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Anuran diversity and community structure in a flooded forest along the middle Juruá River

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Abstract

The Amazon rainforest hosts one of the most diverse anuran assemblages in the world. Despite this there is a severe lack of knowledge on the diversity and composition of anurans across key habitats in the western Brazilian Amazon. This study focused on anuran diversity and community structure in a seasonally flooded forest along the middle Juruá River. Previous studies and inventories on anurans along the river have focused on the upper and lower courses with no studies along the middle section. The study was conducted in a field site along an oxbow lake located 44 kilometers north of the town of Carauari, during the low-water season. Sampling methods were non-lethal using pitfall traps, time-constrained surveys, and accidental encounters. The different capture methods used targeted different species of anurans. In total 243 anurans representing 27 species from 7 different families were registered and identified using external morphology. The relatively high species richness from the rapid survey highlights the anuran diversity in the study area. Furthermore, the spatial distribution of anurans within the study area also reveals heterogeneity in species composition within flooded forests. A comparison of the captured biodiversity with other studies and inventories along the Juruá River and other flooded forests along neighboring rivers offers insight into the biodiversity patterns in the region. This study has also contributed to range extensions of two rarely encountered species and improved the resolution of the distribution of other cryptic species. Additionally, this study discusses the possible drivers of the observed species composition differences and the implications of anthropogenic activity and climate change on the anuran assemblage in the flooded forests of the region.

Keywords: Anuran diversity; Amazonia; Juruá River; Biodiversity; Ecosystem health; Climate change

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List of Abbreviations

PT Pitfall Trap

TCS Time Constrained Survey

AE Accidental Encounter

T(x) Ttrail X=number

TS(x) TranSect x=number

S(x) Stream x=number

Introduction

Tropical rainforests are the most species-rich terrestrial ecosystems on earth (Jablonski et al., 2006; Johnson, 2023). The Amazon rainforest in South America is the largest, containing 6.7 million km² of forest and 1,000,000 km² of freshwater ecosystems, containing approximately one-tenth of the world's known species, including the highest density of amphibians on earth (Charity et al., 2016; Moraes et al., 2021). Most of this is located within the Brazilian Amazon (Burgueño Salas, 2024).

Brazil is home to 1257 known species of amphibians. Of these, 1207 are anurans (frogs and toads) (Frost, 2024), 383 of which are currently found in the Brazilian Amazon (Hoogmoed & Galatti, 2023). This number is increasing (Charity et al., 2016; Moraes et al., 2021), partly due to the use of molecular data that has helped reveal taxonomic boundaries and through increased sampling efforts across the basin (Caminer & Ron, 2020; Fouquet et al., 2007; e.g. Fouquet et al., 2013, 2021, 2022a; Gonçalves Corrêa et al., 2023; Jungfer et al., 2013; Meza-Joya et al., 2019; Rivadeneira et al., 2018). The substantial increase in knowledge of Amazonian anurans in recent years stems from our relatively poor understanding of anuran communities across Amazonia, this underlines the importance of increased sampling efforts to improve our understanding of species richness and assemblage structure (Moraes et al., 2022). Understanding the species assemblage structure and composition is important to understand and ultimately protect the incredible anuran diversity of the Amazon and the important ecosystem services they provide (Leitão et al., 2016).

Amphibians have important ecological functional roles such as nutrient cycling, bioturbation in freshwater ecosystems, pollination, and seed dispersal, and are important predators and prey items (Cortéz-Gómez et al., 2015). They can also play an important role for human communities that rely on the ecosystems amphibians inhabit. For example, they directly benefit humans through their usefulness in medicine and as an important food source (Hocking & Babbitt, 2014). Additionally, they have proven to be an important pest control for crops and a biological control agent for insects that potentially carry diseases that are harmful to humans (Bowatte et al., 2013; Khatiwada et al., 2016). Amphibians are also useful indicators of ecosystem health. Due to their sensitivity to changes in the environment, this may be a useful tool to monitor the integrity of the ecosystems they inhabit (Welsh Jr & Ollivier, 1998). Amphibians are ectotherms which means that surrounding temperatures dictate their body temperature. Combined with their permeable skin this makes them highly vulnerable to changes in their surrounding habitat (Sales et al., 2017).

Worryingly, the Amazon rainforest harbors the highest number of endangered amphibian species on earth (Moraes et al., 2021), a trend that is likely to worsen in the future due to anthropogenic activities (Fearnside, 2017; Lawler et al., 2010). The biggest land use threats in the Amazon

forest and watershed are cattle ranching, infrastructural development and extractive activities such as mining (Fearnside, 2017; Timpe & Kaplan, 2017). In addition to land use changes, future climate scenarios predict longer and more severe droughts and floods in the Amazon (Barichivich et al., 2018; Marengo et al., 2018). The combined impact of the land-use threats and climate change can have devastating impacts on the distribution of anurans, especially in the central and western Amazon (Silva et al., 2018). Nonetheless, retaining habitats that are diverse in microhabitats may help alleviate the pressure of increased temperatures and other extreme climatic events (González-del-Pliego et al., 2020; Scheffers et al., 2014).

Accurate up-to-date information on the distribution, abundance, and diversity of anurans across various ecosystems within the Amazon is key to creating effective conservation plans, especially due to the narrow ranges of many species (Azevedo-Ramos & Galatti, 2002; Lawler et al., 2010; Verdade et al., 2012). It is therefore crucial to gain more information on the anuran assemblage and composition structures in the different ecosystems of western Amazonia (Pantoja & De Fraga, 2012), one of the least sampled regions for anurans in the Amazon (Moraes et al., 2022).

The Amazon can, roughly, be divided into unflooded (terra firme) forests that lie above the maximum flood lines of lakes, rivers, and streams and seasonally flooded forests (Junk, 1997). The two forest types are characterized by different hydrological patterns, light gaps, and associated successional stages (Campbell et al., 1986). In the central Amazon, 17% of the forests are wetlands and 70% of these wetlands are seasonally flooded (Hess et al., 2003).

One of the main types of seasonally flooded forests is the várzea (Junk, Piedade, Schöngart, et al., 2011). Várzea forests are flooded for large portions of the year by white-water rivers (the Juruá, Japurá, Purus, Madeira and main Amazon rivers) which carry large amounts of nutrient-rich sediments from the Andes (Junk, Piedade, Wittmann, et al., 2011). The nutrient-rich sediments are deposited on the low-elevation floodplains during seasonal flooding events, and the high nutrient input and hydrological regimes play important roles in the species composition of both flora and fauna (Assis et al., 2015; Bredin et al., 2020; Haugaasen & Peres, 2005b; Haugaasen & Peres, 2006; Junk, Piedade, Wittmann, et al., 2011). Due to the high reliance on water for amphibians, these differences in hydrological regimes, nutrient input, and consequent differences in forest characteristics can play an important role in amphibian biodiversity patterns across the Amazon (Pantoja & De Fraga, 2012), as it has for other vertebrate taxa (Haugaasen & Peres, 2005b, 2005a).

The Juruá River is a white-water river in the western Brazilian Amazon. There have been very few studies conducted on anurans along the Juruá River. The handful of studies that have been conducted were either in the lower or upper stretches of the river (Gascon, 1996; Moraes et al., 2022; Pantoja & De Fraga, 2012). There are currently no published papers on anurans in the middle portion of the river.

In this thesis, I examine the species composition and assemblage structure of anurans in a várzea forest in the middle Juruá River. The objective of this research is to (1) identify which species of anurans are present in the várzea flooded forests in the region along with their abundance; (2) analyze whether the anuran compositional structure differs throughout the study area in

total and between different capture methods. This is due to the impact of flooding on forest composition, and the importance of hydrology and microhabitats for anurans (González-del-Pliego et al., 2020; Moraes et al., 2021; Prance, 1979). I predict that the species richness will be high and comparable to other studies in várzea forests along the Rio Juruá (Moraes et al., 2022; Pantoja & De Fraga, 2012). Additionally, I predict that the species compositional structure will differ throughout the study area and that it will differ between capture methods. Due to differences in habitat requirements and that different capture methods target different assemblages.

Materials and methods

2.1 Study Area

Fieldwork took place in the western Brazilian Amazon along the middle portion of the Rio Juruá (44 kilometers downstream from Carauari) (Figure 2.1) from the 23rd of September to the 21st October 2023. The study area was next to an oxbow lake which was formed by a bend in the river being cut off from the main river over time (4°32'33.8"S 66°38'56.3"W)(Constantine & Dunne, 2008). Fieldwork was conducted during the low water season. In the high-water season, these várzea forests are flooded by the white water from the Juruá River. The area has an average annual temperature is 24°C, receives approximately 2500mm of precipitation, and has >90% humidity for most of the year (de Vasconcelos et al., 2022).

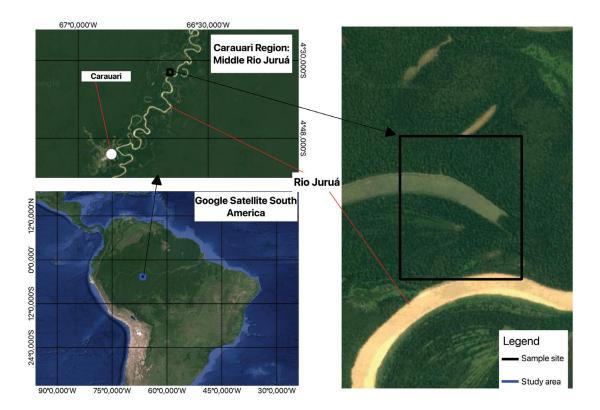


Figure 2.1: The study area is located in the western Brazilian Amazon north of the town of Carauari. Centered around an oxbow lake in the floodplains of the Juruá River.

The floodplains of the Juruá River are inundated approximately 6 months of the year (Assis et al., 2015). The non-flooded period lasts from July to December and the hottest period of the year is from August to November (Hawes & Peres, 2016). The study period was conducted in

2.2. Data collection 5

the hottest season during an abnormally hot and dry year (Espinoza et al., 2024). The study area had an elevation difference of approximately 20 meters from the lowest to the highest point (55-78m a.s.l)(data from Garmin eTREX 32x). The forest had a denser shrub layer on the side of the oxbow lake that was furthest away from the river than on the near side of the lake shown in (Figure 2.2).



Figure 2.2: The study site was around an oxbow lake (panel a). Panel b shows a photo of the typical forest structure on the southern (near) side of the oxbow lake, while panel c was taken on the northern (far) side.

2.2 Data collection

Three transects were set up within the study area, two on the southern side of the oxbow lake and the last on the opposite bank. The two transects on the southern side were spaced 1km from each other with a heading away from the oxbow lake while the last transect was placed on the opposite bank of the oxbow lake with a heading moving away from the streams and lake. In addition to the three transects I also had access trails 1 and 2 to access transects 1 and 3 on the southern side of the oxbow lake (Figure 2.3). The final transect was on the northern side of the oxbow lake and was accessed by boat (Figure 2.3). There were also two streams located at the start of transect 1 and transect 2.

2.2.1 Pitfall traps

Each of the transects had three pitfall trap arrays placed at 0, 250, and 500 meters (Figure 2.3). In total, there were 9 pitfall trap arrays with a total of 36 buckets used. The pitfall trap setup was a "Y" shaped array with 60-liter buckets buried at the intersect and at the ends of the 3 array arms (Figure 2.4a). A drift fence was erected between the buckets using a black plastic sheet with a height of 40 to 50cm to block the path of terrestrial anurans (Figure 2.4b) (Fisher et al., 2008). The buckets were placed approximately 3-4 meters apart. The anurans that encountered the trap array were led along the drift fence until they fell into one of the buckets. Bucket lids were placed on sticks above the buckets to help reduce the amount of sunlight and rain in the traps (Figure 2.4b). This step is important to help minimize the mortality rates of captured individuals (Fisher et al., 2008; Moraes et al., 2022; Sales et al., 2017). To ensure that

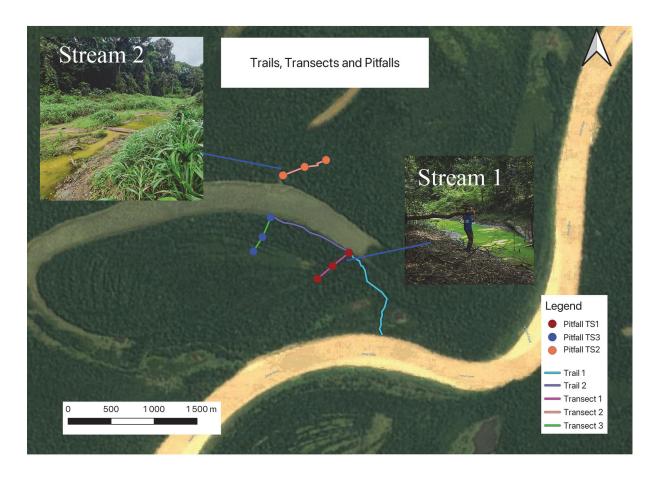


Figure 2.3: The location of the trails, transects, pitfall trap arrays, and the two streams in the study area. Pitfall TS(x), x denotes the corresponding transect number.

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the buckets stayed in the ground, 10-12 holes were drilled in the bottom of each bucket. This equalized any water pressure between the inside and outside of the bucket. Bamboo pieces were placed inside each bucket to allow trapped animals to float in case a trap became flooded.

In total, the traps were open for 12 sampling days with traps 2 and 3 being open from the 29th September-11th October 2023. Transect 1 was open from 30th September to the 12th of October 2023. The pitfall traps were all checked daily.



Figure 2.4: The shape of the (a) pitfall trap arrays and (b) the bucket lids were placed on top of the traps and drift fence.

2.2.2 Time-constrained surveys

Time-constrained surveys (TCSs) were conducted along each trail and transect at night. A TCS limits the sampling by time and is a commonly used survey method for herpetofauna (Guilfoyle, 2010). TCSs implemented in this study lasted for 1 hour, where 5-7 surveyors walked together at a slow pace scanning the vegetation and ground for anurans. All individuals within reach of one of the surveyors were collected. In total, seven one-hour TCSs were performed, covering all transects, trails and stream 1. Only TCSs on the transects were used for the species composition analysis and all TCSs were used for the anuran diversity analysis.

2.2.3 Accidental encounters

The trails and transects were all walked daily to check the traps. This allowed me to conduct daytime surveys, collecting the individuals found within a couple of meters of the trails and transects. These encounters were classified as accidental encounters (AE) because only anurans spotted from a normal walking pace were collected, not actively searching inside dead logs, trees, or other features. Anurans on the trail that sought refuge inside a log or under the leaf litter were searched for but no more than a couple of minutes were spent doing so in an attempt

to minimize sampling bias (Scott et al., 1994). Each transect was walked 12 times (back and forth). In total, this is equal to 35.4km of transects surveyed during the day. The anurans captured on the transects were used for further analysis because the effort was consistent on the transects. The anurans captured along trails 1 and 2 during the day were not used in the species composition analysis because the trails were often walked faster to get to the transects.

2.3 Morphological identification

No anurans were sacrificed in the current work. All individuals were captured using sterile plastic bags and handled using powderless nitrile gloves. These were replaced between each individual to reduce the risk of transmitting potentially harmful pathogens between individuals (AmphibiaWeb, 2009; Greer et al., 2009).

All captured individuals were photographed either in the field site or using a camera cube to get as much detail as possible. They were all weighed using Pesola scales to the nearest 10th for large and 100th of a gram for smaller individuals. The snout-to-vent length (SVL) was measured using a caliper ruler with a precision of 0.03mm. All anurans were measured to the nearest 100th millimeter. They were identified morphologically based on distinguishing features such as body patterns, coloration, and measurements using field guides, species inventories and studies in the western Amazon, and original taxonomic publications (Araujo-Vieira et al., 2020; Caminer & Ron, 2020; Ferrão et al., 2022; Fouquet et al., 2013, 2021; Jungfer et al., 2013; Lynch, 1989; Menin et al., 2006; Meza-Joya et al., 2019; Moraes et al., 2022; Pansonato et al., 2016; Pantoja & De Fraga, 2012; Rivadeneira et al., 2018; Seger et al., 2021; Villacampa et al., 2017). Additionally, I used observations from iNaturalist and consulted experts to help confirm and improve my identifications (A. Fouquet, personal communication, January 2, 2024; L. J. C. de L. Moraes, personal communication, January 11, 2024).

Some species are morphologically cryptic making it difficult to get a confident identification solely based on photographs (Araujo-Vieira et al., 2020). For other species, the morphological characteristics that identify them are not visible until they are fully developed (A. Fouquet, personal communication, January 2, 2024; Villacampa et al., 2017). In both cases, the specimen was identified to the nearest species complex or clade. All anurans were identified based on the taxonomic arrangements from Frost (2024).

2.4 Statistical Methods

2.4.1 Capture rates

The Kruskal-Wallis test was used to assess potential differences in capture rates between transects and survey methods (Lomuscio, 2021). This allowed me to assess whether pitfall traps, time-constrained surveys, or accidental encounters were more effective on some transects compared to others, or whether there was any difference in capture rates in total with all capture methods. Only the transects were used in this analysis because the capture methods were standardized.

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2.4.2 Measuring diversity and sample effort

Hill numbers were used to measure the diversity because they encompass three widely used diversity metrics; species richness (q=0), exponential Shannon diversity (q=1), and inverse Simpson diversity (q=2) (Table 2.1) (Chao et al., 2014). The three diversity metrics show the number of species within the assemblage (q=0), the number of common species (q=1), and the dominant species (q=2) (Hsieh et al., 2016). These results are then extrapolated with 95% confidence intervals using 200 bootstrap replications to model the expected number of species in the várzea forest (Colwell et al., 2012). Diversity accumulation curves were used to assess the completeness of the total sampling effort (Chao et al., 2020). The iNEXT package in R was used to create the accumulation curves for the three hill numbers and calculate the diversity metrics (Hsieh et al., 2016).

Table 2.1: The equations for the three Hill numbers.

Orders	Equations	
q = 0	$\sum_{k=1}^{m} E[f_k(m)]$	
q = 1	$exp[\textstyle\sum_{k=1}^m(-\frac{k}{m}log\frac{k}{m})*E[f_k(m)]]$	
q = 2	$\frac{1}{\sum_{k=1}^m (\frac{k}{m})^2 * E[f_k(m)]}$	

2.4.3 Species composition

To examine the variation in species composition between the transects and between capture methods, I used a non-metric multidimensional scaling (NMDS) ordination based on the Bray-Curtis dissimilarity index (Bray & Curtis (1957)). Bray-Curtis dissimilarity index species composition dissimilarities (Bray & Curtis, 1957; Chao et al., 2006). More similar communities are placed closer together in the ordination plot and less similar communities are further apart (Legendre & Legendre, 2012). The metaNMDS function from the vegan package in R was used to perform the NMDS (Oksanen, 2022).

Permutational Multivariate Analysis of Variance (PERMANOVA) was used to test whether there was a significant difference in species composition between the capture methods and transects (Anderson, 2017). PERMANOVA is a non-parametric multivariate test of difference in species composition among groups (Anderson, 2001). The adonis2 PERMANOVA function was used with 10,000 permutations for each test (Bakker, 2024; Oksanen, 2022). A PERMDISP test using the betadisper function was used as a post-hoc test for the PERMANOVA to test whether differences in dispersion between groups affected the PERMANOVA test (Anderson, 2006; Simpson, n.d.). Both the betadisper and adonis2 functions are from the vegan package in R (Oksanen, 2022).

The Similarity Percentage analysis SIMPER analysis was then used to identify the species that contributed the most to the differences in species composition between the three transects and

between the capture methods (Clarke, 1993). The analysis was conducted using the Bray-Curtis index (Bray & Curtis, 1957). The function returns pairwise comparisons between the capture methods and also for the transects. The five most influential species to dissimilarities were presented in order of average contribution to dissimilarities, along with their average abundance at each transect or using each capture method. The SIMPER function is from the vegan package in R (Oksanen, 2022).

The NMDS analysis of the entire assemblage using all capture methods was organized by capture date, where each date was a sampling unit. This allowed me to identify daily variations in species composition at each site and determine whether the anurans captured on each day were associated with a specific site. For the comparison between methods, the sites were sampling units grouped by capture method.

Results

In total 243 anurans were captured and identified representing 7 families, 14 genera, and 27 species. Hylidae was the most abundant (42.39%) and speciose (14 species), followed by Leptodactylidae (33.33%, 7 species), Bufonidae (16.46%, 2 species), Aromobatidae (6.17%, 1 species). The remaining families Dendrobatidae, Centrolenidae and Pipidae made up less than 1% of the total abundance each with one species from each family. A full species list is provided in the Appendix: Table A.1.

The highest number of amphibians were recorded during the time-constrained surveys (117), followed by pitfall traps (75), and accidental encounters (51). Most of the anurans captured during the time-constrained surveys were from the family Hylidae (72%). Leptodactylidae was the most common pitfall trap capture (52%) and the most commonly captured anurans from accidental encounters were from Leptodactylidae (37%) and Bufonidae (39%).

The most abundant species were Scinax gr. ruber (42) and Leptodactylus petersii (38) by a clear margin, followed by Rhinella castaneotica (27), Adenomera andreae (23), Boana geographica (21), Osteocephalus cf. leprieurii (16), Allobates sp. (15), R. marina (13), and B. cf. steinbachi (10). The remaining species were represented by less than 10 individuals each (Figure 3.1). Most of the captured individuals were adults except L. petersii where 27 of 38 captures were classified as juveniles. Specimens of all captured species are shown in Figure 3.2 - 3.7.

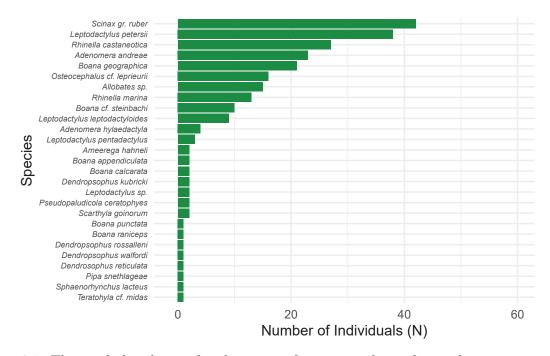


Figure 3.1: The total abundance of each species of anuran in descending order.



Figure 3.2: The species of Anurans found in the genus Boana; (a) Boana cf. steinbachi, (b) B. calcarata, (c) B. appendiculata, (d) B. geographica, (e) B. punctata, (f) B. raniceps. Photos: Joakim Vågen



Figure 3.3: The species of Dendropsophus, Scinax, and Scarthyla found in the study area (a) $Dendropsophus\ rossalleni$, (b) $D.\ kubricki$, (c) $D.\ walfordi$, (d) $D.\ reticulatus$, (e) $Scinax\ gr.\ ruber$, and (f) $Scarthyla\ goinorum$. Photos: Joakim Vågen

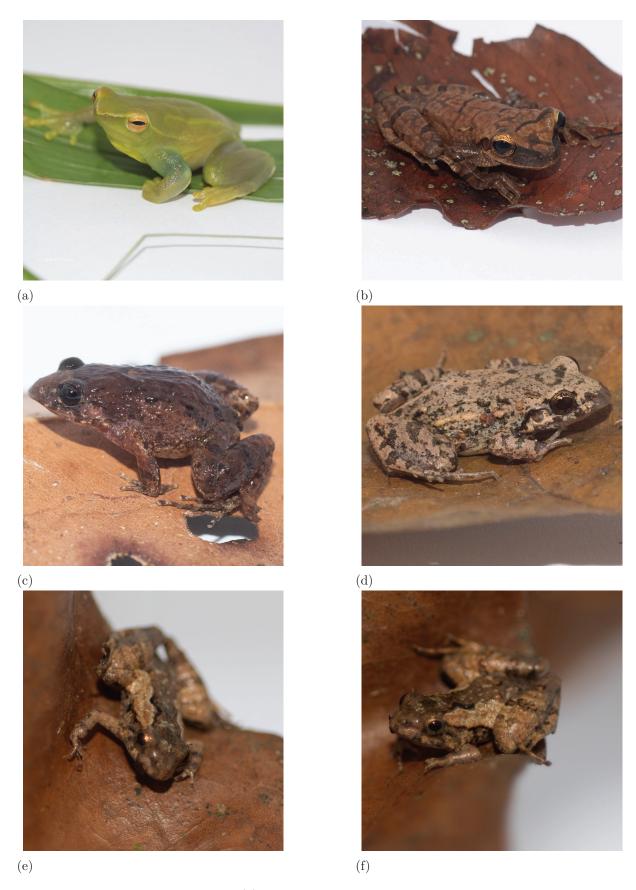


Figure 3.4: The only individual of (a) $Sphaenorhynchus\ lacteus$ found. One of the variations in appearance of (b) $Osteocephalus\ cf.\ leprieurii$. The two species of Adenomera found, (c) $A.\ adenomera$ and (d) $A.\ hylaedactyla$, and (e-f) $Pseudopaludicola\ ceratophyes$ highlighting the elongated tubercle above each eye that is key to identifying this species. Photos: Joakim Vågen



Figure 3.5: The dorsal and ventral patterns and distinguishing features of (a-b) Leptodactylus petersii and (c-d) L. leptodactyloides, (e) L. pentadactylus, and (f) Leptodactylus sp.. Photos: Joakim Vågen



Figure 3.6: Images (a-b) show the phenotypic variation of $Rhinella\ castaneotica$, more variations were found, (c) $R.\ marina$ in adult and (d) juvenile stages, and (e-f) $Allobates\ sp.$. Photos: Joakim Vågen

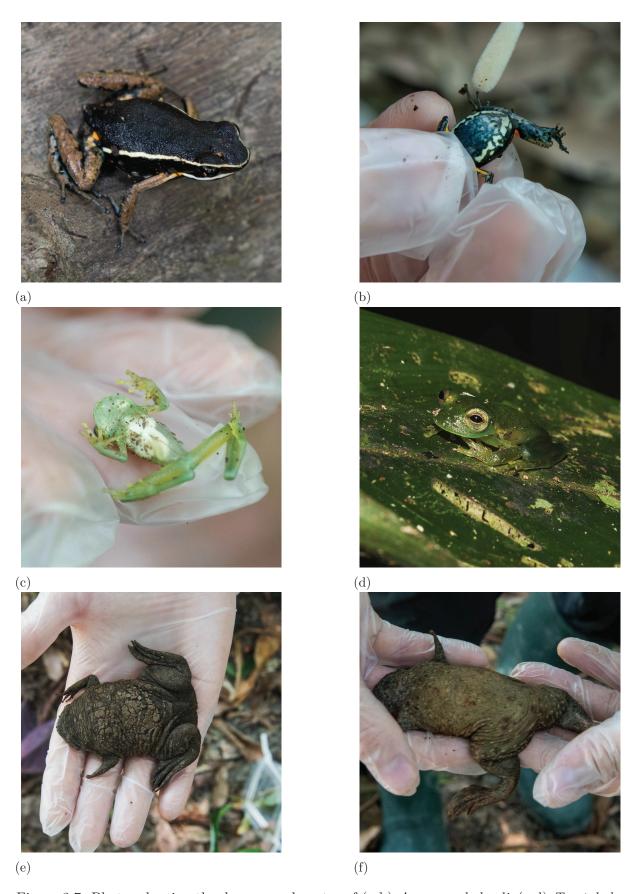


Figure 3.7: Photos showing the dorsum and venter of (a-b) *Ameerega hahneli*, (c-d) *Teratohyla cf. midas*, (e-f) *Pipa snethlageae*. Photos: Joakim Vågen

3.1 Anuran Diversity

The extrapolated species richness of the entire assemblage shows that the sampling effort was not enough to reach an asymptote for the species richness (q = 0) (Figure 3.8). The observed species richness shows 27 species recorded and with a minimum of 31.5 species in the study area indicated by the Chao1 estimator. The curve has reached an asymptote for the exponential Shannon index (q = 1) which indicates that the sampling effort was high enough to representatively capture the common species (13.64 species, asymptotic estimator = 14.64). The sampling effort was also high enough to reveal the dominant species within the study area, indicated by the inverse Simpson index (q = 2; 10.18 species, asymptotic estimator = 10.58) (Figure 3.8).

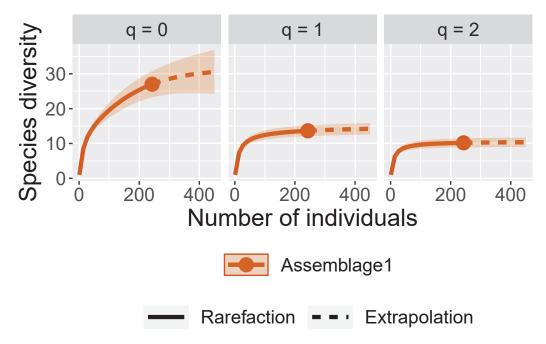


Figure 3.8: The Interpolated (solid lines) and extrapolated (dashed lines) species accumulation curves using Hill numbers (q = 0,1,2).

3.2 Capture Rates

There were no differences in overall capture rates between transects (Kruskal-Wallis Chi-Squared = 0.33, Df = 2, P-value = 0.85). Similarly, there were no differences in capture rates between transects for pitfall traps and accidental encounters (pit-fall traps: Kruskal-Wallis Chi-squared = 1.07, Df = 2, P-value = 0.58, accidental encounters: Kruskall-Wallis Chi-Squared = 0.33, Df = 2, P-value = 0.85), nor between any time-constrained survey sites (time-constrained surveys: Kruskal-Wallis Chi-Squared = 10.69, Df = 6, P-value = 0.098).

3.3 Species Composition

3.3.1 Species composition between transects

The NMDS ordination shows that species composition for each capture date (points) are clustered around each site (centroids) (Non-metric fit, $R^2 = 0.987$) (Figure 3.9). The day-to-day composition appears to be more spread from the average for two of the capture days on TS1. The same applies to TS2 and one capture day stands out on TS3. These differences in dispersion between the sites were not statistically significant (F = 2.6961, Df = 2, P = 0.085). The Adonis (PERMANOVA) analysis shows that the transect had a significant effect on the overall species composition (pseudo-F = 9.07, df = 2, P<0.01), explaining 39.3% of the variation.

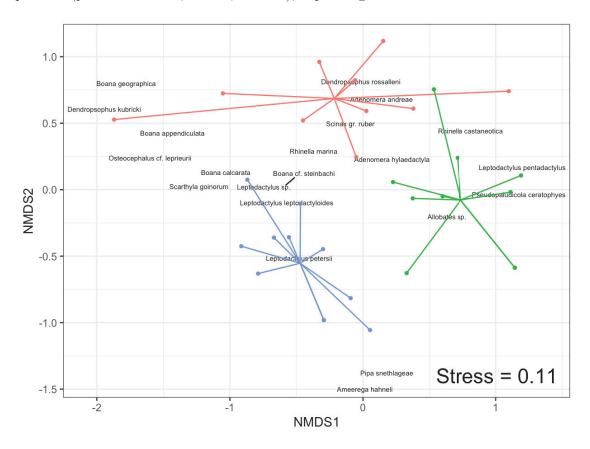


Figure 3.9: NMDS ordination plot of species captured at each of the three transects (Green = Transect 2; Red = Transect 2; Blue = Transect 3) using all three capture methods. Individual points represent sampling days. Species are overlaid and slightly adjusted to reduce overlap while still maintaining relative relationships.

The SIMPER analysis shows that *Allobates sp.* had a large contribution to the average dissimilarity between transect 2 and the two other transects because it was only found on transect 2. Similarly, *Leptodactylus petersii* had the largest contribution to the dissimilarities between transect 3 and the two other transects. Two other influential species were *Adenomera andreae* and *Boana geographica* both abundant on transect 1 (Table 3.1).

Table 3.1: The results from the SIMPER analysis showing the 5 species with the highest average contribution (Avg) to dissimilarities between each pair of transects (TS(1-3)). The columns ava and avb show the average abundance of the species in the pairs, a (left) and b (right) of the pairs in the header (example: first comparison TS1 = ava, TS2 = avb).

Species	Average Contribution (%)	SD	ava	avb
TS1 vs TS2				
$Adenomera\ and reae$	15.68	0.12	4.67	1.33
$Allobates\ sp.$	13.45	0.17	0.00	5.00
$Boana\ geographica$	11.46	0.15	2.67	0.00
$Rhinella\ castaneotica$	8.02	0.07	1.67	2.67
Osteocephalus cf. leprieurii	7.07	0.11	1.67	0.00
TS1 vs TS3				
$Leptodactylus\ petersii$	23.37	0.20	0.33	9.33
$Adenomera\ andreae$	13.60	0.10	4.67	0.33
$Boana\ geographica$	9.31	0.12	2.67	0.00
Osteocephalus cf. leprieurii	7.40	0.07	1.67	1.67
$Rhinella\ castaneotica$	5.47	0.05	1.67	0.00
TS2 vs TS3				
$Leptodactylus\ petersii$	26.85	0.24	0.67	9.33
$Allobates\ sp.$	13.69	0.17	5.00	0.00
$Rhinella\ castaneotica$	11.04	0.10	2.67	0.00
Osteocephalus cf. leprieurii	7.09	0.07	0.00	1.67
Boana cf. steinbachi	4.60	0.05	0.00	1.33

3.3.2 Species composition by capture method

The NMDS ordination shows that the anuran species sampled by pit-fall traps differed from those sampled via time-constrained surveys and accidental encounters (Figure 3.10). The species assemblage captured via pit-fall traps appears to be more consistent than for TCSs and accidental encounters, as the pit-fall samples are more clustered in the ordination diagram (Figure 3.10). TCSs were more variable and the abundance and the composition of species sampled from transect 2 was the most different compared to the other two transects. However, there was no statistically significant difference in dispersion between the capture methods (F = 1.53, Df = 2, P = 0.29). The Adonis (PERMANOVA) analysis revealed that the p-value fluctuated by 0.02 due to the different permutations of the data. This leads to a non-significant p-value in some cases, while in others it is significant. Due to this, I believe there is evidence to suggest that there is a difference in the species composition of anurans captured using the three capture methods (pseudo.- F = 1.6, Df = 2, P = 0.06). Despite the non-significant p-value, the capture method still explained 35% of the variation between the sites.

The SIMPER analysis shows that *Leptodactylus petersii* has the largest average contribution to differences in composition between accidental encounters and pitfall traps (AE vs PT) and for pitfall traps versus time-constrained surveys (PT vs TCS; Table 3.2). It was the most abundant species in the pitfall survey. For accidental encounters versus time-constrained surveys *Rhinella*

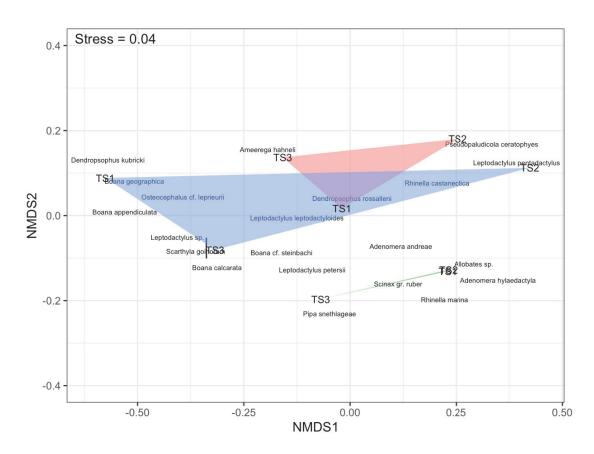


Figure 3.10: NMDS ordination plot using Bray-Curtis dissimilarities sorted by the three capture methods, pitfall traps (PT; green polygon), accidental encounters (AE; red polygon), and time-constrained surveys (TCS; blue polygon) from each of the three transects (TS(1-3)). The species scores are overlaid on the same axis with a slight adjustment to remove overlap.

castaneotica and Osteocephalus cf. leprieurii had the largest contributions (Table 3.2). The former was most abundant from accidental encounters, the latter was more commonly encountered during time-constrained surveys. Boana geographica was captured once through accidental encounters, the rest were through time-constrained surveys. Allobates sp. also contributed to a lot of the dissimilarity between pitfall traps and time-constrained surveys (PT vs TCS) and accidental encounters versus pitfall traps (AE vs PT) due to its abundance in the pitfall traps (Table 3.2). Adenomera andreae was commonly registered in pitfall traps and from accidental encounters, resulting in a high average contribution in all comparisons (Table 3.2).

Table 3.2: The results from the SIMPER analysis showing the 5 species with the highest average contribution (Avg) to dissimilarities between each pair of capture methods. The columns ava and avb show the average abundance of the species in the pairs, a (left) and b (right) of the pairwise header (example: first comparison AE = ava, PT = avb).

Species	Average Contribution (%)	SD	ava	avb
AE vs PT				
$Leptodactylus\ petersii$	20.71	0.26	1.33	8.00
$Allobates\ sp.$	14.20	0.21	0.00	4.67
$Adenomera\ andreae$	11.14	0.09	2.33	4.00
$Scinax\ gr.\ ruber$	9.07	0.05	0.00	3.00
$Rhinella\ marina$	7.15	0.06	0.00	2.33
AE vs TCS				
$Rhinella\ castaneotica$	13.28	0.11	2.67	0.33
Osteocephalus cf. leprieurii	12.49	0.08	0.33	3.00
$Adenomera\ and reae$	11.40	0.09	2.33	0.00
$Boana\ geographica$	10.88	0.14	0.33	2.33
$Leptodactylus\ petersii$	8.09	0.09	1.33	1.00
PT vs TCS				
$Leptodactylus\ petersii$	20.65	0.26	8.00	1.00
$Allobates\ sp.$	13.81	0.19	4.67	0.33
$Adenomera\ and reae$	11.79	0.12	4.00	0.00
Scinax gr. ruber	7.79	0.05	3.00	0.33
Osteocephalus cf. leprieurii	7.47	0.06	0.00	3.00

Discussion

4.1 The várzea forest anuran assemblage

Few studies have focused on anuran species richness and composition in the várzea forests of the western Brazilian Amazon. The number of species and abundance documented in this study surpasses the results from floodplain forests further upstream employing similar sampling methods (Pantoja & De Fraga, 2012). This may suggest a higher abundance and species richness in my study area. However, it is important to note that the two studies were conducted during different seasons (wet-dry transition and dry-wet transition during my study). This may influence the detectability of some species, due to differences in reproductive and general activity levels (Menin et al., 2008; Neckel-Oliveira et al., 2013; Villa et al., 2019). For example, Gonçalves Corrêa et al. (2023) found a higher abundance of anurans representing more species during the months with low rainfall such as (September-November) which is the same period as my study.

The species accumulation curve for species richness (q=0) suggests that additional species are likely to be registered in the study area with increased effort (Figure 3.8). However, my rapid survey still captured 69% of the species richness documented in flooded forests from a long-term monitoring protocol in the lower Juruá River (Moraes et al., 2022). Both the q=1 (exponential Shannon) and q=2 (inverse Simpson) accumulation curves from this study indicate that the composition of common and dominant species was captured (Figure 3.8). Further studies on the anuran assemblage in the várzea forests in the middle Juruá should therefore mostly capture more rare species.

The most abundant and speciose families in this study were Hylidae (14 species) and Leptodactylidae (7 species), a consistent pattern across anuran inventories in the Amazon (Gonçalves Corrêa et al., 2023; Miranda et al., 2015; Moraes et al., 2022; Pantoja & De Fraga, 2012; Taucce et al., 2022). Scinax gr. ruber is one of the most widespread hylids in studies across the Amazon and was recorded both further upstream and downstream (Menin et al., 2006; Moraes et al., 2022; Pantoja & De Fraga, 2012). The other two common hylids in this study, Boana geographica and Osteocephalus cf. leprieurii were also abundant in other studies along the Juruá River, the former both upstream and downstream and the latter only downstream (Moraes et al., 2022; Pantoja & De Fraga, 2012).

The two most common leptodactylids in this study *Leptodactylus petersii* and *Adenomera andreae* both have a wide distribution across the Amazon (AmphibiaWeb, n.d.-b; Azevedo-Ramos & Galatti, 2002). Pantoja & De Fraga (2012) registered neither of them in várzea forests further upstream but Moraes et al. (2022) encountered both downstream. *Leptodactylus leptodactyloides* was not captured by any of the studies along the Juruá River (Gascon, 1996; Moraes et al., 2022; Pantoja & De Fraga, 2012). However, there have been punctual observations along

both the upper and lower stretches of the river (AmphibiaWeb, n.d.-a; iNaturalist, n.d.). *Pseudopaludicola ceratophyes* has only been documented once along the Juruá River (Gascon, 1996). Based on the current range (Pansonato et al., 2016), the individuals encountered in the current study were found approximately 300 kilometers downstream. This suggests a possible range extension downstream along the Juruá River.

Another novelty is *Pipa snethlageae*. This is one of two "macropipa", along with *Pipa pipa*, that have dispersed from western Amazonia eastward along the vast Amazonian waterways (Fouquet et al., 2022b; A. Fouquet, personal communication, January 2, 2024). The latter has been recorded in other studies along the Juruá River, in central Amazonia, and the eastern Amazon (Gonçalves Corrêa et al., 2023; Menin et al., 2006; Moraes et al., 2022; Pantoja & De Fraga, 2012). In contrast, *Pipa snethlageae* has not been recorded in those inventories nor have any punctual observations been registered south of the Amazon River (AmphibiaWeb, 2024; iNaturalist, n.d.). The species is expected to occur across the Amazon basin in flooded habitats (Fouquet et al., 2022b). Its presence in the study area is therefore expected (A. Fouquet, personal communication, January 2, 2024), but it is the first confirmation of its presence south of the Amazon River, at least to my knowledge.

Of the 7 families registered in this study, Centrolenidae was the only family not found in the other studies upstream and downstream along the Juruá River. The species of Centrolenidae captured in this study, *Teratohylas cf. midas* has been registered across various localities across the entire Amazon basin, indicating a pan-Amazonian distribution (Araújo et al., 2018). Along the Juruá it has been recorded approximately 800 kilometers upstream in the state of Acre (Araújo et al., 2018). This observation helps fill in a gap in its distribution across the Amazon. However, studies do suggest that there is a lot of hidden diversity within the species, indicating a species complex (Kok & Castroviejo-Fisher, 2008).

The only members of Bufonidae recorded in this study were *Rhinella marina* and *R. castaneotica*, both of which were widespread in the flooded forests in the Reserva Extrativista do Baixo Juruá (Moraes et al., 2022). Neither were recorded in flooded forests in the Reserva Extrativista do Rio Gregorio further upstream (Pantoja & De Fraga, 2012). These two species were among the most common species captured by Ramalho et al. (2016) along the várzea forests of the Purus River. Indicating that they are both typical of várzea forests.

The family Strabomatidae was not found during this survey, but members of the family were registered upstream in flooded forests (Pantoja & De Fraga, 2012). Moraes et al. (2022) also found one species from the family Strabomatidae further downstream.

4.2 Species composition

The NMDS ordination comparing capture methods shows that pit-fall traps, accidental encounters and time-constrained surveys largely sampled a different set of species, with the largest difference being between pitfall traps and the other two capture methods. However, some species

were sampled using more than one capture method (Table A.2, Table A.3). Most notably, *Leptodactylus petersii*, *Allobates sp.*, *Boana geographica*, *Adenomera andreae*, and *Rhinella cataneotica* were all consistently associated with specific transects, irrespective of the capture method.

These species largely drove the composition differences shown in the between-transect NMDS (Figure 3.9), highlighted in the accompanying SIMPER analysis (Table 3.1). Interestingly, Osteocephalus cf. leprieurii had a high contribution to the dissimilarity between transects 1 and 3, despite having an equal abundance on both transects (Table 3.1). This suggests a false dissimilarity in the SIMPER analysis related to high variance for this particular species (Szöcs & Oksanen, n.d.). However, the other species had more clear affiliations with specific transects. The species composition patterns between the transects may, partially, be driven by differences in reproductive timing and strategy, flood disturbance patterns, detectability, and trophic niche (Caldwell & Vitt, 1999; Gonçalves Corrêa et al., 2023; Hodl, 1990; Ramalho et al., 2018).

Reproductive timing played a large role in the effect Leptodactylus petersii had on the species composition (Table 3.1). Out of 38 L. petersii, 28 (74%) were found on transect 3 and 15 (40%) were captured in a single pitfall trap array. This high capture rate in a single pitfall trap array is explained by the fact that most (71%) of the individuals were juveniles. Only nine individuals were classed as adults (Oliveira-Souza et al., 2020). The juveniles were encountered predominantly in the wettest pitfall trap array, this is explicable by their aquatic larval development (Hodl, 1990). All the adults were found on transect 3, repeating the analysis without juveniles therefore still resulted in a strong association to transect 3 from this species. I therefore decided to keep the juveniles in the species composition analysis. However, sampling at a different time of year can impact the spatial patterns observed in this study due to the high abundance of juvenile L. petersii. Additionally, the presence of juveniles across the whole study area indicates that they are widespread and that the high number observed was by chance, due to the placement of the pitfall trap array.

Adenomera andreae was absent on the transects during the time-constrained surveys but was captured in pitfall traps and accidental encounters. This may have been facilitated by its diurnal activity which increased its detectability during daytime surveys (Caldwell & Vitt, 1999). It was the most common species on transect 1 and a couple of individuals were found on transect 2 and one on transect 3 (Table A.5). The genus Adenomera breeds terrestrially which may help explain its wide distribution even in drier parts of the study area (Hodl, 1990).

An interesting pattern was the dominance of the leaf litter species Allobates sp. on transect 2 and its complete absence in all other sites. This explains its high contribution in the SIMPER analysis between transect 2 and the other two transects. One explanation for this pattern is that transect 2 was connected to the continuous forests, with different flooding gradients inland, while the remaining sites were cut off from the rest of the forest by the oxbow lake, at least partially during the low water season. The pitfall trap arrays on transect 2 were all at higher elevations than the traps on transects 1 and 3 (73-78m asl and 60-71m asl, respectively). The forest structure on the far side of the oxbow lake (transect 2) from the river appeared to be denser than on the side closest to the river (Figure 2.2). This difference may be indicative of less

extensive flooding on the far side of the oxbow lake (de Assis & Wittmann, 2011). Differences in flooding influence potential refuge for leaf litter species, influencing their distribution on a local scale (Gascon, 1996; Ramalho et al., 2018).

Additionally, the oxbow lakes may create islands during the low water season, restricting dispersal and therefore recolonization of leaf litter species that are unable to persist through high frequencies and levels of flooding (MacArthur & Wilson, 2001; Ramalho et al., 2018). Ramalho et al. (2018) noted nested species composition on opposite sides of oxbow lakes where all species found on the side closest to the river were also found on the far side, but the far side had additional species that were possibly less tolerant to more frequent intense flooding. My pitfall traps captured this trend. All species captured in pitfall traps on transect 1 (closest to Juruá River) were captured on transect 2 (opposite side of the oxbow lake) except Allobates sp. (Table A.2).

The high abundances of *Allobates sp.* at single sites was also observed by Gascon (1996), where the individuals were isolated on a dry patch, surrounded by flooded forests during high water levels (in that study referred to as *Colostethus spp.*). *Pseudopaludicola ceratophyes* was another leaf litter species that was only found on transect 2, although only two individuals were found. Contrarily, the leaf litter species *Ameerega hahneli* was only captured on the side of the oxbow lake closest to the main river. Additionally, the leaf litter species *Rhinella castaneotica* was found on both sides. Their presence can be explained by both species' ability to perch and climb floating debris and vegetation to escape predation and floods (Costa-Campos & Pedroso-Santos, 2022; Montanarin, 2016).

Boana geographica was only found on transect 1 from both accidental encounters and time-constrained surveys. Two individuals were mature, the rest were black on the hidden parts of the flanks, indicating that they were reproductively immature (A. Fouquet, personal communication, January 2, 2024; Villacampa et al., 2017). Despite this, their size resembled mature individuals, suggesting they were not recent hatchlings. Interestingly, tadpoles make up an important part of this species' diet (Sant'Anna et al., 2022). It has been observed occupying shrubs surrounding water bodies and actively foraging for tadpoles in the water, Sant'Anna et al. (2022) suggests that this may be linked to its preference for tadpoles as a main dietary component. Its abundance on transect 1, which ran parallel to one of the only remaining wet areas supports this, especially since I observed tadpoles in stream 1.

Interestingly, no hylids were captured during the time-constrained survey on transect 2 on the far side of the oxbow lake. Calls were heard and a few were spotted higher up in trees, but none were close enough to be captured or identified. One reason for this is that the forest was denser on that side of the oxbow lake, making it harder to spot frogs compared to the side closer to the river, where frogs were easily detectable on the more sparse vegetation at eye level. More time-constrained surveys would therefore be necessary to further understand the species composition patterns, especially for hylids.

4.3. Implications 27

4.3 Implications

The sampling took place during an El Niño event which resulted in record temperatures and droughts across the Amazon (Espinoza et al., 2024). This was evident in the study area with most temporary water bodies and muddy areas shrinking or drying completely. However, I did not observe any anuran mortalities and the anuran abundance was high throughout compared to the similar study conducted further upstream (Pantoja & De Fraga, 2012). Yet, the drought may have impacted anuran recruitment. Stream 1 almost completely dried out and eggs laid by Boana boans were laid here. Adult individuals of the species were not observed, but egg clusters are easily identifiable. The males dig circular depressions on the edge of water bodies, and the female deposits her eggs inside these nests (Barbosa et al., 2021). There were multiple nests built along the bank of stream 1 which all dried out with eggs inside during the study period. This highlights the potential impact of severe droughts on the recruitment of species that are reliant on water for reproduction, which applies to most species of anurans in lowland Amazonia (Hodl, 1990). So, despite the high number of recorded anurans, the drought was abnormal and could have impacted the activity levels and future recruitment. More studies should be conducted in climatically normal years to see how the drought may have affected these results.

Increasingly dry low-water seasons can increase distances between ponds (Walls et al., 2013), which is likely how the fully aquatic (Fouquet et al., 2022a) *Pipa snethlageae* ended up in a pitfall trap, trying to find a new pond after its previous pond likely dried out. Shrinking ponds and streams can also increase anuran egg and larvae predation by fish and invertebrates, further increasing the impacts of climatic stress (Neckel-Oliveira & Lannoo, 2007). More extreme climates with more droughts in várzea forests may therefore favor the species that breed in larger more permanent water bodies that are already adapted to egg and larvae predation (Babbitt & Tanner, 2012; Neckel-Oliveira & Lannoo, 2007). Another breeding strategy that may be favored is the opportunistic breeders, as they are more flexible to uncertainties in the timing of favorable climatic conditions (Ford & Scott Jr, n.d.; Marengo et al., 2016). Not all anurans in the Amazon are reliant on direct access to water for breeding such as the genus Adenomera, they produce terrestrial foam nests with larval development inside the nest (Hodl, 1990). The species that are therefore most vulnerable to future climate scenarios are likely the ones that are reliant on temporary waterbodies at specific times of year for reproduction (Babbitt & Tanner, 2012).

Additionally, disturbance through various land-use changes such as conversion to agricultural systems and pastures reduce the species richness and change the composition of anurans (Correa et al., 2015). However, this effect varies depending on the specific agricultural type and habitat matrix (Díaz-Ricaurte et al., 2022). This highlights the need to retain forests that are diverse in microhabitats to minimize the worst effects of climate-induced stress as well as buffer the impacts of land-use changes (González-del-Pliego et al., 2020; Perfecto & Vandermeer, 2008). This also shows the importance of understanding what species are present in the forests as different species will have different life history strategies, habitat requirements, and specializations (Hodl, 1990; Neckel-Oliveira & Lannoo, 2007). Improving knowledge on anuran assemblages and their ecological correlates in different ecosystems across the Amazon can help understand how

future climate scenarios will impact anuran communities as well as help create more informed conservation initiatives (Loyola et al., 2008).

Conclusion

The current study registered a large portion of the species richness and the typical anuran assemblage in the várzea forests of the Juruá River, underlining the importance of rapid biodiversity surveys in new and remote locations across the Amazon basin. This study also revealed heterogeneity in anuran species composition in the study area driven by access to water, reproductive timing and strategy, trophic niche, and possibly through disturbance in the form of flood frequency and intensity. Lastly, this study might have contributed to the range extension of two rarely captured species in western Brazilian Amazonia: *Pseudopaludicola ceratophyes* and *Pipa snethlageae*.

The results presented here show the importance of rapid biodiversity surveys in new and remote locations across the Amazon basin, as they adequately capture typical species and even some rare ones. Future sampling should strive to increase the number of time-constrained surveys on transects, as these were most efficient. However, pit-fall traps captured a very different anuran assemblage and therefore both survey methods should be employed to maximize detection efficiency. Furthermore, I suggest that future sampling of várzea forests should equally sample both sides of oxbow lakes and small elevational differences. This is to further investigate the role of oxbow lakes as dispersal barriers and the effect of flooding frequency at different elevations. Anurans serve as vital indicators of ecosystem health, a thorough understanding of their composition and diversity across várzea forests can provide insights into ecosystem dynamics over space and time. Given the looming threats of climate and land use change, the need for increased sampling efforts cannot be overstated.

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Appendix

Table A.1: All species of Anurans found in the study at different sites and capture methods.

Class: Amphibia				
Order: Anura	Capture location	Capture methods	N	
Family: Aromobatidae				
$Allobates\ sp.$	TS2	PT, TCS	15	
Family: Bufonidae				
$Rhinella\ castaneotica$	T1, TS2, TS1, T1.5	TCS, PT, AE	27	
Rhinella marina	T1, TS2, TS1, T1.5, TS3, T2, S1	TCS, AE, PT	13	
Family: Centrolenidae				
Teratohyla cf. midas	T1	AE		
Family: Dendrobatidae				
$Ameerega\ hahneli$	TS3, T1	AE	4	
Family: Hylidae				
$Boana\ appendiculata$	TS1, TS3	TCS		
Boana calcarata	TS3	TCS		
Boana cf. steinbachi	T1.5, TS3, TS1, S1	TCS, PT, AE	1	
$Boana\ geographica$	T1, T1.5, TS1, S1	TCS, AE	2	
Boana punctata	S2	TCS		
Boana raniceps	T1	AE		
Dendropsophus kubricki	TS1, T1	TCS, AE		
Dendropsophus rossalleni	TS1	AE		
Dendropsophus walfordi	T1	AE		
Dendrosophus reticulata	T1	AE		
Osteocephalus cf. leprieurii	T1, TS3, T1.5, TS1	TCS, AE	1	
Scarthyla goinorum	TS3	TCS		
Scinax gr. ruber	TS2, TS3, TS1, T1.5, T2, S1	PT, TCS	4	
Sphaenorhynchus lacteus	S2	TCS		
NA	TS2	TCS		
Family: Leptodactylidae				
Adenomera andreae	TS2, TS1, T1, T1.5, TS3, S1	PT, AE, TCS	2	
$Adenomera\ hylaedactyla$	TS2, TS1, T1.5, S1	PT, TCS		
$Leptodactylus\ leptodactyloides$	TS3, T1.5, TS1, S1	PT, TCS, AE		
Leptodactylus pentadactylus	S1, T1, TS2	AE, TCS		
Leptodactylus petersii	TS3, TS2, TS1, S1, T1.5	PT, AE, TCS	3	
Leptodactylus sp.	T1, TS3	AE, TCS		
Pseudopaludicola ceratophyes	TS2	AE, TCS		
Family: Pipidae				
Pipa snethlageae	TS3	PT		

Table A.2: The frequency of anurans captured per pitfall trap array. The first number indicates the transect number and the second number indicates the trap number 1-3, 1 is closest to the oxbow lake, 3 is furthest away.

	1-1	1-2	1-3	2-1	2-2	2-3	3-1	3-2	3-3
Adenomera andreae	2	2	5	2	1	0	0	0	0
$A denomera\ hylaedactyla$	0	1	0	1	0	0	0	0	0
$Allobates\ sp.$	0	0	0	9	0	5	0	0	0
Boana cf. steinbachi	0	0	0	0	0	0	0	0	1
$Leptodacty lus\ leptodacty loides$	0	0	0	0	0	0	0	0	1
$Leptodactylus\ petersii$	0	1	0	0	0	1	1	6	15
Pipa snethlageae	0	0	0	0	0	0	0	1	0
$Rhinella\ castaneotica$	2	0	0	1	0	1	0	0	0
Rhinella marina	0	4	1	0	1	0	0	1	0
Scinax gr. ruber	4	1	0	2	0	0	2	0	0

Table A.3: The frequency of anurans captured by time-constrained surveys on the transects.

	TS1	TS2	TS3
Allobates sp.	0	1	0
$Boana\ appendiculata$	1	0	1
Boana calcarata	0	0	2
Boana cf. steinbachi	0	0	3
$Boana\ geographica$	7	0	0
$Dendropsophus\ kubricki$	1	0	0
$Leptodactylus\ pentadactylus$	0	1	0
$Leptodactylus\ petersii$	0	0	3
$Leptodactylus\ sp.$	0	0	1
Osteocephalus cf. leprieurii	5	0	4
$Pseudopaludicola\ ceratophyes$	0	1	0
$Rhinella\ castaneotica$	0	1	0
$Scarthyla\ goinorum$	0	0	2
Scinax gr. ruber	0	0	1

Table A.4: The frequency of anurans accidentally encountered on the transects.

	TS1	TS2	TS3
Adenomera andreae	5	1	1
$Ameerega\ hahneli$	0	0	1
Boana cf. steinbachi	1	0	0
$Boana\ geographica$	1	0	0
$Dendrops ophus\ ross alleni$	1	0	0
$Leptodacty lus\ leptodacty loides$	1	0	1
$Leptodactylus\ petersii$	0	1	3
Osteocephalus cf. leprieurii	0	0	1
$Pseudopaludicola\ ceratophyes$	0	1	0
$Rhinella\ castaneotica$	3	5	0

Table A.5: The frequency of anurans captured on the transects using all capture methods.

	TS1	TS2	TS3
Adenomera andreae	14	4	1
$A denomera\ hylaedactyla$	1	1	0
$Allobates\ sp.$	0	15	0
$Ameerega\ hahneli$	0	0	1
$Boana\ appendiculata$	1	0	1
Boana calcarata	0	0	2
Boana cf. steinbachi	1	0	4
Boana geographica	8	0	0
$Dendropsophus\ kubricki$	1	0	0
$Dendrops ophus\ ross alleni$	1	0	0
$Leptodacty lus\ leptodacty loides$	1	0	2
$Leptodactylus\ pentadactylus$	0	1	0
$Leptodactylus\ petersii$	1	2	28
$Leptodactylus\ sp.$	0	0	1
Osteocephalus cf. leprieurii	5	0	5
Pipa snethlageae	0	0	1
$Pseudopaludicola\ ceratophyes$	0	2	0
$Rhinella\ castaneotica$	5	8	0
Rhinella marina	5	1	1
Scarthyla goinorum	0	0	2
Scinax gr. ruber	5	2	3

