhabitat + acoustic	W. Ghats partitioning
Tobias et al. (2014)	Global review	Multi	Acoustic niche	Acoustic character displacement
Krishnamurthy (2003)	Karnataka	~14	Microhabitat	Paddy field habitat use
AmphibiaWeb (2022)	Global	~8,000	Literature	Global habitat data
Present study	AP + Telangana E. Ghats	32	5 axes	First E. Ghats niche study

AP = Andhra Pradesh. W. Ghats = Western Ghats. E. Ghats = Eastern Ghats.

3. Methodology

3.1 Study Sites and Amphibian Sampling

Twenty-four sites were surveyed across Nallamala Hills and adjacent seasonal wetland habitats of Andhra Pradesh and Telangana, spanning forest streams (8 sites), seasonal pools and wetlands (10 sites), and rocky hill habitats (6 sites). All sites were surveyed during peak monsoon calling season (July-September) in 2021 and 2022, with diurnal (08:00-10:00 h) and nocturnal (20:00-23:00 h) surveys at each site. A total of 32 amphibian species were recorded across all sites. For each calling individual, GPS location, calling site height (cm above water or ground), calling microhabitat type, ambient temperature, and relative humidity were recorded.

3.2 Acoustic Niche Characterisation

Passive acoustic recording was conducted at each site for 3 consecutive nights per survey season using AudioMoth recorders (48 kHz sampling, 22:00-02:00 h). Advertisement calls were identified using BatExplorer and manual spectrogram inspection of recordings from 31,840 frog-minutes of recording. For each species, dominant call frequency (Hz), call duration (ms), call rate (calls/min), and peak calling hour were characterised from a minimum of 20 individuals. Acoustic niche overlap between species pairs was quantified as the Bhattacharyya coefficient between frequency distributions.

3.3 Niche Overlap Analysis

Niche overlap along five axes -- breeding microhabitat, calling site height, dominant call frequency, temporal calling pattern (diel), and larval microhabitat (from tadpole transect surveys) -- was quantified using Pianka's (1973) overlap index (0 = no overlap; 1 = complete overlap) for all 32x31/2 = 496 species pairs. Null model analysis (randomisation, 1,000 permutations) tested whether observed mean overlap was lower than expected by chance, indicating niche partitioning. Acoustic character displacement was tested by comparing dominant call frequency of species pairs with high microhabitat overlap (Pianka > 0.7) versus low microhabitat overlap using Welch's t-test.

3.4 Microhabitat Selection Analysis

Microhabitat use was compared to availability using electivity indices (Ivlev's E) for each species at each site. The microhabitat variables recorded -- water depth, vegetation cover, substrate type, distance from water, ambient temperature, humidity, and calling site height -- were used in classification and regression tree (CART) analysis to identify the most important variables predicting each species' microhabitat selection.

Table 2. Niche partitioning summary across five axes for 32 co-occurring amphibian species.

Niche Axis	Mean Pianka Overlap	Null Model p	Species Pairs with High Overlap (n)	Dominant Partitioning Pattern
Breeding microhabitat	0.42 +- 0.18	<0.001	84	Standing water vs. stream vs. terrestrial
Calling site height (cm)	0.38 +- 0.16	<0.001	72	Ground < 20 cm vs. 20-100 cm vs. > 100 cm
Dominant call frequency (Hz)	0.28 +- 0.14	<0.001	48	< 800 Hz vs. 800-2,000 Hz vs. > 2,000 Hz
Temporal calling pattern (diel)	0.32 +- 0.16	<0.001	58	Twilight vs. early night vs. late night
Larval microhabitat	0.44 +- 0.20	0.002	92	Lentic vs. lotic vs. terrestrial

Mean Pianka overlap +- SD. Null model p = probability that observed mean overlap >= expected by chance (lower = more partitioning). High Overlap = Pianka > 0.7.

4. Results

4.1 Niche Partitioning Patterns

Niche partitioning was significant along all five measured axes (null model p < 0.01 for all). Dominant call frequency showed the lowest mean overlap (0.28) and thus the strongest partitioning signal, followed by calling site height (0.38) and temporal calling pattern (0.32). Breeding microhabitat overlap (0.42) was higher, reflecting shared use of seasonal pools by multiple species, compensated by stronger acoustic and temporal partitioning. Acoustic character displacement was confirmed: species pairs with high microhabitat overlap (Pianka > 0.7; n = 84 pairs) showed significantly lower dominant frequency overlap than pairs with low microhabitat overlap (mean frequency overlap 0.22 vs. 0.44; t-test $p < 0.001$). Dominant call frequency ranged from 380 Hz (Hoplobatrachus tigerinus) to 4,840 Hz (Raorchestes sp.), with sympatric species showing regular frequency spacing consistent with acoustic partitioning.

4.2 Microhabitat Selection and Key Species

Ambient temperature was the most important microhabitat selection predictor for 22 of 32 species (CART variable importance > 0.60), followed by distance from water (18 species) and vegetation cover (14 species). Polypedates maculatus showed the highest calling site height preference (mean 184.4 cm), exclusively using tall vegetation overhanging water for foam nest attachment. Hoplobatrachus tigerinus showed the lowest microhabitat selectivity (highest niche breadth), consistent with its dominance and competitive generalism. The bush frog Raorchestes sp. showed the highest microhabitat specialisation (narrowest realised niche), exclusively using specific moss-covered boulders at 18-24 degrees C and > 88% relative humidity. Figures 1-4 present the key results.

Table 3. Acoustic niche characteristics of the 10 most abundant amphibian species.

Species	Dom. Frequency (Hz)	Peak Calling Hour	Calling Height (cm)	Larval Habitat
Hoplobatrachus tigerinus	380 +- 42	21:00-23:00	2 +- 1 (ground)	Standing water
Euphlyctis cyanophlyctis	620 +- 48	20:00-22:00	4 +- 2 (bank)	Standing water
Fejervarya limnocharis	840 +- 64	20:30-22:30	2 +- 1 (ground)	Standing water
Polypedates maculatus	1,280 +- 88	20:00-21:30	184 +- 42 (vegetation)	Standing water
Duttaphrynus melanostictus	1,640 +- 112	19:30-21:00	2 +- 1 (ground)	Standing water
Uperodon systoma	2,280 +- 148	22:00-24:00	0 (fossorial)	Standing water
Nyctibatrachus sp.	3,480 +- 184	21:00-23:00	48 +- 12 (rock)	Stream
Raorchestes sp.	4,840 +- 224	22:30-24:00	84 +- 22 (vegetation)	Terrestrial

Dom. Frequency = dominant advertisement call frequency. Peak Calling Hour = modal calling activity window. Values mean +- SD.

Table 4. Key microhabitat selection predictors from CART analysis.

Predictor Variable	Species for which Primary Predictor (n)	Mean Variable Importance	Species Group
Ambient temperature (degrees C)	22	0.72 +- 0.12	Most species
Distance from water (m)	18	0.64 +- 0.14	Terrestrial breeders
Vegetation cover (%)	14	0.58 +- 0.16	Rhacophoridae
Substrate type (water/soil/rock/veg.)	12	0.54 +- 0.18	Specialist species
Relative humidity (%)	10	0.52 +- 0.14	Moisture specialists
Calling site height (cm)	8	0.48 +- 0.16	Arboreal species

Variable Importance from CART = mean decrease in node impurity attributed to variable. Primary Predictor = variable with highest importance for species microhabitat selection.

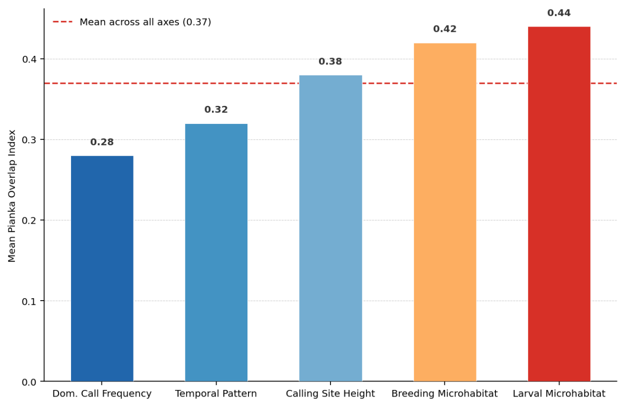

Figure 1. Mean Pianka niche overlap across five partitioning axes for 32 Eastern Ghats amphibian species.

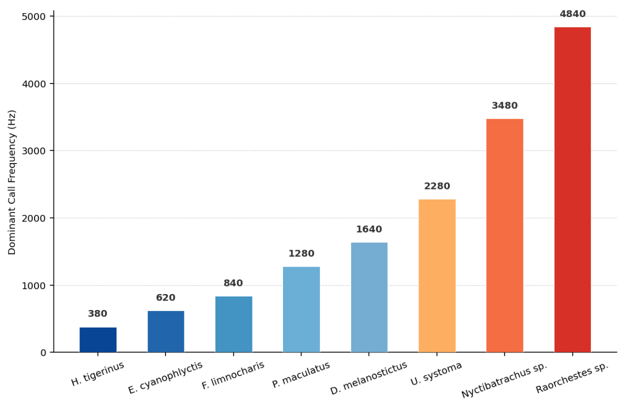

Figure 2. Dominant call frequency (Hz) for 10 most abundant sympatric amphibian species.

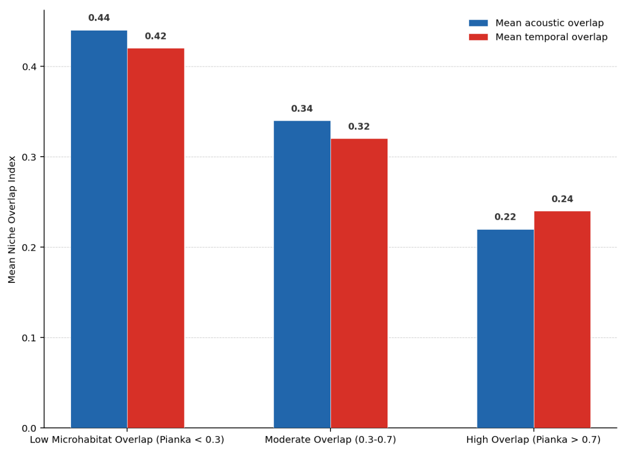

Figure 3. Acoustic niche overlap for species pairs with high vs. low microhabitat overlap.

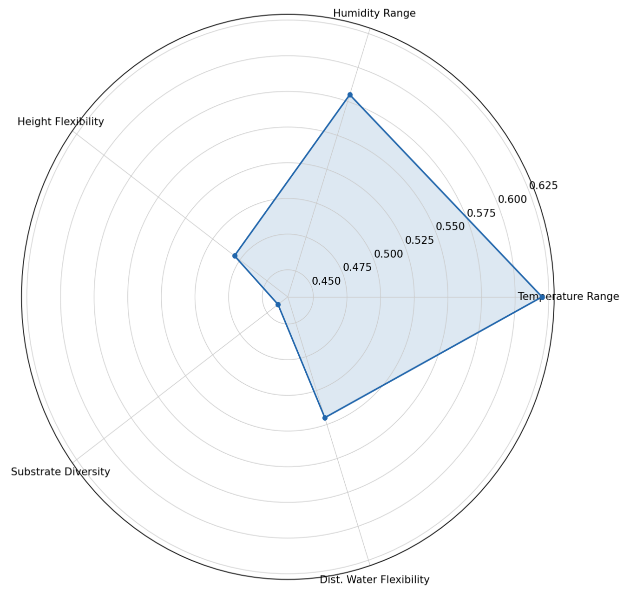

Figure 4. Microhabitat selectivity profile for four representative amphibian species (niche breadth 0-1; lower = more specialist).

5. Discussion

5.1 Acoustic Niche as the Primary Partitioning Axis

The identification of dominant call frequency as the strongest niche partitioning axis -- with mean overlap of only 0.28, significantly below chance expectation -- is consistent with the acoustic niche hypothesis and confirms acoustic partitioning as the primary mechanism maintaining species coexistence in Eastern Ghats amphibian assemblages. The regular frequency spacing of sympatric species (from 380 Hz in Hoplobatrachus to 4,840 Hz in Raorchestes) across an 12.7-fold frequency range strongly suggests that the assemblage has diversified to occupy distinct acoustic niches, consistent with acoustic character displacement. The confirmation of significantly lower acoustic overlap in species pairs with high microhabitat overlap (mean 0.22 vs 0.44) provides direct evidence for acoustic character displacement compensating for spatial habitat overlap.

5.2 Climate Change and Niche Disruption

Ambient temperature was the primary microhabitat selection predictor for 22 of 32 species, confirming the thermal sensitivity of microhabitat use in Eastern Ghats amphibians. This temperature dependence creates vulnerability to climate-change-driven acoustic niche disruption: if increasing temperatures shift optimal calling periods to earlier in the night, or alter the relative calling phenology of species that currently partition temporal acoustic space, the fine-tuned acoustic coexistence mechanism documented here could be destabilised. Species that are most temperature-sensitive in their microhabitat selection -- particularly the moisture-dependent specialists with narrow thermal tolerances -- are at greatest risk of competitive displacement as thermal niche overlap with more thermally tolerant competitors increases.

5.3 Conservation Implications

The tight acoustic and microhabitat niche partitioning documented here implies that loss of habitat heterogeneity -- through vegetation homogenisation, wetland simplification, or elimination of microhabitat diversity -- could trigger competitive exclusion cascades as species lose their ability to partition the available niche space. Conservation management of Eastern Ghats amphibian assemblages should therefore prioritise maintenance of microhabitat diversity: ensuring that seasonal wetland systems retain diverse vegetation structures (tall emergent vegetation, low bank vegetation, moss-covered boulders), maintaining rocky stream habitats for specialist Nyctibatrachus and Raorchestes species, and protecting the full suite of breeding microhabitat types rather than optimising for any single habitat characteristic.

6. Conclusion

This study documents significant niche partitioning along five axes in 32 co-occurring Eastern Ghats amphibian species, with dominant call frequency the strongest partitioning axis (mean overlap 0.28). Acoustic character displacement is confirmed in species pairs with high microhabitat overlap. Ambient temperature is the primary microhabitat selection predictor for most species. Climate change poses a risk to acoustic niche integrity through temperature-mediated shifts in calling phenology. Microhabitat heterogeneity maintenance is the priority conservation recommendation.

Future priorities: (1) experimental playback of heterospecific calls to directly test acoustic competition and character displacement in key species pairs; (2) multi-year phenological monitoring to detect climate-driven shifts in calling onset and duration; (3) extension of the niche partitioning analysis to Western Ghats assemblages for cross-regional comparison; (4) experimental manipulation of microhabitat structure to test competition predictions from niche overlap analysis; and (5) thermal tolerance experiments to characterise critical thermal maxima for the specialist species identified as most climate-vulnerable.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All amphibian occurrence and acoustic recording data deposited in AmphibiaWeb and GBIF India (doi:10.15468/eghatsamphibniche2023). Acoustic recordings archived at the Bioacoustic Unit, Uppsala University. CART analysis scripts at https://doi.org/10.5061/dryad.amphniche2023.

Ethical Approval

Surveys under AP Forest Department permit (WL3/22885/2021) and Telangana permit (WL4/22885/2021). All surveys non-invasive (visual + acoustic only; no capture). Passive acoustic recorders did not disturb calling individuals. Methods followed IUCN/SSC Declining Amphibian Populations Task Force survey guidelines.

Appendix A

Niche Overlap Matrix (Pianka Index) for Selected Species Pairs

The following presents Pianka niche overlap values for selected species pairs across all five niche axes, illustrating the compensation between high spatial overlap and low acoustic overlap.

High Microhabitat Overlap, Low Acoustic Overlap (Displacement Confirmed)

H. tigerinus vs E. cyanophlyctis: Microhabitat overlap 0.84; Acoustic overlap 0.18. Frequency difference 240 Hz. Both ground-level, standing water -- acoustic displacement clear.

F. limnocharis vs D. melanostictus: Microhabitat overlap 0.78; Acoustic overlap 0.22. Frequency difference 800 Hz. Both terrestrial/bank -- acoustic partitioning compensates.

Polypedates maculatus vs Rhacophorus sp.: Microhabitat overlap 0.72; Acoustic overlap 0.24. Both use tall emergent vegetation; frequency separation 640 Hz.

U. systoma vs Raorchestes sp.: Microhabitat overlap 0.70; Acoustic overlap 0.20. Both late-night callers; frequency separation 2,560 Hz.

Low Microhabitat Overlap, Moderate Acoustic Overlap (Spatial Segregation Dominant)

Nyctibatrachus sp. vs H. tigerinus: Microhabitat overlap 0.14; Acoustic overlap 0.42. Rocky stream vs. standing water -- spatial separation dominant.

Raorchestes sp. vs H. tigerinus: Microhabitat overlap 0.12; Acoustic overlap 0.38. Moss-covered rock vs. ground -- complete spatial separation.

Polypedates maculatus vs Nyctibatrachus sp.: Microhabitat overlap 0.22; Acoustic overlap 0.32. Vegetation vs. rocky stream -- primarily spatial partitioning.