
LARVAL ANURAN ASSEMBLAGES IN TROPICAL RAINFOREST STREAMS IN BORNEO

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Abstract.—We investigated the diversity and factors influencing species composition of larval anurans within rainforest streams of northeast Borneo. We sampled tadpoles at 50 riparian plots for a combined period of 10 mo and recorded 17 tadpole species representing six anuran families: Bufonidae, Dicroglossidae, Megophryidae, Microhylidae, Ranidae, and Rhacophoridae. Of the 15 habitat variables measured, we found that stream velocity, microhabitat width, and number of odonate larvae significantly influenced composition of the larval assemblage. Subsequently, we assigned larval anurans into five habitat guilds. This study provides the first quantitative data on the species organization of larval anurans in Borneo. This finding is both of ecological interest and of practical importance for future conservation and management of frogs in species rich tropical ecosystems.

Key Words.—Brunei Darussalam; community ecology; frogs; tadpoles

INTRODUCTION

Out of the multiple drivers of global amphibian declines, habitat destruction and fragmentation pose two major threats in Southeast Asia (Sodhi et al. 2004; Rowley et al. 2010). Amphibians are notably susceptible to habitat modification and fragmentation (McDiarmid and Altig 1999; Young et al. 2001; Stuart et al. 2004; Gallant et al. 2007) due to their complex life cycles (Delis et al. 1996, Vos and Stumpel 1996) and the fact that they are vulnerable to environmental variations both in aquatic and terrestrial ecosystems during development (Duellman and Trueb 1994; Vallan 2000; Borges-Júnior and Rocha 2013). Therefore, investigations on all amphibian life stages should be made top priority, particularly in tropical regions where assemblages are diminishing before insights on their ecological roles can be obtained (Haas and Das 2011).

The idea that the tadpole phase can be equally as vital as the adult phase specifically for the perpetual existence of an anuran species at a specific area and for general success and distribution is generally plausible (Haas and Das 2011). Additionally, larval anurans can have significant effects on ecosystem structure and function by shifting patterns of primary productivity, algal communities, and nutrient dynamics in various freshwater habitats (Kupferberg 1997; Flecker et al. 1999; Altig et al. 2007; Hocking and Babbitt 2014). In spite of their ecological importance, most studies concerning anuran community ecology have focused primarily on adults and their ecological requirements and interactions (e.g., Inger and Voris 1993; Eterovick 2003; Wells 2007; Ernst and Rödel 2008; Keller et al.

2009) and only a few included larval stages (e.g., Inger et al. 1986; Peltzer and Lajmanovich 2004; Borges-Júnior and Rocha 2013; de Almeida et al. 2015). Additionally, studies that examine the diversity patterns of tadpole communities themselves are lacking (Eterovick and Fernandes 2001; Eterovick and Barros 2003).

Factors affecting tropical tadpole assemblages particularly in streams have long been understudied (Wells 2007). Nonetheless, recent research in tropical streams found that a suite of environmental variables determines species richness of tadpoles to a varying extent (Parris and McCarthy 1999; Peltzer and Lajmanovich 2004; Eterovick and Barata 2006; Both et al. 2009; Strauß et al. 2010). Lotic aquatic habitats in the tropics may differ in their structural features including limnological characteristics such as conductivity, temperature, dissolved oxygen, pH (Rome et al. 1992; Peltzer and Lajmanovich 2004; Both et al. 2009), hydroperiod (Baber et al. 2004; Moreira et al. 2010), depth and size of rivers (Gascon 1991; Parris and McCarthy 1999; Eterovick and Barata 2006; Strauß et al. 2010), canopy openness (Halverson et al. 2003), and availability of temporary ponds (Rodrigues et al. 2010). Furthermore, biotic factors such as predation and competition may also influence larval assemblages to a varying degree depending on the hydroperiod of aquatic habitats (Heyer et al. 1975; Morin 1983; Hero et al. 2001). Previous studies have found that predators exert significant top-down regulation of larval assemblages by causing fatality among tadpoles (Woodward 1983; Werner and McPeck 1994; Wilbur 1997; Alford 1999; Grafe et al. 2004). In the Amazon rainforest, fishes posed a strong predation pressure on anurans leading

to the reduction in frog populations (Hero et al. 1998). Consequently, habitat selection by frogs was directly attributed to the distribution of fishes. On the other hand, the correlation between macroinvertebrate predators and tadpoles can either be positive (Babbitt 2005), negative (Werner and McPeck 1994), or show no association (Baber et al. 2004; Werner et al. 2007). Nonetheless, many researchers view fish as the principal predators of tadpoles in streams and other permanent habitats (Heyer et al. 1975; Azevedo-Ramos and Magnusson 1999; Hero et al. 2001) but invertebrate predators such as dragonfly larvae have a greater influence in ponds and temporary habitats (Azevedo-Ramos and Magnusson 1999).

Borneo counts more than 180 species of anurans whereby 130, or just over 70%, are endemics (Inger et al. 2017; Frogs of Borneo. The frogs of East Malaysia and their larval forms. Available from <http://www.frogsofborneo.org/> [Accessed 21 July 2019]); however, 51 of the frog species on the island remain with unknown larval stages (Haas and Das 2011). Furthermore, except for Inger et al. (1986), most studies on Bornean frog communities have paid more attention to the adult stages (e.g., Keller et al. 2009; Porter 2010; Ahmad Sah et al. 2019; Konopik et al. 2015; Goutte et al. 2017). Studies of larval anurans often limit their focus to descriptions of tadpoles for identification purposes and report the type of microhabitat where the tadpole can be found (e.g. Inger 1985; Haas and Das 2008; Haas et al. 2012; Haas et al. 2014; Oberhammer et al. 2015).

Published information on factors that determine tadpole assemblages on Borneo is non-existent. Such knowledge will unequivocally enhance our current understanding of the habitat characteristics responsible for shaping frog species diversity in tropical forests (de Almeida et al. 2015) particularly in Bornean rainforests. Our aim is to answer four questions. (1) How high is the species richness and abundance of tadpoles in rocky, rainforest streams? (2) Which factors affect the structure and distribution of tadpoles? (3) Is there a correlation between the presence of tadpoles and predators in a microhabitat? (4) Does the morphology of larval anurans influence their habitat selection?

MATERIALS AND METHODS

Study sites.—The study took place within the Ulu Temburong National Park and its buffer zone in Brunei Darussalam within the periods of February to March 2014 and September 2014 to May 2015 (Fig. 1). Pristine lowland mixed-dipterocarp forest predominantly covers the 50,000-ha national park with patches of submontane forests existing at higher elevations. The terrain is generally rugged with the presence of numerous medium to small-sized streams that flow into the larger Belalong and Temburong rivers. Air temperature during the study

periods ranged from 24.2–26.5° C and relative humidity ranged from 93.3–100%. We selected 10 independent first and second-order streams ranging from 2.28–7.81 m in average width. Within each stream, we established five 5 × 10 m plots at irregular intervals to encompass stream heterogeneity. Distance between neighboring plots was at least 20 m. We visited each plot seven times during the day typically between 0800–1700. We rotated visits between streams to control for seasonal variation. We visited each stream with 3–237 d between visits (mean = 29.9 ± 44.5 d [standard deviation]). We visited one stream only five times due to its dangerous conditions during floods. The average time to sample one plot/visit ranged from 11–73 min, depending on the number of tadpoles and macroinvertebrates encountered.

Sample collection.—At least two people sampled tadpoles by starting the plots from downstream to upstream. In each plot, one person (the netter) placed and held a modified net (1 × 1 m and 1.5 mm mesh size) with one end submerged into the bottom of the stream facing the water current. Another person (the kicker) stood about a meter in front of the net, kicking and disturbing the stream bed for one minute to dislodge tadpoles and macroinvertebrates from the substrates while approaching the net. We repeated this process until all the different microhabitats within each plot were sampled exhaustively. We sampled smaller microhabitats such as side pools and rock walls using a handheld dip net and streams varied in microhabitats (Fig. 2). We transferred specimens from nets into a tray, sorted from other macroinvertebrates, and counted them. For each tadpole captured, we measured its snout to tail length (STL) with a plastic Vernier caliper to the nearest 0.1 mm. Initially, we brought a few samples of each tadpole species back to the laboratory for photography and identification. We preserved the samples in 75% ethanol for future reference. Thereafter, we identified species in the field using morphological characters. We also noted presence of egg clutches and adult frogs. We counted fish and dragonfly larvae and measured them to account for the presence and abundance of tadpole predators. We returned all animals to their respective habitats.

On each visit, we measured air and water temperatures as well as relative humidity using a sling psychrometer. We measured maximum and minimum stream widths and depths at each plot with a meter tape. We recorded the widths and depths of each microhabitat (e.g., side pools, potholes, runs, and riffles) in which tadpoles were encountered. We measured current velocity with a JDC Flowatch flow meter (JDC Electronic SA, Waadt, Switzerland) within the middle of the water column of each microhabitat for each visit. We measured stream conductivity using a handheld conductivity meter (YSI Pro, Yellow Springs, Ohio, USA).

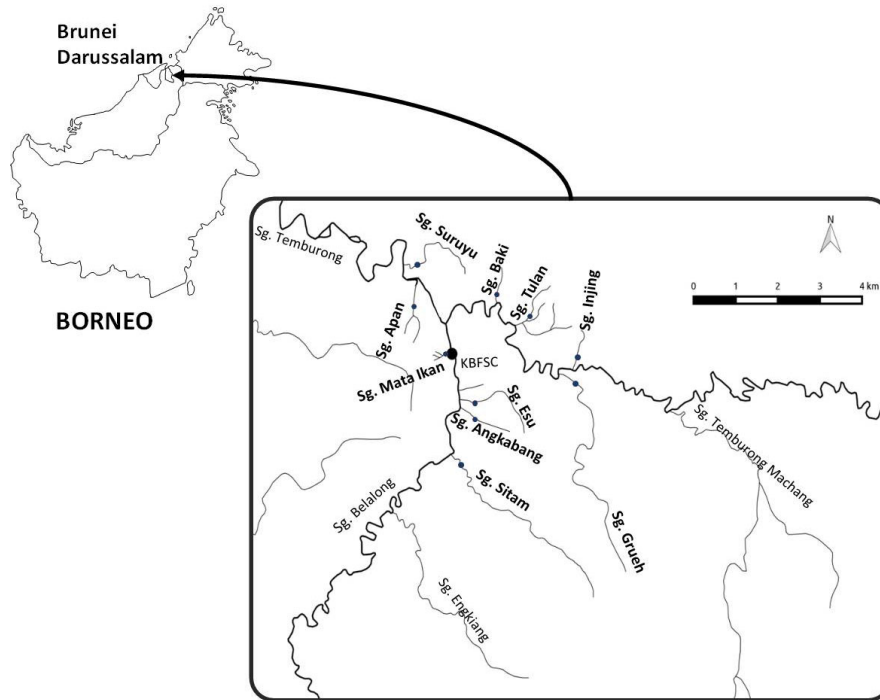


FIGURE 1. The location study areas in the Ulu Temburong National Park within Brunei Darussalam. Bold labels indicate study streams with the center of stream transects indicated by small dots. The large dot indicates the location of the Kuala Belalong Field Studies Centre (KBFS). Map redrawn with permission from the Institute of Biodiversity and Environmental Research, University Brunei Darussalam.

We quantified the density of riparian vegetation at each plot by counting each individual plant, which we categorized into one of the five strata; (1) height < 10 cm, (2) 11–100 cm, (3) 101–200 cm, (4) 201–300 cm, and (5) > 301 cm. We determined canopy cover at each plot using a spherical densiometer. To determine stream slope at each plot within a 10 m stream segment, we followed the protocol in LaPerriere and Martin (1986). We took these parameters only once throughout the study period.

Statistical analyses.—Because we did not mark tadpoles individually, we conservatively estimated tadpole abundance from the maximum number of individuals of each species captured on a single survey in each stream. Because we sampled tadpoles by replacing them after each survey, counting all the tadpoles of one species would lead to an inflated estimate of abundance (or pseudoreplication) as on subsequent visits we would possibly encounter the same tadpole(s) as on a previous visit. For example, on the Mata Ikan stream in plot 1, the counts for *Leptobranchium abboti* on each of the seven visits were zero, six, 15, 14, 22, 20, and six individuals, and thus we took 22 as a conservative estimate of the abundance of that species in that plot. The true number would be somewhere between 22–83 individuals depending on recapture likelihood. Stream abundances are the sum of the conservative counts from

each of the five plots (see Supplemental Information for the raw counts). We then determined the values of abundance-based coverage estimators (ACE), Chao 1, and Jack 1 to get an estimate of the true species richness of tadpoles for each study stream (R Core Team 2015). We calculated species diversity using the Shannon index (H) and its respective evenness (J) for each stream (R Core Team 2015). We used the sum of the maximum numbers found in each plot to calculate these indices for each stream after log transformation.

We assessed the effects of the environmental parameters on larval assemblage composition by running a non-metric multidimensional scaling (NMDS) ordination using the Bray-Curtis (Sørensen) index as distance measure (R Core Team 2015). We accepted two ordination axes with the stress of 0.12 as the optimal model with reasonable interpretive ability. We fit environmental parameters into the ordination plot by applying the function `envfit` with 999 permutations. We plotted only the variables with significant correlations with ordination axes onto the final biplot.

We present descriptive statistics as means \pm standard deviations unless stated otherwise. For all tests, we considered $P \leq 0.05$ statistically significant. We performed all statistical analyses in the R statistical software version 3.2.2 (R Core Team 2015) with the packages `RVAideMemoire` for G tests and `vegan` for NMDS.

RESULTS

Species richness and abundance.—We encountered 17 species of tadpoles from six families (Bufonidae, Dicroglossidae, Megophryidae, Microhylidae, Ranidae, and Rhacophoridae) in all riparian plots within the UTNP (Fig. 3). Five tadpole morphotypes could not be assigned to the species level. The species accumulation curve started to level off on the 17th survey and reached an asymptote on the 50th survey (Fig. 4). Additionally, calculations of true species richness with the ACE, Chao1, and Jack1 estimated only 17 species of tadpoles in the study streams. This suggests that the 68 surveys were enough to detect all larval species and that further surveys, using the same techniques, would not likely yield any additional species. We found that *Meristogenys poecilus* (Speckle-legged Torrent Frog) was the most abundant species in the study sites while we encountered only a few individuals of *Chalcorana megalonesa* (White-lipped Stream Frog) and *Limnonectes kuhlii* (Kuhl’s Creek Frog) over the study period (Fig. 5; Supplemental Information). Moreover, the rank abundance curve formed a gentle slope suggesting both high species evenness and richness.

Species diversity between streams.—The species richness of tadpoles varied among the 10 study streams with Baki having the highest species number (14) and Sitam with the lowest number of species (three; Table 1). Shannon diversity was highest in Tulan, and lowest in Sitam. Species evenness was the highest for Suruyu, followed by Esu, Tulan, Baki, Mata Ikan, Apan, Grueh, Engkabang, Sitam and Injing. Species diversity, however, was not significantly different between the 10 stream sites (G test = 3.36, $df = 9$, $P = 0.948$).

Larval community analysis.—We found a strong association between the fitted values and the ordination distances as calculated in the goodness-of-fit plot (linear fit $r^2 = 0.899$). Of the 15 measured variables, only three variables showed significant correlations with the ordination axes (Table 2; Fig. 6). Stream velocity and width of microhabitat showed strong positive correlation with NMDS 1 while the number of odonate larvae had a weak positive association with NMDS 2. Larval species that were positively associated with NMDS 1 were *Meristogenys poecilus* and



FIGURE 2. Representative example of (A) the streams studied (Sg. Grueh) and (B) the variation in microhabitats sampled within the 5 × 10 m plots, (Sg. Mata Ikan). Microhabitats were (1) large open pools, often but not always at the base of small waterfalls, (2) rock-pools at the stream margins that fill irregularly, (3) extensive gravel and leaf-litter beds with low stream velocity, (4) small to medium-sized waterfalls or riffles, and (5) small riffles and runs. (A photographed by Ulmar Grafe and B by Hanyrol Ahmad Sah).

Meristogenys sp. (torrent frogs; Table 3). Conversely, species that showed negative association with NMDS 1 were *Leptobranchella* sp. (large-eyed litter frogs), *Leptobranchium abboti* (Lowland Large-eyed Litter Frog), *Leptotalax* sp. (slender litter frogs), *Limnonectes* sp. (swamp frogs), *Megophrys nasuta* (Bornean Horned Frog), *Rhacophorus belalongensis* (Belalong Tree Frog) and *Stauroids* sp. (foot-flagging frogs). Furthermore, larval species correlating positively with NMDS 2 were *Chalcorana megalonesa*, *Limnonectes kuhlii*, and *Rhacophorus pardalis* (Harlequin Tree Frog). On the other hand, *Ansonia longidigita* (Long-fingered Slender Toad), *Ansonia* aff. *platysoma* (Flat-bodied Slender Toad), *Limnonectes leporinus* (Giant River Frog),

TABLE 1. Richness (number of species), Shannon diversity index (H'), and evenness (J') values of larval anuran assemblages for 10 study streams in Brunei Darussalam.

	Apan	Baki	Engkabang	Esu	Grueh	Injing	Mata Ikan	Suruyu	Sitam	Tulan
Richness	13	14	13	7	6	7	11	4	3	11
Shannon diversity index	1.45	1.59	1.11	1.50	0.91	0.22	1.47	1.29	0.18	2.00
Evenness	0.57	0.62	0.44	0.84	0.51	0.12	0.61	0.93	0.17	0.84

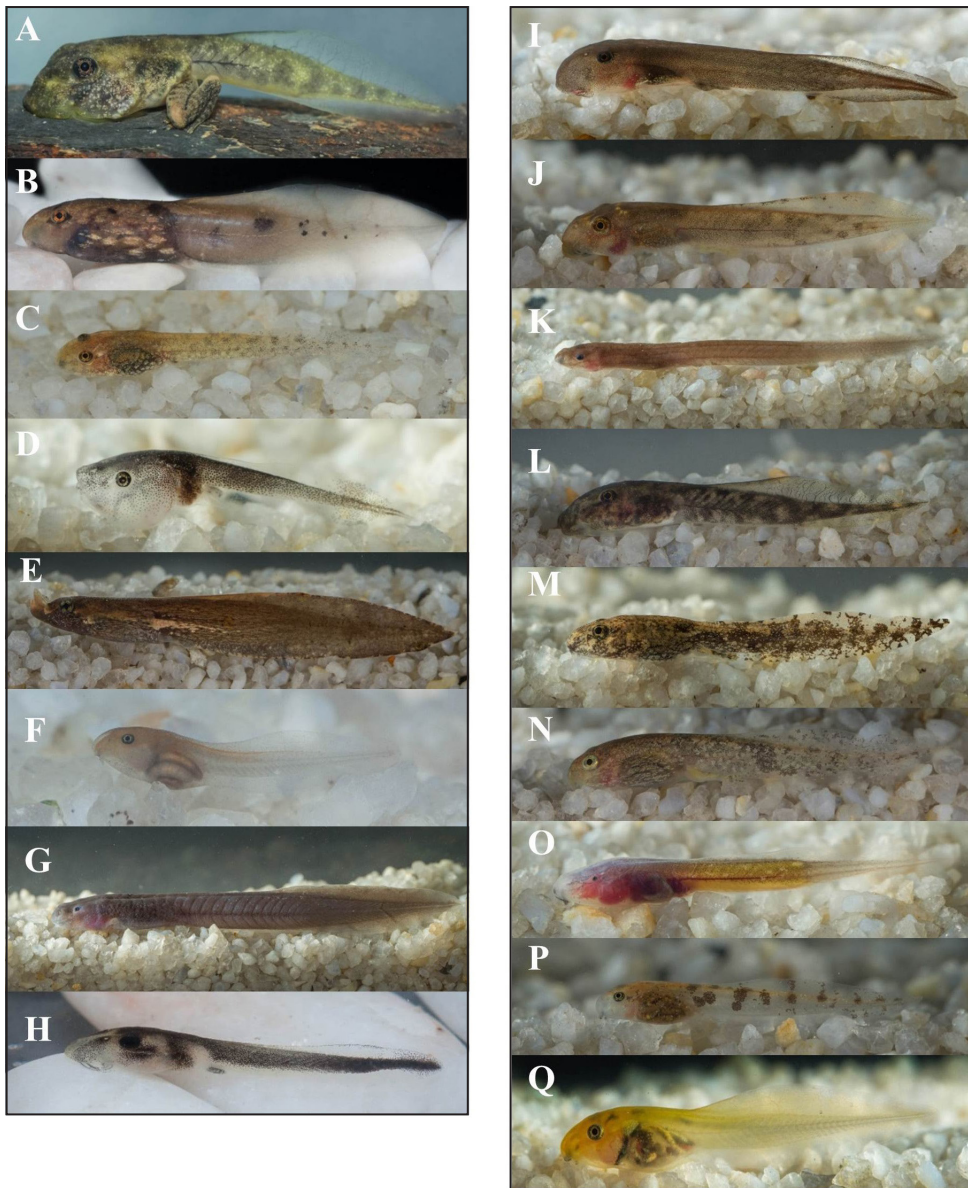


FIGURE 3. Larval anurans encountered at riparian plots sorted from the commonest to the rarest (size not to scale): A) *Meristogenys poecilus* (Speckle-legged Torrent Frog), B) *Leptobrachium abbotti* (Lowland Large-eyed Litter Frog), C) *Limnonectes* aff. *palavanensis* (Smooth Guardian Frog), D) *Microhyla petrigena* (Pothole Narrow-mouthed Frog), E) *Megophrys nasuta* (Bornean Horned Frog), F) *Rhacophorus pardalis* (Harlequin Tree Frog), G) *Leptotalax* sp. (slender litter frogs), H) *Ansonia longidigita* (Long-fingered Slender Toad), I) *Ansonia* aff. *platysoma* (Flat-bodied Slender Toad), J) *Rhacophorus belalongensis* (Belalong Tree Frog), K) *Leptobrachella* sp. (large-eyed litter frogs), L) *Meristogenys* sp. (torrent frogs), M) *Limnonectes leporinus* (Giant River Frog), N) *Limnonectes* sp. (swamp frogs), O) *Staurois* sp. (foot-flagging frogs), P) *Limnonectes kuhlii* (Kuhl's Creek Frog), and Q) *Chalcorana megalonesa* (White-lipped Stream Frog). (Photographed by Hanyrol Ahmad Sah).

Limnonectes aff. *palavanensis* (Smooth Guardian Frog), and *Microhyla petrigena* (Pothole Narrow-mouthed Frog) had negative associations with the NMDS 2 axis.

We grouped species into five habitat guilds based on their strong association between the fitted values and the ordination distances (linear fit $r^2 = 0.899$) and their clustering in the ordination biplot (Fig. 6). Species with positive NMDS 1 values and negative NMDS 2 values were designated torrent species. In contrast, those with

strong negative NMDS 1 values and only slightly positive NMDS 2 values were termed rock-pool species. Open-pool species had both negative association with NMDS 1 and NMDS 2. Another group of species with both negative correlation with NMDS 1 and NMDS 2 were assigned generalist/gravel-bed species. Whereas, the last group of species with slight to moderate negative NMDS 1 values but strongly negative NMDS 2 values were referred to as small microhabitat: side-pool/riffles/mini-waterfall species.

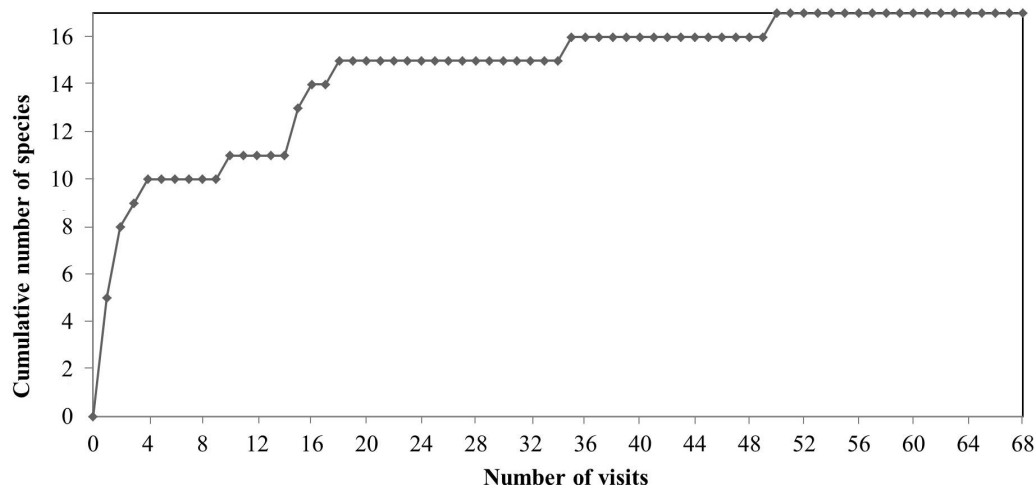


FIGURE 4. Curve of the cumulative number of tadpole species found during plot visits in Ulu Temburong National Park, Brunei Darussalam.

DISCUSSION

The larval phase of anurans, specifically for tropical species, is the least understood life-history stage, but it is likely that selection is the strongest during this period (Heyer et al. 1973; Grafe et al. 2004). In spite of the growing knowledge on the ecology of single tadpole species in Borneo (e.g. Haas et al. 2006; Shimada et al. 2007; Haas et al. 2012; Haas et al. 2014; Oberhammer et al. 2015), the organization of larval communities in Borneo remains largely understudied. The current study provides a novel investigation on tadpole diversity and factors that influence a community assemblage of rainforest stream larval anurans in northeastern Borneo.

Larval richness.—A vast majority of frogs in Borneo breed in forest streams (Inger et al. 2017; Frogs of Borneo. 2019. *op. cit.*) while a few others deposit their eggs in ponds, puddles on the forest floor, pitcher plants and various other phytotelmata. In the current study, we encountered 17 species of larval anurans in 10 study streams, with Baki having a maximum of 14 species. Inger et al. (1986) encountered 29 species or distinct larval forms over a period of 22 y covering a larger number and wider variety of streams as well as microhabitats across a large area of Malaysian Borneo. Conversely, larval species richness for the current study is slightly higher when compared to that sampled by Heyer (1973) from northeastern Thailand with 15 larval forms. Currently, Madagascar has the most species rich larval communities with up to 25 species per stream (Vences et al. 2008; Strauß et al. 2010). In contrast, the tropical forest streams of Brazil host up to 10 species per stream (Hero et al. 2001; Eterovick 2003; Eterovick and Barata 2006; Afonso and Eterovick 2007).

The overall species richness of tadpoles in our study streams is an underestimate of the true species richness.

The species count should be higher by about four species because individuals identified as *Leptobranchella* sp., *Leptotalax* sp., and *Staurois* sp. could actually represent two or three species. We could not distinguish the different species from the same genus based solely on morphology.

Abundance of tadpoles.—Overall, *Meristogenys poecilus* followed by *Leptobranchium abbotti* and *Limnonectes* aff. *palavanensis* were the most abundant tadpoles at our study sites. The variation in the number of individuals of each species might be attributed to (1) a higher number of individuals of these species breeding during the study period, (2) a larger clutch size

TABLE 2. Correlation coefficients (r^2) of environmental and biotic variables with nonmetric multidimensional scaling (NMDS) ordination axes. P values are listed as $**P < 0.001$ and $*P < 0.05$.

Variable	NMDS1	NMDS2	r^2	Pr(>r)
Stream width	0.99	-0.16	0.58	0.061
Stream depth	-0.17	-0.98	0.08	0.777
Canopy cover	-0.64	-0.77	0.27	0.336
Slope	-0.49	-0.87	0.22	0.42
Vegetation height				
< 10 cm	-0.98	0.20	0.32	0.265
11–100 cm	0.95	-0.32	0.42	0.156
101–200 cm	0.07	-1.00	0.17	0.499
201–300 cm	-0.99	-0.14	0.01	0.978
> 301 cm	-0.53	-0.84	0.15	0.564
Velocity	1.00	0.06	0.65	0.026*
Width of microhabitat	0.82	0.57	0.67	0.022*
Depth of microhabitat	-0.33	-0.94	0.17	0.501
Conductivity	-0.54	0.84	0.13	0.646
Number fish	-0.99	0.15	0.50	0.099
Number odonate larvae	-1.00	0.09	0.80	0.001**

TABLE 3. Correlation of species with ordination of larval anuran community structure and vectors of nonmetric multidimensional scaling (NMDS) projections. Common names of species are in order of appearance: *Megophrys nasuta* (Bornean Horned Frog), *Leptotalax* sp. (slender litter frogs), *Rhacophorus belalongensis* (Belalong Tree Frog), *Chalcorana megalonesa* (White-lipped Stream Frog), *Limnometes kuhlii* (Kuhl's Creek Frog), and *Rhacophorus pardalis* (Harlequin Tree Frog), *Leptobrachella* sp. (large-eyed litter frogs), *Leptobrachium abbotti* (Lowland Large-eyed Litter Frog), *Staurois* sp. (foot-flagging frogs), *Meristogenys poecilus* (Speckle-legged Torrent Frog), *Meristogenys* sp. (torrent frogs), *Ansonia longidigita* (Long-fingered Slender Toad), *Ansonia* aff. *platysoma* (Flat-bodied Slender Toad), *Limnometes leporinus* (Giant River Frog), *Limnometes* aff. *palavanensis* (Smooth Guardian Frog), *Limnometes* sp. (swamp frogs), and *Microhyla petrigena* (Pothole Narrow-mouthed Frog). *P* values are based on 999 permutations and an asterisk (*) = $P \leq 0.05$.

Species guilds	NMDS1	NMDS2	r^2	Pr(> <i>r</i>)
Open-pool				
<i>Megophrys nasuta</i>	-0.96	-0.29	0.21	0.443
<i>Leptotalax</i> sp.	-0.97	-0.26	0.45	0.106
<i>Rhacophorus belalongensis</i>	-0.78	-0.63	0.17	0.527
Rock-pool				
<i>Chalcorana megalonesa</i>	-1.00	0.09	0.33	0.322
<i>Limnometes kuhlii</i>	-1.00	0.09	0.33	0.322
<i>Rhacophorus pardalis</i>	-1.00	0.09	0.33	0.322
Generalist/gravel-bed				
<i>Leptobrachella</i> sp.	-0.90	-0.43	0.60	0.036*
<i>Leptobrachium abbotti</i>	-0.76	-0.66	0.23	0.416
<i>Staurois</i> sp.	-0.85	-0.52	0.22	0.439
Torrent				
<i>Meristogenys poecilus</i>	0.68	-0.73	0.15	0.562
<i>M.</i> sp.	0.72	-0.70	0.14	0.581
Side-pool/riffles/mini-waterfall				
<i>Ansonia longidigita</i>	-0.34	-0.94	0.39	0.172
<i>A.</i> aff. <i>platysoma</i>	-0.50	-0.87	0.30	0.302
<i>Limnometes leporinus</i>	-0.23	-0.97	0.50	0.076
<i>L.</i> aff. <i>palavanensis</i>	-0.25	-0.97	0.14	0.614
<i>L.</i> sp.	-0.72	-0.69	0.28	0.323
<i>Microhyla petrigena</i>	-0.24	-0.97	0.14	0.692

produced by these species, (3) variable duration of the tadpole stage, or (4) a bias in detecting certain species of tadpoles. We note that our abundance rank distribution is based on plot data alone and does not reflect tadpole abundances along the full stretch of a stream. In particular, *Chalcorana megalonesa*, *Limnometes kuhlii* and *Staurois* sp. were among the rarely encountered species in our plots although the adults of these species are among the most frequently seen frogs at streams. Finally, some tadpoles, such as those of *L. kuhlii* and *L. abbotti*, hide during the day and thus were probably under-sampled in this study.

Factors affecting larval distribution.—Ordination indicated that species assemblage composition of larval anurans at our study streams was linked to stream velocity, width of microhabitat, and number of odonate larvae. Generally, most tadpoles avoid shallow portions of streams with strong currents (Eterovick and Barata 2006) and may seek refuge in the stream substrate when velocity is high (Kupferberg et al. 2011). Strauß et al. (2010) suggested that selective pressures created by stream current are likely to be more powerful in fast-flowing stretches of streams, where larval anurans not suited to this situation will be carried away in the event of high-water flow, particularly after heavy rain. The composition of the larval assemblage was skewed towards species that appear to prefer microhabitats with no current. Only a few species of tadpoles in Borneo exhibit morphological adaptations to strong currents (Inger et al. 2017; Frogs of Borneo. 2019. *op.cit.*). This includes all known larval forms of *Ansonia*, *Meristogenys*, a few species of *Rhacophorus*, and *Huia cavitympanum*. These species will also survive in slow-flowing portions of streams, although they may have to compete with other tadpoles better suited to these conditions. Of the genera *Ansonia*, *Meristogenys*, and *Rhacophorus*, only a few representatives are found in slow-moving portions of streams. In the case of *Ansonia* and *Meristogenys*, they retain the morphological features for torrenticolous habitats. Tadpoles within the genus *Rhacophorus* are primarily found in slow-flowing water bodies, with only *R. angulirostris* showing adaptations for fast water habitats (Haas and Das 2011).

Most tadpole species in Madagascar prefer habitats that are wide, deep, and with gentle slopes (Strauß et al. 2010). Only a few species of tadpoles from this study follow this trend. Tadpoles using such habitats generally stay at the bottom where water current may be weak or insignificant (Eterovick and Barata 2006). Our findings show that most Bornean tadpoles inhabiting first and second-order streams favored smaller microhabitats. According to Heyer et al. (1975), small microhabitats such as small puddles are typically used by opportunistic breeders. To ensure reproductive success, such breeders characteristically lay a clutch of numerous eggs in small, transitory habitats, often partitioning clutches between oviposition sites (Goyes Valleyos et al. 2019). This is consistent with the larval habitat and reproductive strategy of *Microhyla petrigena*.

Numerous studies have recognized aquatic predators as the principal biotic factor influencing the assemblage composition of tropical stream and pond-dwelling tadpole communities both spatially and temporally (reviewed in Wells 2007). We observed a number of tadpoles with damaged tail fins that we attribute to predation. Injury to the tail fin is prevalent in habitats with a lot of invertebrate predators (Blair and Wassersug

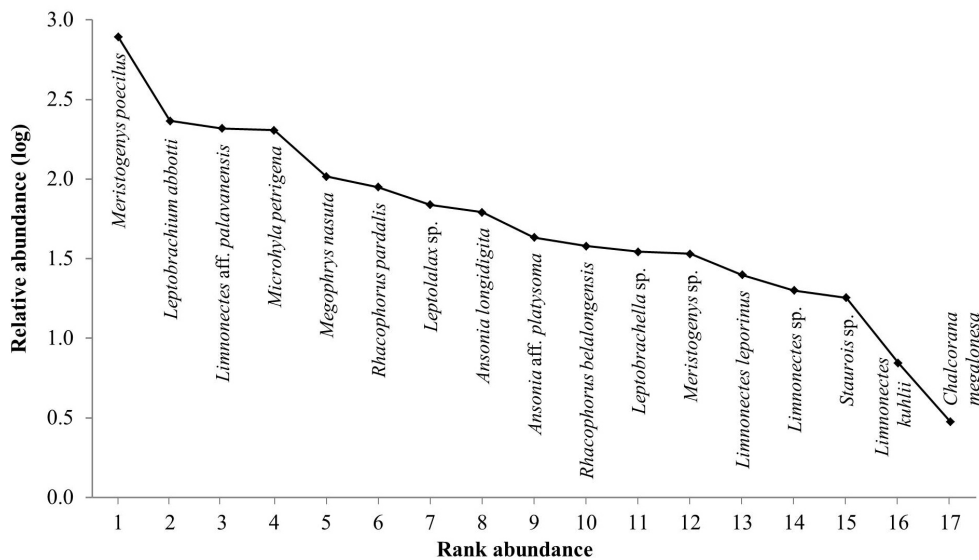


FIGURE 5. Rank abundance curve for the larval anurans encountered in the Temburong National Park, Brunei Darussalam.

2000; Hoff and Wassersug 2000) but such damage has minor effects on the survival of tadpoles compared to the lethality of body strikes (Van Buskirk et al. 2003).

Odonate larvae are rapacious predators of anuran larvae that make use of tactile and visual signals to find their prey (Richards and Bull 1990). They can have substantial impacts on the survival and relative abundance of tadpoles by preying selectively on particular species (Gascon 1992). Despite this, the distribution of *Chalcorana megalonesa*, *Limnonectes kuhlii*, and *Rhacophorus pardalis* showed significant preference for habitats with increasing abundance of odonate naiads. Predators of different kinds can impose different ecological pressures on their prey (Borges-Júnior and Rocha 2013). As a countermeasure,

tadpoles have evolved different anti-predatory strategies including shifts in behavior, morphology, and pigmentation (Azevedo-Ramos et al. 1992; Schmidt and Amézquita 2001; McIntyre et al. 2004). For example, to increase survivorship, tadpoles can reduce their motility in the presence of dragonfly naiads (Azevedo-Ramos et al. 1992; Chovanec 1992; Werner and McPeck 1994). This may also include spending less time foraging (Relyea 2007; Richter-Boix et al. 2007; Saidapur et al. 2009; Smith and Awan 2009).

Adult versus tadpole distribution at streams.—

Keller et al. (2009), surveying adult amphibians within 5 × 10 m riparian plots in five of the same streams as in this study, found 27 species of adult frogs. We

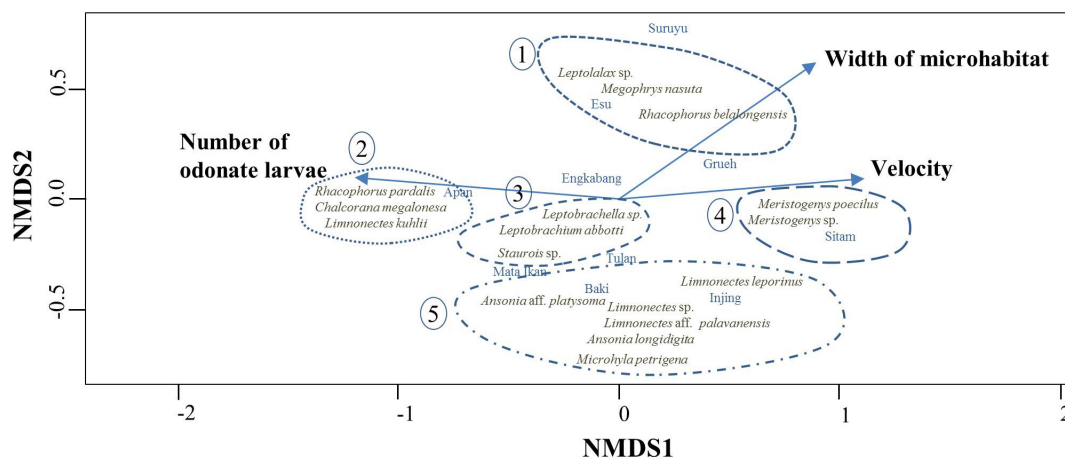


FIGURE 6. Nonmetric multidimensional scaling (NMDS) ordination of the anuran larval community composition from the 10 study streams (names in blue) in the Ulu Temburong National Park, Brunei Darussalam. Arrows depict significant variables, direction of arrow indicates correlation with that axis, and length of arrow shows the strength of the correlation. The tadpoles separate into five distinct microhabitat guilds: 1. Open-pool species, 2. Rock-pool species, 3. Generalist/gravel-bed species, 4. Torrent species, 5. Small microhabitat: side-pool/riffles/mini-waterfall species.

encountered the tadpoles of only a subset of these species. For example, we did not encounter *Pulchrana picturata* (Spotted Stream Frog) and *P. signata* (Stripped Stream Frog), two of the most common medium-sized stream-breeding frogs that deposit their eggs in stream side pools (Inger et al. 2017; Frogs of Borneo. 2019. *op. cit.*). This is an enigma and needs further study. Our plots may have covered fewer stream-side pools than the Keller et al. (2009) study. Likewise, we also did not encounter tadpoles of other stream breeders such as *Borneophrys edwardinae* (Rough-backed Horned Frog) and this reflects their true rareness. To our surprise, we encountered a large number of *Limnometes* aff. *palavanensis* tadpoles although adults are uncommon at streams. Adult males guard eggs in the leaf litter and typically carry tadpoles to small pools of water on the forest floor (Goyes Vallejos et al. 2019). Our data suggests that stream-side pools are being used frequently as well. Interestingly, these stream-side pools are free of dragonfly naiads, whereas pools within the forest are not.

We found a good match between adult and larval microhabitats for *Leptolalax* and *Ansonia*. We found adult *Leptolalax* distributed at calm stream sectors (Keller et al. 2009). Similarly, we found the larval forms of *Leptolalax* at open pools in calm water. Likewise, adults of both *Ansonia* species and their tadpoles were encountered at small waterfalls or riffles.

For several species we found the larval forms in different stream sectors from that of the adults. We found adult *Limnometes leporinus* and *Meristogenys* at streams with larger areas of stagnant water (Keller et al. 2009), whereas the distribution of larval *L. leporinus* was associated with small side pools and *Meristogenys* tadpoles showed preference for fast-flowing sections of streams. In addition, we frequently found adults of *Leptobranchium abboti*, *Megophrys nasuta*, *Rhacophorus belalongensis*, and *Staurois* at waterfalls (Keller et al. 2009). This indicates that, at least for these species, the habitat parameters that affect the distribution of adult frogs have only minor, or no, effects on larval diversity. Thus, while adults select oviposition sites (Inger et al. 1986; Alford 1999; Afonso and Eterovick 2007; Magnusson and Hero 1991), tadpoles may select appropriate aquatic microhabitats not associated with stream sites used by adults (Strauß et al. 2010).

Several studies have found that the availability of microhabitat to tadpoles relies, largely, on the choice of breeding sites by the adults (e.g. Inger et al. 1986; Murphy 2003; Kopp et al. 2006; Eterovick and Ferreira 2008). Some landscape features can affect adult distribution directly (Parris and McCarthy 1999; Lomolino and Smith 2003; Parris 2004; Keller et al. 2009) thus, leading them to favor certain oviposition sites, which subsequently influence tadpole distributions (Evans et

al. 1996; Alford 1999; Eterovick and Barros 2003). For example, adults may avoid habitats with high densities of predators and high risk of desiccation, restricting the microhabitats that will be available to tadpoles (Murphy 2003; Kopp et al. 2006). This selectivity is vital as appropriate reproduction sites can influence hatching success, tadpole performance, recruitment and subsequently, parental health (Magnusson and Hero 1991).

Ecomorphological adaptations of tadpoles.—Microhabitat choice by tadpoles is often closely linked to morphological modifications and specialized feeding behavior (Inger et al. 1986; Altig and Johnston 1989). In Bornean streams, the tadpoles of *Meristogenys* and *Huia* have heavy bodies that are widely rounded and ventrally flat (Shimada et al. 2007). Below the snout are broadened suctorial lips followed by a large abdominal sucker (i.e., gastromyzophorous larvae; Inger 1966). All these features enable them to adhere to rocks and retain position within fast flowing stretches of streams (Inger 1985). The abdominal sucker also helps tadpoles to feed by scraping food off rocks while clinging on substrate in otherwise very difficult situations (Inger et al. 1986). Other examples include the tadpoles of *Ansonia*, which have expanded suctorial oral disks (Frogs of Borneo. 2019. *op. cit.*) and *Rhacophorus belalongensis* with a cup-like sucker mouth. These structures also help them to cling onto rocks in strong currents. None of these modified structures would perform well on silty substrates (Inger 1985). Furthermore, the slimy and elongated bodies of larval *Leptobranchella* and *Staurois* permit them to wriggle in between cracks, which help them escape strong currents in riffles and torrents. Such behavior would not be suitable over massive areas of bedrock (Inger 1985). In contrast, larvae of *Megophrys* possess rather fascinating mouthparts. Their mouth labia are expanded allowing surface film feeding (Frogs of Borneo. 2019. *op. cit.*). Overall, these adaptations may restrict the occurrence of these species to certain habitats only.

In summary, the current study emphasizes the importance of streams as oviposition sites and habitats for many frogs and their larval forms in Borneo. Here, we also provide the first quantitative data on the organization of anuran larvae in the rainforest streams from the northeastern part of Borneo. Our findings show that stream velocity, width of microhabitat and number of odonate larvae were significant predictors of tadpole assemblage composition. Conversely, different sets of environmental parameters including stream size, density of understory vegetation, and presence of waterfalls were associated with the assemblage composition of adult anurans (Keller et al. 2009). While it is vital to conserve streams of various sizes (Parris and McCarthy

1999), it is also paramount to protect streams containing heterogeneous microhabitats. In particular, low-order streams in forested headwaters that harbor many Bornean endemics are in need of priority conservation action (Pui and Das 2016). Such generalizations have significant implications for the conservation and management of tropical amphibians.

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ULMAR GRAFE is a Professor of Biology at University Brunei Darussalam, Brunei Darussalam (Borneo). A native of Germany, he undertook his undergraduate and M.Sc. studies at the University of Würzburg, Germany, and the State University of New York at Albany, USA. Ulmar received his Ph.D. from the Department of Neurobiology and Behavior at Cornell University, Ithaca, New York, USA, where he studied communication and sexual selection in African reed frogs. Ulmar is interested in understanding the functional role of amphibians in tropical ecosystems and human altered landscapes, the evolutionary ecology of frog-biting midges, the behavioral ecology of southeast Asian frogs, the sensory ecology of Bornean bats, and the mechanisms of prey capture in pitcher plants. He has conducted research in Brunei Darussalam, Germany, Ivory Coast, Malaysia, Puerto Rico, USA, Zambia, and Zimbabwe. He is coauthor of the book *A Field Guide to the Frogs of Borneo* and serves as subject editor to the *Journal Biotropica*. (Photographed by Juan Osorio Caceres).