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Frogs in sight and sound: Passive acoustics and visual surveys reveal complementary species detection in tropical rainforest anurans

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Abstract

Amphibian surveys in remote tropical rainforests are often constrained by rugged terrain, dense vegetation, limited accessibility, and high logistical demands associated with observer-based methods. Passive acoustic monitoring (PAM) using autonomous recording units (ARUs) has emerged as a promising, non-invasive tool for biodiversity assessments, however, its effectiveness can vary across taxa and landscapes. We conducted a comparative evaluation of PAM with traditional Visual Encounter Surveys (VES) to document the anuran community of a tropical wet evergreen forest within the Indo-Burma biodiversity hotspot. Our results show that PAM effectively detected most of the visually observed species, as well as many vocally active cryptic, arboreal, and fossorial species that were missed by VES. Its suitability for deployment in inaccessible areas underscores its potential for large-scale assessments. However, VES detected non-calling and conspicuous species, highlighting the limitation of a single-method approach. A mixed method—integrating PAM with VES yielded a more comprehensive inventory. These findings provide crucial insights into optimising amphibian monitoring protocols and support the adoption of integrated survey methodologies for long-term assessments, particularly in landscapes where conventional methods are constrained by terrain and effort.

Keywords

Species richness, Arunachal Pradesh, Bioacoustics, Monitoring, Tiger reserve, Namdapha National Park

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Introduction

Tropical rainforests support a high diversity of amphibians—one of the most evolutionarily ancient and ecologically sensitive vertebrate groups (Stuart et al. 2005, Wells 2010, Penhacek et al. 2024). Anura, consisting of frogs and toads, is the largest order within Amphibia, covering over 85% of all described species (Frost 2024). Amphibian discoveries have accelerated in recent years, with approximately 780 new species described between 2016 and 2020, majority of which were anurans (Womack et al. 2022). Despite numerous ongoing discoveries, many species in rainforest regions likely remain undocumented, primarily due to insufficient sampling and cryptic speciation (Funk et al. 2011). These regions are severely under-sampled because of inaccessibility caused by rugged topography, dense vegetation, seasonal flooding and, in some cases, socio-political instability—all of which impede comprehensive biodiversity assessments (Feeley and Silman 2011, Jenkins et al. 2013). These challenges are particularly acute for amphibians, many of which are nocturnal and small-sized—posing a significant challenge to traditional observer-based visual encounter survey (VES) methods. Furthermore, comprehensive monitoring of biodiversity requires repeated assessments, ideally conducted over extended periods and wide spatial scales (Lindenmayer and Likens 2010), which demands significant efforts for an observer-based field survey.

Bioacoustics approach such as passive acoustic monitoring (PAM) involves deploying autonomous sound recording devices to detect vocalising species, without the need for physical presence. It has emerged as a powerful method for amphibian research, which provides reliable estimates of vocally active species (Blumstein et al. 2011). Unlike VES, which is limited by weather, terrain and observer effort, PAM offers continuous, non-invasive data collection, flexible for prolonged sampling periods and in inaccessible areas (Marques et al. 2013, Melo et al. 2021).

Over the last decade, greater availability and affordability of PAM devices driven by technological advancements have increased the opportunity to acoustically survey wildlife (Gibb et al. 2018). Yet, in terrestrial ecosystems, bats, followed by birds are the most studied using PAM, while only 12% of the PAM studies until 2018 focussed on anurans (Sugai et al. 2018).

Many studies have compared PAM with VES in inventorying anurans, but their findings differ, shaped by differences in landscape features, habitat complexity, and species assemblage (Acevedo and Villanueva-Rivera 2009, Brauer et al. 2016, Boullhesen et al. 2021). We assess the relative effectiveness of PAM and VES in the rainforests of Northeast India, which is a part of the Indo-Burma region— one among the eight hottest biodiversity hotspots of the world with high amphibian diversity, yet understudied (Myers et al. 2000, Pawar and Birand 2001). Threatened by habitat modifications, the need to assess the biodiversity in Northeast India has received attention from researchers in the recent past. However, large-scale surveys remain challenging due to inaccessibility and difficult terrain (Ohler et al. 2018).

In this study, we compare and contrast the performance of passive acoustic monitoring (PAM) with visual encounter survey (VES) method, to inventory the amphibian community in a tropical wet evergreen forest in Indo-Burma biodiversity hotspot. Additionally, we test if the combined PAM-plus-VES method yields a significantly better result in estimating the study area's regional amphibian species richness. The overall goal here is to determine the most efficient and feasible method, which can be used to accelerate the creation of a comprehensive amphibian inventory for the Indian region of Indo-Burma biodiversity hotspot.

Materials and methods

Study Area

The study was conducted in Namdapha Tiger Reserve (NTR), a 1985 sq. km protected area in Arunachal Pradesh, India (Fig. 1), situated within the Indo-Burma biodiversity hotspot (Myers et al. 2000). NTR is home to extensive rainforests (Champion and Seth 1968), and is considered as the northernmost low-land tropical wet evergreen forest in the world (Proctor et al. 1998). Due to its wide elevation range (200–4571m), the forest types transition from wet evergreen forests to wet temperate forests with increasing altitude (Champion and Seth 1968). The park's habitat heterogeneity supports highly diverse species assemblage, including several endemic species. Given the park's rugged terrain, the dense undergrowth and limited accessibility, non-invasive surveys, such as camera trapping were preferred over visual transect based methods, in the past (Datta et al. 2008).

Data Sampling

We selected 14 sampling locations in the tropical evergreen forest zone of NTR for the survey (Fig. 1), based on existing literature (Sarkar and Sanyal 1984, Dinesh and Radhakrishnan 2019), previous exploration surveys (conducted in 2022) and the information provided by the local people. Each sample location (site) corresponded to one of the following four habitats; (1) lake/pond; (2) river stream; (3) road-side water puddle; (4) swamps within the forest.

We used Song meter micro units (Wildlife Acoustics, Inc.) for passive acoustic monitoring. Each PAM unit was powered by three AA alkaline batteries and silica bags were placed inside to prevent moisture accumulation. We stored the digital recordings on microSD cards inserted in the units.

We configured the devices using the Song Meter Configurator mobile App (v 1.5.15). The sampling rate was set to 44.1kHz, Gain was set to 18 dB and individual recordings were saved as 60 minutes files.

We collected data through PAM and VES methods at the beginning of the wet season (May–June 2023) in Northeast India to avoid the risk of floods and landslides in the following months. We configured PAM units to record from dusk to midnight (18:00 to 23:59 hours), coinciding with the peak activity period of amphibians. At each of the 14 sampling sites, we installed one PAM unit to record for six hours. We securely strapped each device to a tree or plant, positioning it approximately 1.5 meters above the ground (Walls et al. 2014).

At each ARU installed location, we conducted a nocturnal visual encounter survey (VES) (Scott et al. 1994) between 18:00 to 23:59 hours on the day following acoustic data collection. Three surveyors searched for anurans at each site for a fixed duration of two hours using flashlights. The VES sampling effort at each site was 6 man hours (3 persons * 2 hours), which is consistent with the PAM sampling effort of 6 hours (1 unit * 6 hours).

Data Analysis

We used Raven Pro (v 1.6) for analysing the sound files retrieved from PAM units. After discarding corrupt files and those with excessive noise (rain), we obtained 3360 minutes of recordings. The sampling effort was standardised to 10 min for each hour of recording (Melo et al. 2021, Ribeiro Jr et al. 2022). The 10 min continuous segment within each hour was randomly selected. Thus, for each site, 60 minutes (6 (hours) * 10 (min/h)) of call recording was considered as the sample for analysis. Analysis involved listening to the recordings and visually scanning the spectrogram in Raven Pro with frame length set to 60 seconds (Wimmer et al. 2013, D'Anunciação et al. 2022). We set the spectrum function to a Hanning window of 256 samples and DFT size of 1024 samples. Two team members with adequate knowledge of anuran calls listened to the recordings and identified the species. We annotated the identified calls and measured the dominant frequency using peak frequency measurement in Raven's selection spectrum function (Bernardes et al. 2015). Dominant frequency is defined as the frequency at which the maximum power is observed in a call selection.

We estimated the gamma species richness for VES and PAM methods separately using a non-parametric bootstrap approach (Efron and Tibshirani 1994), wherein 14 sites were resampled with replacement for 1000 times and the number of unique species in each replicate was recorded. We used the resulting distribution of the estimated richness to calculate the 95% confidence interval (Efron and Tibshirani 1994, Chiu et al. 2014). Given that the sampling sites were independent and the sampling effort was consistent, this resampling-based method is flexible and is widely applied in ecological studies (Gotelli and Colwell 2001). We compared the bootstrap derived species richness estimates of the two methods using the non-parametric Mann-Whitney U test (Mann and Whitney 1947).

Additionally, we used Jaccard's index to measure the similarity between the set of amphibian species detected by PAM and VES methods. We grouped the species based on ecological traits to investigate the method-specific detection patterns (Davis et al. 2025). The analysed traits were—(1) the vertically stratified habitat; (2) body size using Snout Vent Length (SVL)—small(<=30 mm), medium(31–60 mm), large (>60 mm); (3) dominant call frequency—low(<2 kHz), mid (2–4 kHz), high (>4 kHz). For each of the above groups, we calculated the species richness across detection methods, based on rarefied species accumulation curves with 95% confidence intervals. To examine species richness and sampling adequacy, we constructed species accumulation curves (SAC) for (1) PAM, (2) VES, and (3) PAM+VES methods, wherein the number of sampled sites was chosen as the effort. R software (v 4.1.3) and iNEXT package (Hsieh et al. 2016) were used to run the above analysis. To estimate the effort required to detect all the species, we extrapolated the species detections to thrice the minimum observed sample size (Hsieh et al. 2016).

Results

PAM vs VES

We identified a total of 19 amphibian species belonging to 17 Genera and 6 Family (Frost 2024) from 720 minutes of passive acoustic recordings (Table 1). We detected 19 species of amphibians belonging to 17 Genera and 7 Family (Frost 2024) from visual encounter surveys (Table 1). Both PAM and VES detected seven endemic amphibian species (Fig. 2). The bootstrap-derived 95% confidence interval for species richness ranged between 14–19 species for each PAM and VES methods (Fig. 3). We observed a clear overlap in the estimated richness confidence intervals, indicating a similarity in the output of the two methods. The Wilcoxon rank sum test confirmed that there was no significant difference in the regional species richness between methods ($W = 494174$, $p > 0.1$).

However, a marginal difference was observed in the composition of species detected by the two methods. The Jaccard similarity coefficient (or Jaccard Index) was 0.652, which implies that 65.2

% of the total species were recorded by both methods, while 17.4% of species were unique to each method. The species detected by PAM and VES were analysed based on ecological traits, including vertical habitat stratification, body size and dominant call frequency (Fig. 4). Our results show that PAM was effective in detecting arboreal and fossorial anurans, whereas VES detected a greater number of species inhabiting terrestrial and stream habitat. Body size influenced detection patterns, with PAM marginally outperforming VES in detecting smaller anurans (SVL < 30mm). Additionally, PAM performed better in detecting species with a dominant frequency in the mid range (2–4.5 kHz) (Fig. 4).

Interestingly, the upper limit of the bootstrap confidence interval of richness for both VES and PAM methods was not greater than the observed richness (Fig. 3). We investigated this disparity by evaluating the sampling adequacy. We constructed species accumulation curves (SAC) based on the species detection history across sampling locations. For both the methods, a positive but decelerating trend in cumulative species richness was observed with increasing sampling sites, indicating that new species continue to be detected albeit at a slower rate (Fig. 5). The rate of species accumulation at the tail end of the rarefaction curve—calculated by measuring the slope of the last 3 points, was 0.46 for PAM and 0.46 for VES. This indicates that, on an average, 0.46 new species were added with each additional site.

Mixed Method

When we combined both the survey methods (mixed method), a total of 23 species were recorded, which is 21% more than the observed species in either of the methods (PAM or VES). Using bootstrap resampling, the 95% confidence interval was between 16–23 species (Fig. 3). The mixed method richness estimate was significantly higher than PAM estimate ($W = 940992$, $p < 0.0005$) and VES estimate ($W = 939942$, $p < 0.0005$). Similar to the accumulation curves of VES and PAM, sampling inadequacy was observed in the mixed method SAC where 0.53 additional species were detected with each new site. The extrapolated curve approached an asymptote at approximately three times the current sample effort, suggesting that around 40 sites would be required to create a comprehensive inventory for the study area (Fig. 5).

Discussion

Amphibians are the most threatened vertebrate class and their extinction rate shows no sign of decline (Luedtke et al. 2023). At the same time, the steady increase in the rate of newly described amphibian species is indicative of a large pool of unknown species (Womack et al. 2022). This indicates that the true rate of threat to this class is higher than currently known. This study recognises the necessity to assess and monitor the poorly known amphibians of the Indo-Burma biodiversity hotspot. To tackle the safety and accessibility challenges associated with nocturnal visual surveys in this landscape, we tested the efficiency of passive acoustic monitoring of anurans as an alternative to traditional visual encounter survey. We find that PAM is a reliable method in estimating the amphibian species richness, especially in remote and inaccessible regions. However a mixed method wherein PAM is complemented with a VES yielded more comprehensive results. Our findings provide crucial evidence for large scale assessment and monitoring of amphibians in rugged terrains which are treacherous for manual surveys in tropical rainforests.

In our study, we found that both visual encounter surveys and passive acoustics yielded the same landscape level species richness with identical bootstrap derived 95% confidence intervals. Similar results were observed in Andean forests, where equivalent amphibian species richness was observed across methods (Boullhesen et al. 2021). The PAM richness estimate was also similar to earlier visual surveys conducted in Nadmapha Tiger Reserve. In 1985, Sarkar and Sanyal (1984) conducted an expedition and reported 14 amphibian species (Sarkar and Sanyal 1984). A more recent survey conducted in 2009 reported 22 different amphibian species in NTR (Dinesh and Radhakrishnan 2019). Based on our findings, we recommend passive acoustic monitoring as an alternative to VES for assessing and monitoring anurans, particularly in the vastly unexplored and inaccessible rainforests of Northeast India. However, developing a comprehensive inventory for this region requires examining the species composition detected by each method.

Our results showed that 15 species were common to both methods while four unique species were detected by PAM and VES respectively (Table 1). Analysis by ecological traits, revealed that PAM was effective in detecting vocal amphibians which were either cryptic or occupied concealed niches. VES failed to detect *Nasituxalus* sp. and *Zhangixalus smaragdinus* , likely because they are arboreal and hence outside the observer's field of view. Barnes & Quinn (2023) detected arboreal anurans from ARUs alone, highlighting the distinct advantage of PAM over VES in detecting tree-dwelling frogs (Barnes and Quinn 2023). Visually spotting species in the high canopy is a major challenge, while locating those hiding in subterranean environments is even more difficult. Our ARUs succeeded in detecting *Limnonectes* sp. 1., which usually calls from small holes in the surface covered with leaf litter. Additionally, through PAM, we identified a cryptic species of the genus Raorchestes (*Raorchestes* sp 1.), based on the differences in call structure and dominant frequency from *Raorchestes* sp 2. and *Raorchestes* sp 3.. Thus, PAM outperformed VES by detecting calls from species that were otherwise difficult to detect visually, including arboreal, fossorial, and cryptic species. These detections also suggest that the landscape harbours complex environments with vertically structured amphibian habitats (Oliveira and Scheffers 2019). Complex habitats with dense vegetation are known to attenuate high-frequency calls (Wiley and Richards 1978), whereas abiotic noise can mask low-frequency calls (Buxton et al. 2017). This explains the detection of more species with mid frequency calls (2–4.5 kHz) through PAM.

Four amphibian species — *Amolops adicola*, *Duttaphrynus melanostictus*, *Odorana livida* and *Limnonectes* sp. 2. were uniquely detected by VES. Many Odorrana species produce complex ultrasonic calls (Shen et al. 2011, Arch et al. 2012). It is likely that *Odorana livida* was not detected through PAM because its calls were outside the detection frequency range of our ARUs. *Amolops adicola* occurs in riverine habitats with peak calling and breeding activity documented in the month of October (Patel et al. 2021). Since our study was undertaken between May and June, it is likely that *A. adicola* was not vocalising during this period for it to be detected by PAM. The high ambient noise generated by torrential streams likely contribute to low species detections by PAM (Towsey et al. 2014, Buxton et al. 2017). This is consistent with our findings, where more numbers of species were recorded through VES compared to PAM in streams. The *Limnonectes* sp. 2. detected in VES was commonly found in road puddles and was not observed vocalising during visual surveys. Similar to *A. adicola*, it is possible that this species breeds during a different season. The exclusive detection of *D. melanostictus* by VES may be attributed to its terrestrial and conspicuous nature, along with its low frequency and low intensity calls that may be masked by ambient noise, limiting its detectability by PAM. Echoing other similar findings, we conclude that VES performs well in detecting amphibians that are either non-vocal, have low-intensity or infrequent calls (Dodd 2010, Guzy et al. 2014), or occur in habitats with high ambient noise such as streams.

Noting the complementary nature of VES to acoustic method, we compared the performance of the mixed method (PAM+VES) with its counterparts. The mixed method yielded significantly higher amphibian species richness estimates for the studied landscape. These findings support combining visual and passive acoustic surveys for comprehensive assessment of amphibian communities (Boullhesen et al. 2021, Hoefer et al. 2023).

The observed species richness in all the three methods (PAM, VES and PAM+VES) was equal to the upper limit of the bootstrapped derived confidence interval. This can be because of the presence of rare species—those detected at only one or few sites. Nearly 50% of the total species detected in the mixed method were observed at a maximum of two sites. The presence of a high number of rare species in communities reflects complexity in habitats and environmental heterogeneity, highlighting its conservation importance (Magurran and Henderson 2011). However, the percentage of rare species and the discrepancy in observed richness (vs CI) could also be because of insufficient sampling. A limited or uneven sampling effort across the study area can result in a downward bias of bootstrap derived richness estimates. In all the three methods non-asymptotic species accumulation rarefaction curves were observed (Fig 5), reflecting the incomplete detection of the community richness (Gotelli and Colwell 2001).

In this study, the chosen sampling locations were primarily based on previously surveyed accessible locations selected from literature and did not cover the complete altitudinal range of the Tiger Reserve. Accessibility and safety have been an impediment to conduct nocturnal visual surveys in this region. This study reveals PAM as an efficient alternative to VES, and offers the advantage of sampling for a longer duration. Thus we recommend using passive acoustic devices to estimate the anuran species richness in NTR by sampling across minimum 40 sites (based on extrapolated SAC) covering the altitudinal gradient and diverse habitats. Wherever possible, we suggest that PAM should be complemented with a VES or sampling should be undertaken across multiple seasons of a year.

Conclusion

This study provides the first comparative account of passive acoustic monitoring and visual encounter survey approaches for anurans in India. The findings highlight the effectiveness of PAM in detecting anurans in structurally complex tropical rainforests. Since PAM is non-invasive and logistically feasible in remote and inaccessible terrain, we advocate for its implementation in Northeast India and its neighbouring countries that share similar landscapes. However, to create comprehensive inventories and conduct long-term monitoring of anurans, we recommend a mixed-method approach combining visual and acoustic surveys.

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Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Data Availability

The datasets generated during and/or analysed during the current study are available in the supplementary file.

Table 1 List of Anuran species identified through passive acoustic monitoring (PAM) and visual encounter survey (VES).

Family	Species	PAM	VES
Bufonidae	*Duttaphrynus melanostictus*		Yes
Ceratobatrachidae	*Alcalus fontinalis* †	Yes	Yes
Dicroglossidae	*Minervarya* sp.	Yes	Yes
	Limnonectes sp 1.	Yes	
	Limnonectes sp 2.		Yes
Megophryidae	*Xenophrys ancrae* †	Yes	Yes
Microhylidae	*Microhyla eos* †	Yes	Yes
Ranidae	*Amolops marmoratus*	Yes	Yes
	Amolops adicola		Yes
	Hylarana leptoglossa	Yes	Yes
	Nidirana noadihing†	Yes	Yes
	Odorrana livida		Yes

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Rhacophoridae	*Gracixalus patkaiensis*†	Yes	Yes
	Kurixalus naso	Yes	Yes
	Nasutixalus sp.	Yes	
	Polypedates himalayensis	Yes	Yes
	Raorchestes sp 1.‡	Yes	
	Raorchestes sp 2.‡	Yes	Yes
	Raorchestes sp 3.‡	Yes	Yes
	Rhacophorus namdaphaensis†	Yes	Yes
	Rhacophorus bipunctatus	Yes	Yes
	Feihyla shyamrupus†	Yes	Yes
	Zhangixalus smaragdinus	Yes	

† *species endemic to India.*
‡ *cryptic species.*

Figure 1 Map showing the sampled locations in the study area (Namdapha Tiger Reserve), which lies within the Indo-Burma global biodiversity hotspot.

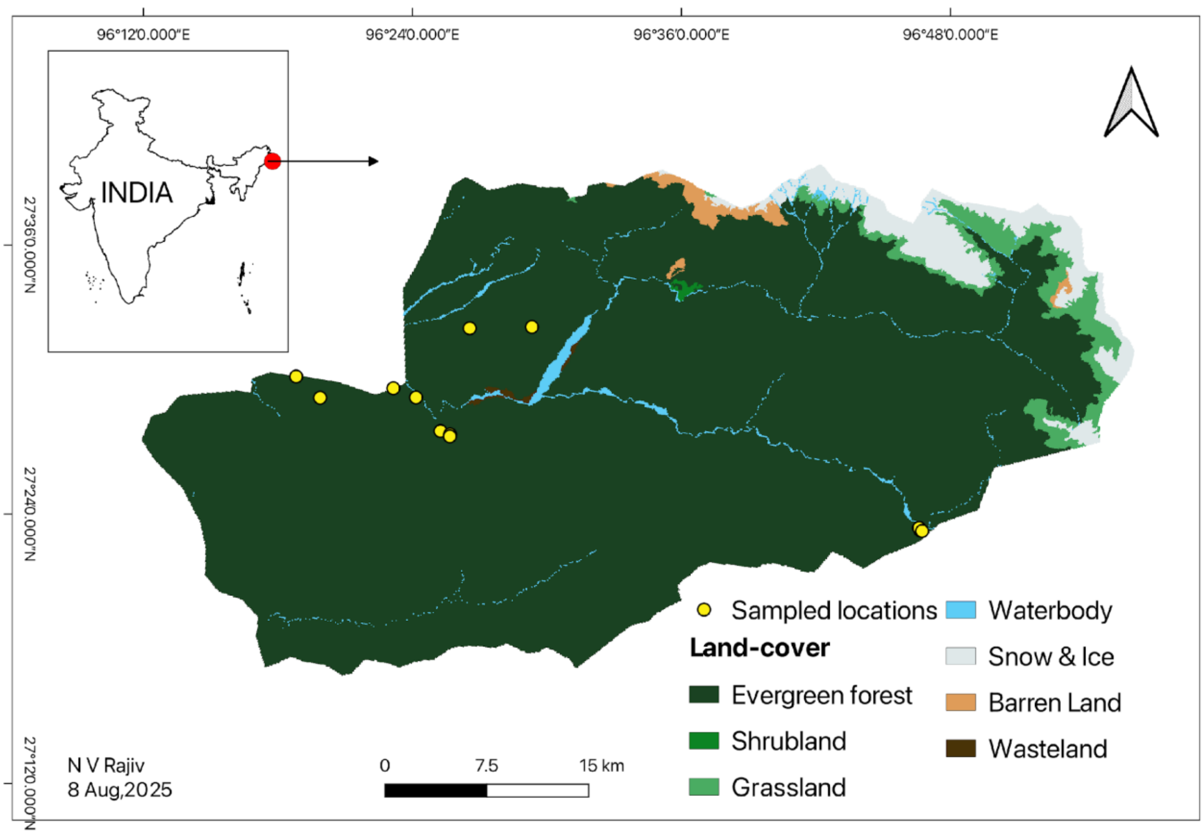

Figure 2 Endemic species detected during the survey. **top** (left to right) *Alcalus fontinalis*, *Feihyla shyamrupus*, and *Gracixalus patkaiensis*; **bottom** (left to right) *Xenophrys ancrae*, *Microhyla eos*, and *Nidirana noadihing*. Images by Abhijit Das.

Figure 3 Observed anuran species richness (circles) with 95% confidence intervals (horizontal bars) obtained from passive acoustic monitoring (PAM) only, visual encounter survey (VES) only, and mixed method (PAM+VES).

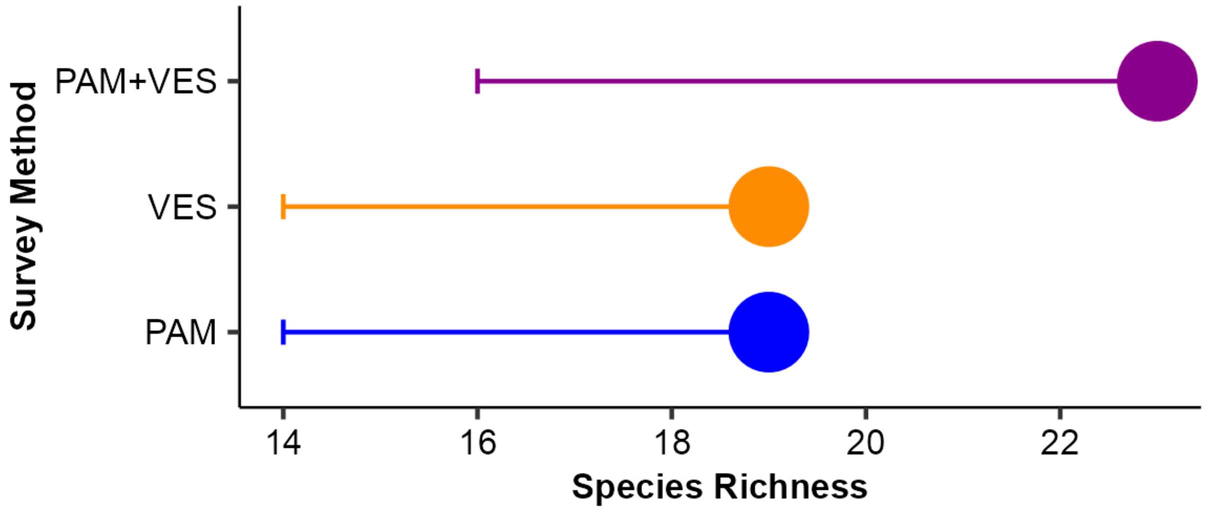

Figure 4: Number of anuran species detected in PAM and VES based on ecological traits. **Top** vertically stratified habitat; **Bottom-left** body size (snout vent length: small <= 30 mm, medium = 31–60 mm, large > 60 mm); **Bottom-right** dominant call frequency (low < 2 kHz, Mid = 2–4.5 kHz, High > 4.5 kHz). The error bars indicate 95% confidence interval calculated from species accumulation curves using iNEXT package (Hsieh et al. 2016).

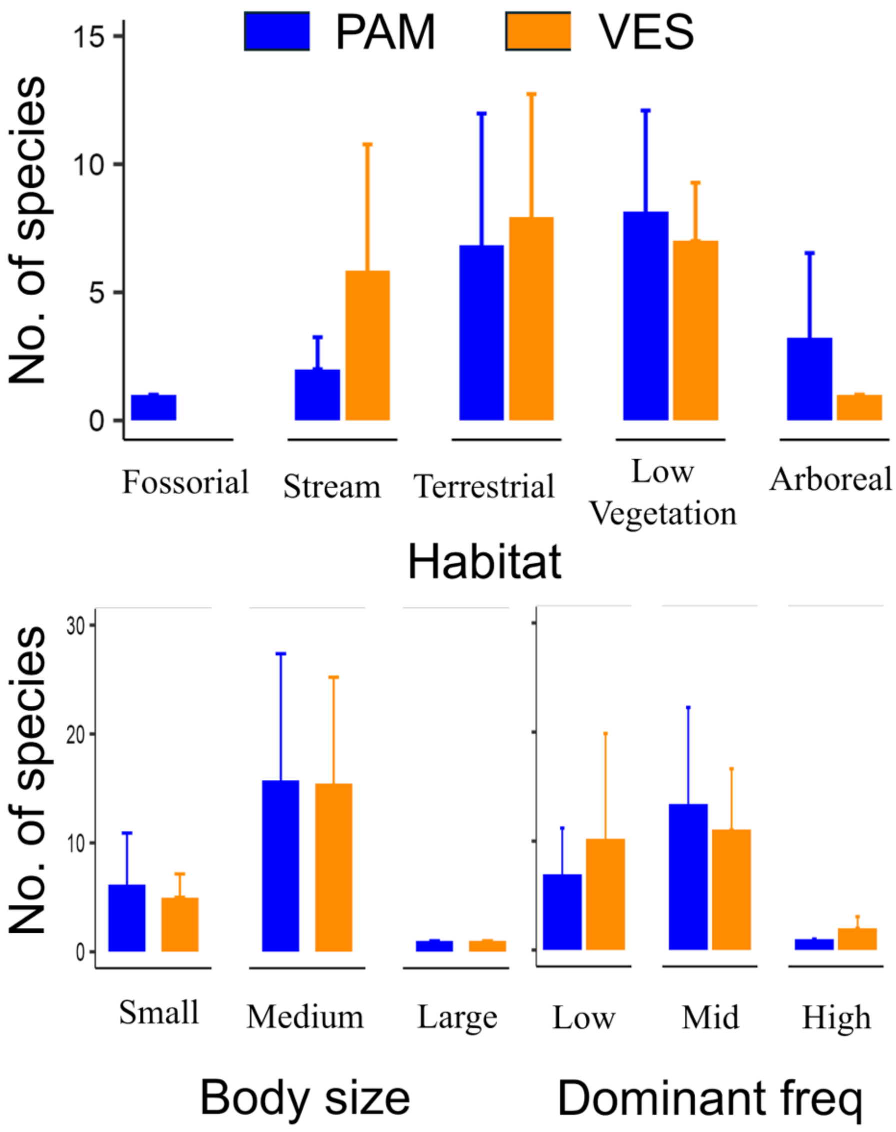

Figure 5 Species accumulation curve of species richness with number of sampled sites as effort for PAM-only, VES-only and PAM+VES methods. The shaded area around the curves represent the 95% confidence intervals.