Herpetological Journal

Environmental correlates of species richness and composition of riparian anuran communities in rainforests of north-western Borneo: a metacommunity perspective

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The diversity of stream anurans in Southeast Asia is highly endangered by habitat loss and fragmentation. To optimise conservation planning, their distribution patterns and habitat requirements need to be better understood. In this study, we investigated the distribution and habitat requirements of stream-associated anurans across four sites in north-western Borneo. The sites showed differences in species richness and composition. At a local scale, only microhabitat parameters and stream dynamics had a significant explanatory power on species composition. At a regional scale, environmental variables and geographical distances were both correlated with species composition, with adjacent locations having more similar species assemblages than distant locations. In order to protect the diversity of riparian anurans of north-western Borneo, protected areas need to include distant sites within the same region in addition to a diversity of habitats.

Key words: Amphibians, Anura, beta diversity, Borneo, Brunei, ecology, frog, Malaysia, stream

INTRODUCTION

Amphibians have been identified as the most threatened vertebrate group with nearly a third being listed as threatened (IUCN, 2015). An additional quarter of the species are listed as "data deficient" (IUCN, 2015), and are likely to be more threatened than the fully assessed species, with on average 81% of their ranges totally outside protected areas (Howard & Bickford, 2014; Nori & Loyola, 2015). One of the limitations for amphibian conservation planning in tropical countries is the scarcity of records linking spatial turnover of species to their environments. Southeast Asian amphibian diversity, in particular, is understudied and highly endangered. This region is exceptional in its species richness and endemism (Sodhi et al*.,* 2004), and new species are still being described at a high rate (Grosjean et al., 2015; Inger et al*.,* 2016; Stuart et al., 2006). Southeast Asia also contains a high number (36%) of amphibian species listed as "data deficient" and a fifth are listed as threatened (Howard & Bickford, 2014; Rowley, 2010). The major factors responsible for the disappearance of anurans are habitat loss, habitat fragmentation and disease (Becker et al., 2007; Pounds et al., 2006; Rowley et al., 2010; Sodhi et al., 2008; Sodhi et al., 2010; Stuart et al., 2004).

Borneo ranks among the most vulnerable biodiversity hotspots worldwide (Bellard et al., 2014). Between 1973 and 2010, Borneo has lost 30.2% of its forest cover, which is nearly twice the rate of humid tropical forests globally (Gaveau et al., 2014). The majority of this forest loss occurred in coastal lowlands (below 500 m asl), and selective logging and land conversion to particularly oil palm plantation has been intense (Gaveau et al*.,* 2014). Historically, Borneo has been the major source of vertebrate radiations within Sundaland, stressing the island's importance as an evolutionary hotspot (de Bruyn et al., 2014). To safeguard its biodiversity, identifying areas requiring high conservation efforts is thus an urgent priority (Struebig et al., 2015).

In order to put effective conservation plans into action, a precise understanding of species diversity, distribution patterns, and habitat requirements is needed. Both local and regional (metacommunity) scales of analyses inform broader conservation planning. While the species diversity within a site (alpha diversity) contributes to the relative importance of an area, the rate of species turnover between sites (beta diversity) dictates the optimal spatial arrangement of conservation areas (McKnight et al., 2007). Adjacent sites tend to have similar species compositions (Ernst, & Rödel, 2005; 2008; Dahl et al., 2009; Vasudevan et al., 2006) and the

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difference in species assemblages between sites reflects past and present differences in environment, ecological interactions, and biogeographic history, including barriers to dispersal and speciation mechanisms (Ricklefs & Schluter, 1993). Environmental factors such as understorey vegetation structure, canopy coverage, and stream dynamics influence local species richness and community composition of amphibians (Pearman, 1997; Bastazini et al., 2007; Gillespie et al., 2005; Keller et al., 2009; Konopik et al., 2015). It is thus essential to consider both geographic distance and environmental factors when determining the best arrangement for conservation areas.

Keller et al. (2009) investigated the importance of environmental heterogeneity versus geographic distances among streams at a local scale in north-western Borneo. The authors found that species composition was influenced by environmental factors and spatial distances, without a correlation between geographic distance and environmental similarity at this scale. In this study, we investigate the distribution pattern and habitat requirements of stream-associated anurans across north-western Borneo at a larger scale. We compare a total of four lowland rainforest sites and 107 plots (including the 50 plots from the study conducted by Keller et al. 2009), varying in between-site distance from 40 to 90 km within 5400 km², a spatial scale that can inform on meso-scale influences such as dispersal, local extinction and spatial heterogeneity (Harrison & Cornell, 2008; Ricklefs, 2004).

MATERIALS AND METHODS

Study sites
We surveyed four sites: Ulu Temburong National Park, Bukit Teraja Protection Forest, Tasek Merimbun Heritage Park (all located in Brunei Darussalam), and Gunung Mulu National Park (Sarawak, Malaysia). These sites were chosen for their well-preserved lowland mixed-dipterocarp forest.

Ulu Temburong National Park (UTNP)
UTNP is a 46210-hectare protected area situated in the Temburong district of eastern Brunei Darussalam. This hilly lowland mixed-dipterocarp forest is the best studied area in Brunei for amphibian diversity, and hosts 69 out of the 84 amphibian species recorded in the country (Grafe & Keller, 2009; Grafe & Das, 2014). Among these species, 39 are considered stream-associated. We surveyed three streams, all located within five kilometres of the Kuala Belalong Field Studies Centre (KBFSC, 32°38.26'' N, 09°33.86'' E, 50–100 m above sea level). The Apan is a medium-sized (3-8 m wide) stream, while the Belalong and Temburong are large (15–30 m wide) streams. Six plots were set along each stream. Each plot was surveyed eight times between 15 February and 24 March 2010. In addition, we used the data collected by Keller et al. (2009) following the same method in ten smaller streams in the same area.

Bukit Teraja Protection Forest proposed extension (BTPF)
Bukit Teraja is located near the border with Sarawak, in the Belait district in western Brunei Darussalam (4°17.00"N 114°25.20"E). The area surveyed lies between the existing Bukit Teraja Protection Forest (mixed dipterocarp) and the Ulu Mendaram forest conservation area (peat swamp forest). The region has never been extensively surveyed for amphibians. We surveyed two streams, Kancil and Ular, both three to seven metres wide (50–130 m above sea level). As the site is not part of a national park, and the lower parts of the streams are used by nearby villages and for recreational purposes, we chose the sites upstream of several waterfalls in order to minimise human disturbance. Five plots in each stream were surveyed eight times between 5 April and 24 May 2010.

Tasek Merimbun Heritage Park (TMHP)
TMHP is a 7800-hectare area in the Tutong district (4°36' N, 114°41' E, 50–80 m above sea level) of western Brunei Darussalam that includes peat swamp and lowland mixed dipterocarp rainforest (Das et al., 2008). Four narrow streams (1.5–3 m wide) within the rainforest were surveyed. Five plots in each stream were surveyed eight times between 2 June and 6 July 2007.

Gunung Mulu National Park (GMNP)
GMNP is a UNESCO World Heritage site of 52864 hectares (3°56'–4°16' N, 114°47'–115°00' E) in northern Sarawak, Malaysia. The park provides a wide diversity of forest types, with a great altitudinal gradient from 20 to 2376 metres, and is thus a place of high amphibian diversity. The park contains over 90 amphibian species (Dehling, 2008), 30 of which are low-elevation stream frogs. We surveyed two streams at low elevation (50–200 m above sea level): an upstream part of the Melinau Paku and the Nyipa. Four plots in the Nyipa were visited three times, and five plots in the Melinau Paku were visited four times, all between 19 and 30 April 2010.

Survey protocol
We used the standardised stream frog survey protocol as outlined in Keller et al. (2009). Rectangular plots of ten by five metres were set across streams (or along one bank for larger streams), such that the water body was always, at least partially, included within the plot. Plots were exhaustively searched for frogs both visually and acoustically for at least 20 min. Tadpoles were not taken into account. The positions of the plots were chosen in order to reflect best the different habitats existing in the stream. To ensure independence between plots, they were separated from each other by a minimum of 20 metres. Plots were visited at night between 1900 and 0100 hours.

Environmental parameters
Environmental variables shown to be of importance for the structure of riparian amphibian assemblages (Gillespie et al., 2005; Keller et al., 2009) were measured at each plot: slope, width, and maximum depth of the stream in addition to substrate and vegetation structure.

Table 1. List of the anurans recorded in the literature for lowland mixed-dipterocarp rainforests in the Ulu Temburong National Park (UTNP), Gunung Mulu National Park (GMNP), Tasek Merimbun Heritage Park (TMHP) and Bukit Teraja Protection Forest (BTPF). IUCN (2015) conservation status: LC=least concern, NT=near threatened, VU=vulnerable, EN=endangered, DD=data deficient. Degree of endemism: 1=endemic to Borneo 0=not endemic to Borneo. Record for each site: P=encountered in the plots (included in the environmental factors analysis), S=encountered in the streams studied outside the plots (included in the beta diversity analysis), A=encountered in the area but not in the stream (excluded from the analysis), L=literature. (1) *Limnonectes kuhlii* and *Hylarana raniceps* are here considered as single species, while they are designiated groups of cryptic species occurring across south-east Asia. The phylogeny of these groups is being revised and the species might be re-attributed a posteriori to the sites later on. The species of the genus *Meristogenys* have been grouped since the adult forms do not differ greatly in form or colour (except *M. kinabaluensis* which was absent from all the sites), but can be differentiated from one another with their larval form. The IUCN status of the species of this genus is either VU or NT (except for *M. orphnocnemis* which is LC).

Species	IUCN	Endemism	UTNP	GMNP	TMHP	BTPF
Bufonidae						
Ansonia albomaculata	NT	1	P	P		
A. leptopus	NT	1	P	P		
A. longidigita	NT	1	P	P		
A. platysoma	EN	1	S	L		
Ingerophrynus divergens	LC	0	P	P		P
I. quadriporcatus	LC	0			P	
Pedostibes hosii	LC	0	S			
P. rugosus	NT	1	S			
Pelophryne signata	NT	0	A			
Phrynoidis asper	LC	0	P	S	P	S
P. juxtasper	LC	0	P	S		
Ceratobatrachidae						
Alcalus baluensis	LC	1	P	P		P
Dicroglossidae						
Fejervarya limnocharis	LC	0	A	L		
L. ibanorum	NT	1	P	P		
L. ingeri	NT	1	P	S	P	A
L. kuhlii (1)	LC	0	P	P		P
L. hikidai	LC	1			P	
L. leporinus	LC	1	P	P	P	P
L. malesianus	NT	0		P		
L. palavanensis	LC	0	S	L		
L. paramacrodon	NT	0	A			
Occidozyga baluensis	NT	1	A			A
O. laevis	LC	0	A	L		
Megophryidae						
Borneophrys edwardinae	VU	1	S			
Leptobrachella mjobergi	LC	1	P	P		
L. parva	VU	1	P	P		
Leptobrachium abbotti	LC	1	S	S		
L. montanum	LC	1	P			
Leptolalax fritinniens	NT	1	P	P		
L. gracilis	NT	0	P	P		S
L. pictus	VU	1	A	S		
M. nasuta	LC	0	P	P		
Microhylidae						
Chaperina fusca	LC	0	P			P
Kalophrynus pleurostigma	LC	0	A	L		
K. subterrestris	NT	0	A			
Kaloula baleata	LC	0		L		A

Table 1. *Continued.*

Species	IUCN	Endemism	UTNP	GMNP	TMHP	BTPF
Metaphrynella sundana	LC	1	A	L		
Microhyla borneensis	LC	1	A	A		
M. perparva	NT	1		A		A
M. petrigena	NT	1	A			
Ranidae						
Huia cavitympanum	LC	1		P		
Hylarana glandulosa	LC	0	P	S	P	P
H. nicobariensis	LC	0				A
H. picturata	LC	1	P	P		
H. raniceps (1)	LC	0	P	P	P	
H. signata	LC	0	P	S	P	P
Meristogenys sp. (1)		1	P	P		
Odorrana hosii	LC	0	P	L		
Staurois latopalmatus	LC	1	P	P		
S. guttatus	LC	0	P	P		P
S. parvus	NT	1	P	P		
Rhacophoridae						
Feihyla kajau	NT	1	P	L		
Kurixalus appendiculatus	LC	0		A		A
Nyctixalus pictus	NT	0	A	A		
Philautus hosii	NT	1	P	S		
P. tectus	VU	1	P	P		S
Polypedates colletti	LC	0		A		
P. leucomystax	LC	0	A	L		
P. macrotis	LC	0	A	S		
P. otilophus	LC	0	A	L		
Rhacophorus belalongensis	DD	1	P	P		
R. cyanopunctatus	LC	0	A	S		
R. gauni	NT	1		S		
R. harissoni	NT	1	P	L		
R. nigropalmatus	LC	0	A	L		S
R. pardalis	LC	0	P	L		
R. rufipes	NT	1	A	L		

The slope of the stream, which reflects the stream dynamics, was measured following the method described by La Perrier & Martin (1986): parallel to the stream flow, in the middle of the plot, and averaged on the length of the plot. The number of plant stems was counted for three height categories, corresponding to plant sizes used as substrate by different species of frogs: below ten cm, between ten cm and one metre, and over one metre. In addition, the surface covered by different substrates (rock, sand, gravel, logs, and detritus) within the plot was estimated. These factors were considered constant during the whole survey period and therefore measured only once per plot.

Highly dynamic environmental parameters, such as the maximum width and depth of the stream, were measured for each visitation. Indeed, changes in weather conditions at the site, or even far upstream, may strongly affect stream dynamics, sometimes switching from a slow-flowing, pond-like situation to a torrent within minutes.

Statistical analyses

Correlations between habitats, species composition, and geographic distances among streams

We calculated distance matrices based on dissimilarity between streams. We used Euclidean distance for the distance matrix based on habitat parameters and Bray-Curtis index for distance matrices based on species composition. Real geographic distances (in km) between streams constituted the distance matrix for geographic distances. We compared pairs of distance matrices with Mantel tests and the species composition and habitat dissimilarity while controlling for geographic distances with partial Mantel tests based on Pearson's correlation and 1000 permutations. We tested correlations between species composition, habitat, and geographic distances for all sites and for UTNP alone.

Table 2. Mantel tests for all sites together and UTNP alone. Tests are based on Pearson's product-moment correlation and for 1000 permutations. The distance matrix for environmental factors is based on Euclidean indices. The distance matrix for species is based on Bray-Curtis indices. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1; *p*-values are based on 1000 permutations.

ALL sites together	r	p-value	
Species*Environment	0.4154	0.002	**
Species*Geographic	0.6934	0.001	***
Environment*Geographic	0.4441	0.007	**
Partial Mantel test Species*Environment*Geographic	0.2371	0.047	*
UTNP only			
Species*Environment	0.6221	0.014	*
Species*Geographic	-0.08921	0.712	
Environment*Geographic	-0.01473	0.527	

Environmental variables and species composition
To investigate how species assemblages were distributed according to environmental variables, we used non-metric multidimensional scaling (NMDS) with an unconstrained method and ordinated plots in regard to their species composition. We used Bray-Curtis dissimilarities and randomised starting coordinates in order to produce a global optimal solution. We calculated species scores as weighted averages of plots scores. We then fitted environmental factors to the ordination, in order to identify which habitat parameter shaped the species composition of the different plots.

RESULTS

Over all sites, we encountered 37 species within the study plots (Table 1). Species accumulation curves were asymptotic for each site (Online Appendix), indicating that most of the species present were detected. Species assemblages were correlated with both environmental factors and geographical distance between sites, with a much stronger correlation with geographical distance (Table 2). Environmental factors and geographical distance were correlated, and their interaction influenced species assemblages (Table 2). Within the UTNP, species composition was not significantly correlated with geographical distance between plots but was significantly correlated with the environmental factors (Table 2).

All the environmental variables were significantly correlated with the ordination axes (Table 3) and were
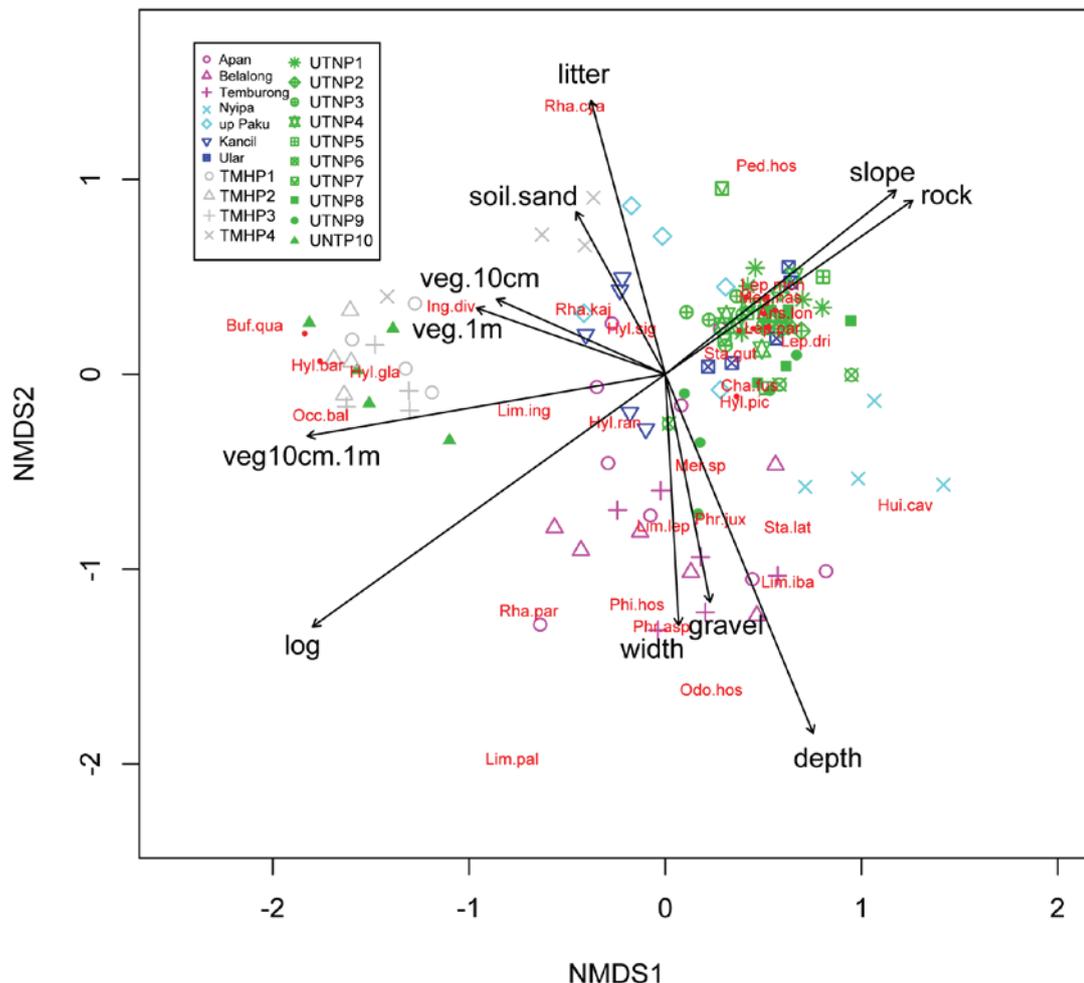

Fig. 1. Non-metric multidimensional (NMDS) scaling of the plots based on species composition. Species are designated by their abbreviated names in red. Arrows represent the direction of the gradient for the diverse environmental factors, with a length proportional to the correlation with the ordination.

Table 3. Environmental variables fitted to NMDS axes. Variables: vegetation: veg.10cm=plants <10cm; veg10cm.1m=plants between 10cm and 1m; veg.1m=plants above 1m. Ground coverage within the plot: soil; sand; gravel; rock; log (fallen trees or branches); litter (leaf litter). Stream dynamic: width and depth (both maximal within the plot); slope=average slope of the stream in the plot. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1; p-values are based on 1000 permutations.

	NMDS1	NMDS2	r^2	$Pr(>r)$	Significance
veg 10cm	-0.912359	0.409391	0.0926	0.008991	**
veg10cm.1m	-0.985226	-0.171257	0.3575	0.000999	***
veg.1m	-0.942921	0.333018	0.1088	0.004995	**
slope	0.779762	0.626076	0.2374	0.000999	***
soil.sand	-0.478680	0.877989	0.0940	0.008991	**
gravel	0.191377	-0.981517	0.1482	0.000999	***
rock	0.816300	0.577628	0.2487	0.000999	***
log	-0.811331	-0.584587	0.5120	0.000999	***
litter	-0.260256	0.965540	0.2202	0.000999	***
width	0.053352	-0.998576	0.1738	0.000999	***
depth	0.378832	-0.925465	0.4136	0.000999	***

highly correlated to one another. Unsurprisingly, plots from the same sites tended to share similarities in environmental factors (Fig. 1). TMHP streams were narrow, shallow, flat, and highly vegetated, with a substrate composed essentially of bare soil or sand and leaf litter, with no gravelly or rocky areas. The small streams of UTNP had quite homogeneous environmental parameters in comparison to the other sites: all these streams were small and steep with rocky or gravelly substrate and poor understory vegetation. BTPF streams were narrow, with a medium slope and understory vegetation cover, and covered with leaf litter. The plots of the large streams of UTNP and of the streams of GMNP were more dispersed in the matrix. The total number of riparian species over all the four sites (*n*=45) was twice as high as the average species richness at any individual site (range from 8 to 38, mean=23).

DISCUSSION

The composition of stream-associated anurans was influenced by both the microhabitat and the geographic distance between sites. The importance of these factors varied according to geographic scale. At a local scale, environmental factors played an essential role, as seen for the UTNP alone (also shown in Keller et al., 2009). The substrate type, the dynamics of the stream, and the understorey vegetation structures all had significant explanatory power regarding species assemblages. Indeed, understorey vegetation in the vicinity of streams can serve as support for frogs calling for mates, foam nesting, or hanging a clutch of eggs. Depending on its height, the plant may serve different species of frogs. For example *Rhacophorus belalongensis* was most commonly found on vegetation higher than one metre, whereas *Leptobrachella mjobergi* was usually found on leaves less than ten centimetres above ground. The dynamics of the stream is also of great importance for stream-breeding frogs, because stream characteristics

need to match the requirements of the future tadpoles, which may be highly specialised. For example, tadpoles of *Meristogenys* spp. and *Huia cavitympanum* live in fast-flowing currents that are well oxygenated and provide a high flow of nutrients. The tadpoles of *Megophrys spp.*, on the other hand, inhabit slow streams, which allow them to filter the surface of the water with their funnel-shaped mouth.

At a regional scale (40–90 km), geographical distance between sites was more correlated to species composition than environmental parameters, although microhabitats did also influence species composition. These results contrast with those of Ernst & Rödel (2008) who found a spatial structure but no environmental correlation with leaf-litter anuran communities in Ivory Coast and Guyana, even though the distances between sites were smaller than those in the present study (0.2–6.3 km; Rödel & Ernst, 2004). The influence of geographical distances between sites on their respective species composition reflects the history of species and populations rather than their habitat needs. Our study focused solely on riparian species of lowland rainforests; similarity decay across sites would most probably be stronger if species across all habitat types and elevations were included. Moreover, the rate of similarity decay in species composition with geographic distance seems to be a property of the region itself (Dahl et al., 2009). The same geographical distance between two sites would thus have a different impact in different regions.

With twice as many riparian anuran species at the regional level than at the local level average, north-western Borneo's high regional diversity is not only due to high local (alpha) diversity, but also to a high regional turn-over (beta diversity). North-western Borneo is thus amongst the most diverse tropical regions, with the quotient for the Western Ghats of India being 2.6 (Vasudevan et al., 2006) and 2.0 and 2.7 for New Guinea and Bolivia respectively (Dahl et al., 2009). The implications of this result, in terms of conservation, are

important beyond Borneo itself. In order to protect the diversity of riparian anurans, it is necessary to not only focus on a few hotspots, but to focus conservation efforts on a network of sites within the same region. Moreover, our study focused solely on riparian species, and we can expect this quotient to increase if all forest species are included in this index. In addition, our study assessed beta diversity over an area of only 60x90 km or 5400 km^2 with regional turnover certainly to be much higher at a larger scale.

This study directs attention to the high species turnover of amphibians in north-western Borneo and the role of environmental factors predicting their pattern of distribution. Amphibians play a major role in tropical forest food webs (Konopik et al., 2014; Reagan & Wade, 1996) and their value as a surrogate group for global conservation planning is widely accepted (Buckley & Jetz, 2008). Large-scale spatial planning requires detailed distributional data and the underlying environmental correlates and ecological processes that determine such patterns (Struebig et al., 2015; Runting et al., 2015). Despite their importance, amphibians are often still absent from impact assessments in the tropics (e.g. Kitzes & Shirley, 2015) largely because the factors regulating their distribution are understudied. We emphasise the importance of assessing the environmental predictors of amphibian distribution on multiple spatial scales as regional influences on richness of local communities are ubiquitous (Harrison & Cornell, 2008).

This study provides the baseline to investigate rainforest amphibian assemblages and for future comparisons with anthropogenically degraded forests. Recently, canopy cover was identified as a principle predictor of primary forest frog species richness across a disturbance gradient in northern Borneo (Konopik et al., 2015). Although efforts are being made by the Malaysian and Bruneian governments to promote ecotourism and protect lowland forests, deforestation for oil palm plantations, the creation of production forests, hydroelectric dams, fire, and urbanisation remain major threats to biodiversity including amphibians (Faruk et al., 2013: Fitzherbert et al., 2015; Gaveau et al., 2014; Grafe & Das, 2014; Kitzes & Shirley, 2015). It is therefore an urgent priority to establish a network of protected areas which will efficiently shelter a maximum number of species.

ACKNOWLEDGEMENTS

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