

Amphibian species diversity in the proposed extension of the Bukit Teraja Protection Forest, Brunei Darussalam

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Abstract

Amphibian species diversity was investigated within the lowland mixed-dipterocarp forest of the proposed extension of the Bukit Teraja Protection Forest (BTPF), Brunei Darussalam in north-west Borneo. A combination of both visual encounter and acoustic sampling techniques were conducted opportunistically as well as in six selected stream transects, each containing five 5x10m plots. A total of 39 species of frogs from seven families (Bufonidae, Ceratobatrachidae, Dicroglossidae, Megophryidae, Microhylidae, Ranidae, and Rhacophoridae) were identified from the BTPF. Most notably, four new records for Brunei were discovered: *Hylarana nicobariensis*, *Kaloula baleata*, *Limnonectes malesianus*, and *Microhyla perparva*. This brings the total number of amphibian species in Brunei Darussalam to 84. Canonical correspondence analysis showed that out of 13 measured environmental variables maximum stream depth and % soil/sand of ground cover were significantly correlated with anuran assemblage composition. Species overlap between the proposed extension of the Bukit Teraja Protection Forest and the Ulu Temburong National Park (UTNP) determined by the coefficient of biogeographic resemblance (CBR) showed low species complementarity between these two regions. This emphasizes the need to upgrade the proposed extension of the BTPF to a protection forest to ensure the conservation of regional amphibian biodiversity.

Index Terms: anurans, biodiversity, conservation, species assemblages, tropical lowland rainforest

1. Introduction

The distributions of terrestrial vertebrates have informed global and local conservation priorities.¹ However, more fine-scale and targeted surveys will be necessary to identify priorities at a scale practical for local action. In the case of amphibians, not all regions have been equally targeted, with amphibian distributions on Borneo remaining particularly incomplete.² Small-ranged amphibians with specific habitat requirements are particularly vulnerable to falling through the grid of large-scale meta-analyses. There is a recognized need for conservation actions particularly in Borneo where the rates of deforestation are high due to logging and land conversion for oil-palm plantations and urbanization.^{3,4} Furthermore, studies that explore the effects of both environmental variables and

biotic effects on amphibian assemblage composition in the tropics are limited.^{5,6} Such information serves to predict distribution patterns of data-deficient species and can direct conservation efforts.

Borneo provides an excellent model for studying amphibian species diversity and factors influencing diversity. Borneo, the third largest island in the world, is widely known as an area of high biodiversity^{7,8} hosting nearly 200 species of amphibians.² The level of endemism of frogs in Borneo is high with about two-thirds of its frog species endemic to the island.² This number will continue to rise as additional frog species are being discovered every year.² Wildlife inventories are the basic tool for conservation, laying the

foundation for prioritizing areas for conservation.⁹⁻¹³

Research on amphibian assemblages regarding spatial and environmental effects have produced contrasting outcomes. In sub-tropical eastern Australia, dominant environmental effects dominated anuran species composition on a regional scale.¹⁴ In contrast, anuran assemblages in pristine and disturbed forests of the afro- and neotropics were mostly affected by pure spatial effects with pure environmental effects controlling assemblages in disturbed areas only.¹⁵⁻¹⁶ However, within pristine habitats, it was found that it was impossible to predict assemblage compositions on a species-specific level with habitat variables.¹⁶ It was deduced that in pristine habitats, priority effects and lottery recruitment were more important than species-specific responses to the environment, even though species have, for instance, explicit breeding habitats. Furthermore, investigations on the community assemblages of leaf-litter and canopy frogs in pristine forests identified the importance of spatial effects and spatially structured environments.¹⁶⁻¹⁸

The current study was undertaken in Brunei Darussalam located on the north coast of Borneo. Brunei's land area (5,766 km²), although representing only less than 1% of the whole of Borneo, is still approximately 56% forested.¹⁹ Seventeen percent of Brunei's forests are undisturbed or pristine and are currently protected as either protection or conservation forest or national park. A variety of forests exist including mixed-dipterocarp rainforest, lower montane forest, upper montane forest, tropical heath forest and others.²⁰ These forests are among the richest in the world²¹ and they support many different frog species. For example, Grafe and Das¹⁹ list a total of 70 species of frogs of seven families (Bufonidae, Cetatobatrachidae, Dicroglossidae, Megophryidae, Microhylidae, Ranidae and Rhacophoridae) for the lowland mixed-dipterocarp forest of Ulu Temburong National Park alone. However, as more changes occur as a result of

increased road and dam constructions, new settlement schemes, and fire, the forest cover will continue to be reduced.²⁰ Therefore, there is an urgent need to study these habitats to ensure conservation of frogs in this small but highly diverse country.

Riparian frogs were chosen for this study because most frog species on Borneo are stream-associated and the environmental variables affecting their assemblages tend to be group-specific, i.e. correlated with differences in life-history patterns as well as habitat affiliation.^{2, 15}

The main objectives of the study were to (1) provide an inventory of amphibians within the proposed extension of the Bukit Teraja Protection Forest, (2) investigate whether environmentally similar sites have similar species assemblages, and (3) evaluate the area for its conservation value in particular its complementarity to other forested areas, such as Ulu Temburong National Park.

2. Materials and Methods

2.1 Study area

The study was conducted within the lowland mixed-dipterocarp forest of the proposed extension of the Bukit Teraja Protection Forest (see **Figure 1**) Belait District, Brunei Darussalam from April 2010 to May 2011, as well as on 8 June 2014 and 25 January 2018. Only opportunistic surveys were conducted in 2014 and 2018. Mean air temperature during fieldwork was 25.5°C (\pm SD of 0.9°C) and mean water temperature was 25.2°C (\pm SD of 0.8°C). The area comprises Bukit Teraja Protection Forest and the Heart of Borneo proposed extension of the Bukit Teraja Protection Forest (BTPF). This area covers an elevational range from under 30–415 m above sea level with Bukit Teraja being the highest point. The Bukit Teraja Protection Forest has a total area of more than 6000 hectares of undisturbed lowland mixed-dipterocarp forest. While the BTPF has approximately 2,500 hectares of mostly undisturbed mixed-dipterocarp forest, about 325

ha of the BTPF is peat swamp forest that borders the peat swamp forest of the Ulu Mendaram Conservation Forest²² (see **Figure 1**).

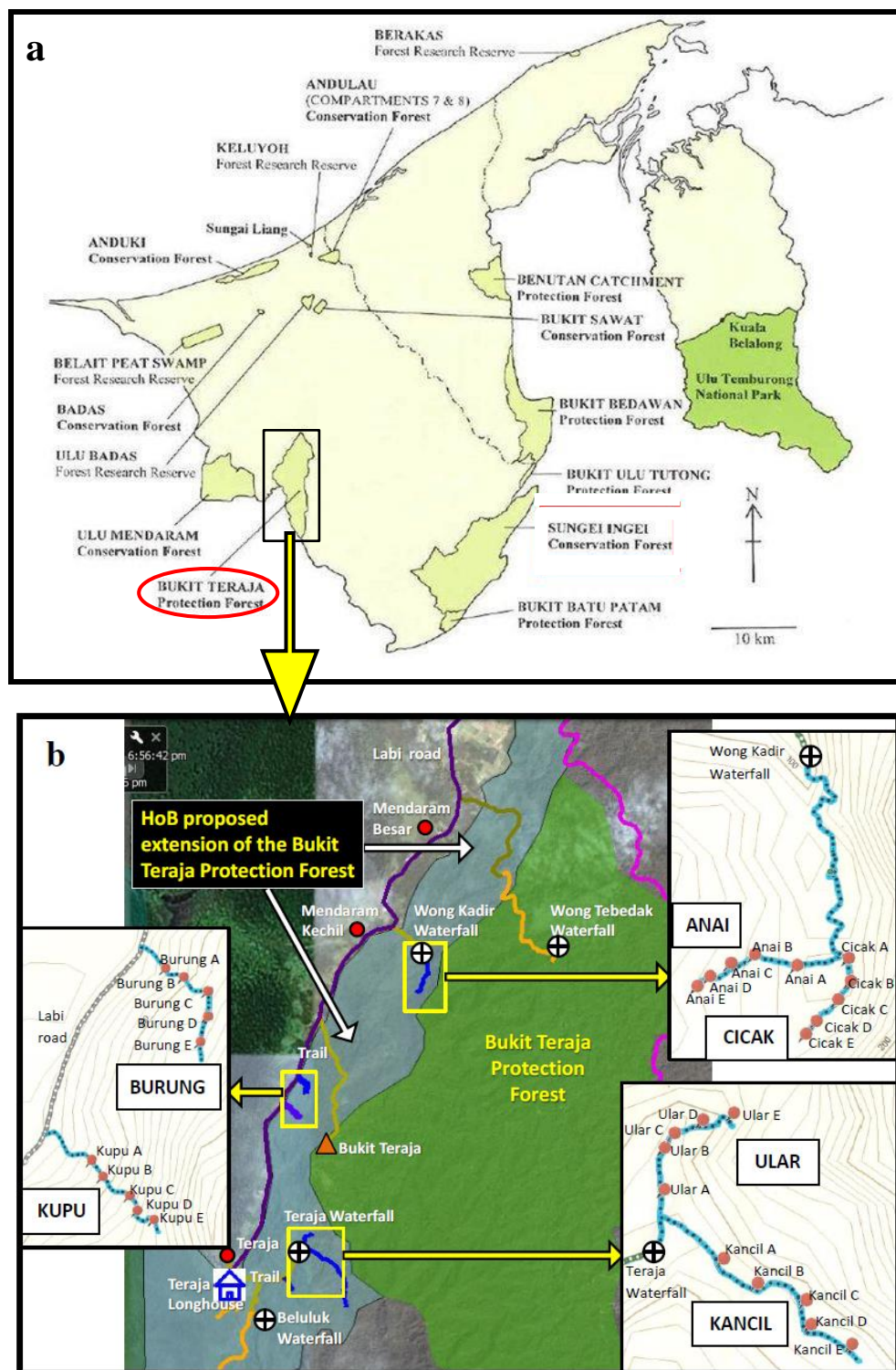


Figure 1. Maps showing (a) the location of the Bukit Teraja Protection Forest and its surrounding area²¹ and (b) the close-up view of the Protection Forest (green) and the proposed extension of the Bukit Teraja Protection Forest (blue), showing all the stream transects and 30 study plots (Google map by Peter Engbers)

Six stream transects of small to medium sizes were selected within the BTPF. These streams were labelled Ular, Kancil, Anai, Cicak, Kupu and Burung. Ular and Kancil were located upstream of the Teraja waterfall, Anai and Cicak were upstream of the Wong Kadir waterfall, and Kupu and Burung ran perpendicular and upstream from the Labi-Teraja road (see **Figure 1**). Five 5 x 10 m plots were established within each stream transect. Plot locations were selected haphazardly with irregular intervals to cover stream heterogeneity. Distance between neighbouring plots was at least 20 m. Each stream plot was visited eight times during the study period. We visited each plot at irregular intervals timing our visits to insure an even spread of plot visits throughout the study period.

2.2 Species capture and identification

A combination of both visual and acoustic encounter surveys were conducted to sample frogs between 1900–2330 h. Transect walks were conducted by 1–4 people. Survey effort was normalized by increasing or decreasing search time per plot according to the number of surveyors. The mean time spent within each plot searching for frogs was 10.6 min (\pm 2.9 min SD). Any encountered individuals were identified and when identification was not possible photographs were taken or samples were brought back to be identified. Frogs removed were released back the next day roughly at the spot of capture. The substrates on which the frogs were encountered (leaf, branch, ground) and height from the ground were recorded. Opportunistic surveys required actively searching for animals over large areas in order to increase the probability of encountering as many different species as possible. Samples of each new species were preserved in 75% ethanol and kept in the UBD Natural History Museum for future reference. Identification of frogs was facilitated by Malkmus²³, Das²⁴ and Inger et al.² Scientific names follow Frost²⁵ except for the genus *Hylarana* as we do not accept the splitting of this monophyletic genus.

2.3 Environmental characterization

We measured maximum stream width and depth, stream slope, density of riparian vegetation and canopy cover as these have been shown to influence the assemblage structure of riparian frogs.^{14,26,27,28,29} Density of vegetation was measured by counting each individual plant within five height categories; < 10 cm, 10 cm–1 m, 1–2 m, 2–3 m and >3 m. Canopy cover at each plot was determined using a spherical densiometer. To determine ground cover in each plot, the ground was divided into % soil/sand, % rock, % gravel and % log roughly by eye. Maximum stream width and depth were measured on each visit and averaged over the study period, whereas the other largely invariant parameters were determined only once during the project. Descriptive statistics are given as mean \pm SD unless stated otherwise.

2.4 Species diversity

Species accumulation curves for all six transects combined were plotted. To get an estimate of the true species richness of frogs for the BTPF the values of abundance-based coverage estimator (ACE) and Chao 1 were determined using EstimateS Win 8.20.³⁰ ACE and Chao 1 are non-parametric estimators that predict species richness based on species abundance. Since toe clipping was not done to mark each individual species found, the maximum number of individuals of each species captured on a single night per stream transect was assumed to be the abundance of that species in each stream. Rank abundance graphs were plotted and frogs categorized as abundant, common or rare, depending on whether they were encountered in all 6 streams, in 2–5 transects or in only one stream transect. Species diversity in each stream transect was calculated by Fishers' alpha index using EstimateS Win 8.20³⁰ and similarity between streams was determined by Morisita's similarity index in Krebs³¹. The Kruskal-Wallis test, a non-parametric test, was used to determine the differences in stream characteristics among the six streams using SPSS (version 17).

2.5 Community analysis

Canonical correspondence analysis (CCA), a multivariate direct gradient analysis, in the program CANOCO (version 4.5)³² was used to analyze the relationship between environmental variables and species abundance of frogs. Species with one individual only (i.e. *Philautus tectus*, *Chaperina fusca* and *Rhacophorus nigropalmatus*) were excluded from this analysis. The environmental variables utilized in the CCA were therefore, mean stream depth and width, stream slope, canopy cover, density of vegetation (< 10 cm, 10 cm-1 m, 1-2 m, 2-3 m and >3 m vegetation) and percentage ground cover (% soil/sand, % rock, % gravel and % log). In this technique, the ordination axes are constrained by linear combinations of the selected environmental variables.^{33,34,35} CCA was chosen as it is robust to analysis with numerous correlated variables³⁷ and allows the identification of variation patterns that are best explained by the particularized environmental variables.³⁴ To determine the relative importance of the variables, the forward step-wise selection procedure was then performed. In this procedure, each of the variables was analyzed separately for individual explanatory power (marginal effects) as well as the effect that each variable had in addition to the variables that have already been chosen (conditional effects).³⁸ Monte Carlo permutation tests (with 999 random permutations) were run to test the significance of these effects as well as the statistical significance of the first canonical axis and of all canonical axes. We used Moran's *I* (R package *ade4*) to test environmental parameters for spatial autocorrelation for all plots and within streams.

2.6 Complementarity analysis

Species overlap between the proposed extension of the Bukit Teraja Protection Forest and the Ulu Temburong National Park (UTNP) was determined by the coefficient of biogeographic resemblance (CBR).^{38,39,40} Complementarity analysis gives an indication of the degree of similarity in the species composition between two geographically separated areas.⁴⁰ The index was

calculated as: $\text{Overlap/Similarity} = 2C/(N1 + N2)$ where *C* is the number of species in common to the two regions (i.e., the BTPF and the UTNP) and *N1* and *N2* are the number of species in the first and the second region, respectively. The value of CBR ranges from 0 (no species in common i.e. low complementarity) to 1 (all species are shared in both regions).³⁹ The checklist of frog species for the UTNP was obtained from Grafe and Das.¹⁹

3. Results

3.1 Species diversity

In total, 39 species of frogs representing 46% of frog species in Brunei were recorded from the proposed extension of the Bukit Teraja Protection Forest (see **Table 1**). These anurans belong to seven families: Bufonidae (4 spp), Ceratobatrachidae (1 sp), Dicroglossidae (10 spp), Megophryidae (2 spp), Microhylidae (6 spp), Ranidae (8 spp), and Rhacophoridae (8 spp). All individuals were identified to the species level except for one individual of *Ansonia*. According to the Global Amphibian Assessment,⁴¹ twenty-five species are classified as least concern, nine species are near threatened and only one species i.e. *Philautus tectus* is listed as Vulnerable. Only two individuals of *P. tectus* were encountered during the study period; one individual outside a riparian plot at the Teraja Waterfall and another inside a riparian plot at the Wong Kadir Waterfall. The majority of the frogs encountered in BTPF were either adults or juveniles except for *Leptobrachium abbotti* and *Microhyla borneensis*, which were a young metamorph and a tadpole, respectively.

Out of the 36 frog species, 22 species were encountered in varying habitats outside the riparian plots within the BTPF via opportunistic surveys. The four species *Hylarana nicobariensis*, *Kaloula baleata*, *Limnonectes malesianus*, and *Microhyla perparva* were new records for Brunei. The four new records bring the total number of frog species in Brunei to 84.

The overall species accumulation curve for all six streams combined at the BTPF started to level off on the 27th survey and reached an asymptote on the 46th survey (see **Figure 2**). This suggests that most of the riparian anuran community have now been detected. Both ACE and Chao 1 computed only 14 species in the stream transects. This implies that if additional surveys were to be conducted, no new species will likely be encountered.

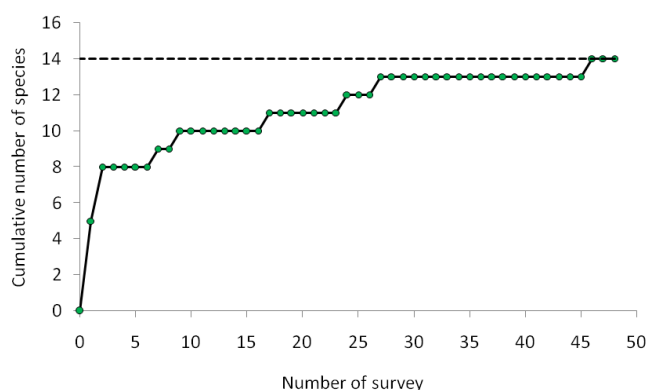


Figure 2. Species accumulation curve for the proposed extension of the Bukit Teraja Protection Forest during 48 visits. Dotted line represents both values of ACE and Chao 1.

3.2 Species richness, compositions and rank abundance at different streams

Overall, the most abundant species in the BTPF was *Limnonectes* aff. *kuhlii* with a total of 38 individuals (see **Figure 3**). Species that were encountered only once within plots were considered rare (i.e. *Chaperina fusca*, *Philautus tectus* and *Rhacophorus nigropalmatus*). The rest of the species had intermediate abundances and thus were considered common.

Values of the Morisita's similarity index between Ular-Kancil, Ular-Cicak, Anai-Kupu, and Kupu-Burung were 1 or slightly more than 1. Thus, these streams showed complete similarity in species composition. Cicak-Kancil, Cicak-Anai and Burung-Anai also showed strong similarity. On the contrary, poor similarities were detected between Ular-Kupu, Ular-Burung, Kancil-Kupu and Kancil-Burung.

Moran's *I* showed a lack of spatial autocorrelation for all plots and within streams. All combinations of streams and environmental parameters were not significant ($P > 0.05$) and distance did not explain much of the environmental variance (mean $I = -0.14 \pm 0.09$).

The Canonical correspondence analysis explained only 49% of the total variation indicating that some other important variance was not included. Axis 1 and Axis 2 showed high correlations between species and environmental variables ($r = 0.888$ and $r = 0.877$), and explained 31.8 % and 26 % of the total variance, respectively. Only mean depth and % soil/sand showed very significant difference ($P = 0.005$ and $P = 0.006$, respectively) when all of the variables were combined and tested for conditional effects.

Both canonical coefficients and intraset correlations show that Axis 1 is a gradient of increasing depth of stream and % sand/soil, whereas Axis 2 is a gradient of increasing depth and decreasing % soil/sand.

The assemblage of *Hylarana baramica*, and *Ingerophrynus divergens* was influenced by stream depth (see **Figure 4**). Both species are known to breed in stream-side pools.² *Limnonectes leporinus* showed preference for shallow streams. *Staurois guttatus* preferred areas with less sand. Conversely, the presence of *Phrynoidis asper* was influenced by the presence of soil or sand. In contrast, the *Hylarana glandulosa*, *H. megalonesa*, *H. signata*, *A. baluensis* and *Limnonectes* aff. *kuhlii* assemblage was clustered in the centre of the ordination diagram. This suggests that these species had no habitat preferences based on the chosen ecological variables. Thus, these species were grouped as generalists.

3.3 Species complementarity between Teraja and Ulu Temburong National Park

The BTPF with 39 and the UTMNP with 70 species had 30 species of frogs in common. The two regions had a low complementarity (CBR = 0.550).

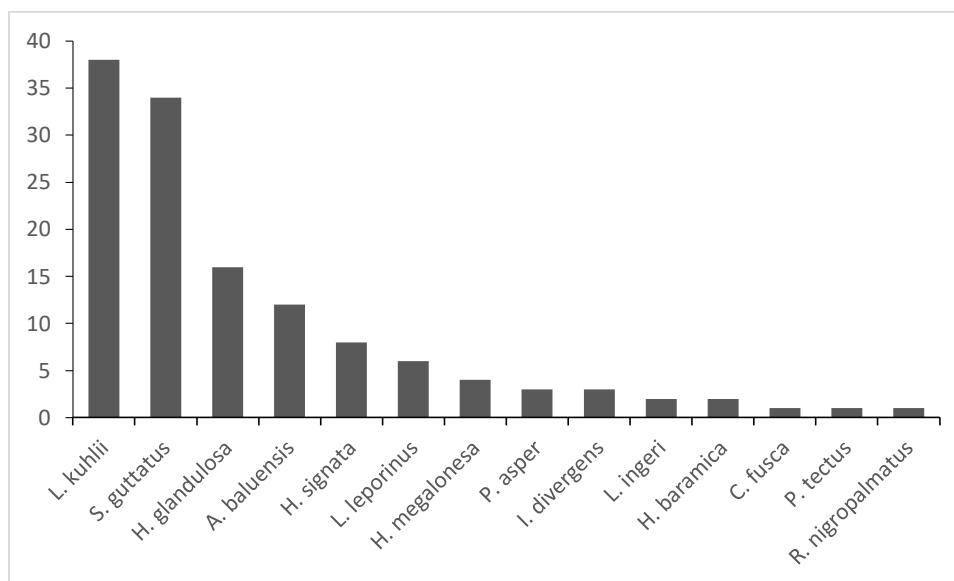


Figure 3. Rank abundance of species found in all riparian plots.

4. Discussion

4.1 Species diversity

Extensive studies of the amphibians of Brunei have only been done in restricted parts of the country including Ulu Temburong National Park^{24,27,42} and Tasek Merimbum Heritage Park.⁴⁴

This is the first detailed study of anuran diversity in the proposed extension of the Bukit Teraja Protection Forest. The current survey identified 39 species of frogs and thus provides a baseline inventory of anuran species diversity of this area. Anuran diversity of the BTPF is relatively low when compared to other sites with similar lowland forest type within Borneo such as the Ulu Temburong National Park¹⁹ (70 species), Nanga Tekalit in Sarawak⁴⁴ (60 species) and Crocker Range National Park in Sabah⁴⁶ (59 species) and Danum Valley (50 species).⁴⁶ However, among these sites the BTPF has the lowest elevational profile possibly providing a lower variety of suitable breeding sites.

Several more promising areas within the BTPF remain unexplored including the Beluluk Waterfall, Talingan Waterfall and Tebedak Waterfall as well as the Bukit Teraja Protection

Area itself. Species such as *Ingerophrynus quadriporcatus*, and frogs from the genus *Kalophrynus* might occur in area but were not encountered during the surveys. Further surveys will most likely result in the rise of the number of amphibians in the BTPF.

4.2 New records

The current study extends the knowledge of the range distribution of frogs in Borneo. The four frogs (*Hylarana nicobariensis*, *Kaloula baleata*, *Limnonectes malesianus*, and *Microhyla perparva*) found in this study have already been known to occur in the Malaysian and the Indonesian parts of Borneo as well as in other parts of south-east Asia. It can now be confirmed that these species occur in Brunei and that the BTPF might possibly be one of the few places in Brunei where these species can be found. This finding also emphasizes that the inventory of Brunei's amphibians is far from complete.

4.3 Species richness, distribution and abundance of riparian frogs

Fisher's alpha indicated that Kancil was the most diverse stream and the Burung was the least diverse although Burung had more species than

Kancil (nine and seven species, respectively). This is probably because of the difference in species evenness. Burung might have more species but only a few species were dominating in abundance.

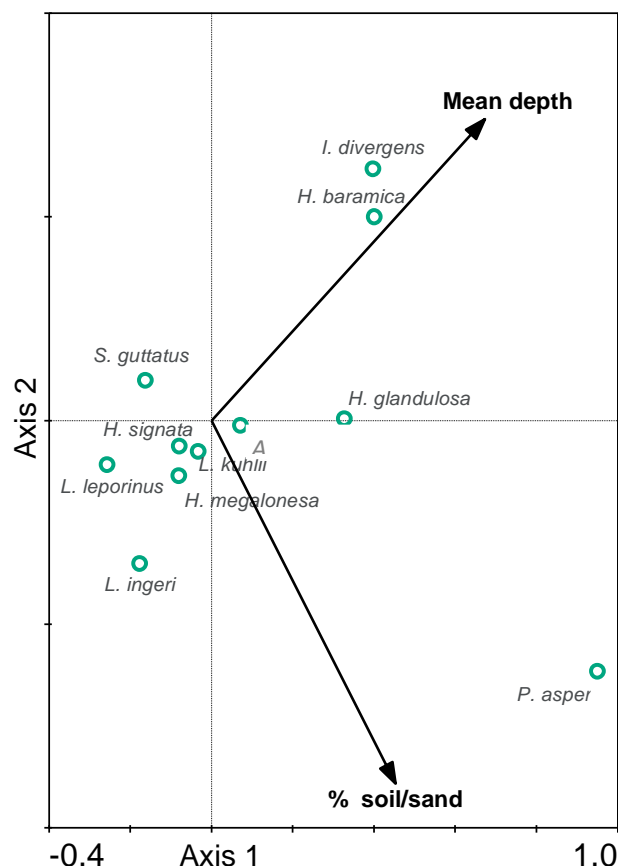


Figure 4. CCA biplot of the relations between environmental variables and frog assemblage. Arrows are environmental variables. Direction of arrow indicates correlation with that axis and length indicates the strength of the correlation.

Hylarana glandulosa, *Alcalus baluensis* and *Limnonectes* aff. *kuhlii* were the three most widely distributed species in all six streams. *Hylarana glandulosa* is generally found in peat swamps.^{2, 47} The close proximity of the peat swamp forest of the Ulu Mendaram Conservation Area might explain its occurrence in Teraja. Moreover, the presence of some juveniles of *H. glandulosa* in streams reflected that this species might use streams as dispersal routes. *Limnonectes* aff. *kuhlii* is probably the most common frog species in the lowland rainforest of Brunei, reportedly found in

small streams with rocky bottom.^{24, 47} However, the individuals of *L. aff. kuhlii* in this study were encountered at streams with sandy bottom. As this species is likely to be a complex of cryptic species, it cannot be ruled out that the differences in habitat use between study areas reflect habitat preferences of two different species within the complex. Alternatively, this reflects its ability to occupy and survive in many different habitats. Another species that showed wide distribution at all studied streams except for Anai was *Limnonectes leporinus*. *Limnonectes leporinus* has been known to dwell along medium and large streams.^{2, 48} Thus, Anai being the smallest stream it might not be preferred by *L. leporinus*. *Staurois guttatus* and *Hylarana signata* were both absent in Kupu and Burung. This may reflect the intermittent nature of these streams (i.e. both streams are short and probably dry out in periods without rainfall with a concomitant drop in humidity to which *S. guttatus* is sensitive).

Abundance for most species at streams was very low (see **Figure 3**). *Chaperina fusca*, *Philautus tectus* and *Rhacophorus nigropalmatus* were only found once inside riparian plots. *P. tectus* was also found outside a plot in Ular. Given that *P. tectus* is listed as vulnerable occurring only in primary forest streams (see **Table 1**) its presence in Ular and Cicak indicate that these stream habitats were pristine. *C. fusca* were also found in Kancil, Burung and Kupu but all individuals were found outside plots. *Rhacophorus nigropalmatus* is known to live very high in the canopy of primary lowland rainforest and only comes down from the trees to breed in forest ponds such as pig or rhino wallows.^{2, 47} Interestingly, the only individual of *R. nigropalmatus* in this study was found above a pool at one of the waterfalls in Burung.

4.4 Environmental influences on frog assemblages
Canonical correspondence analysis of the anuran assemblages in the BTPF revealed that species composition was influenced by two stream characteristics: stream depth and the presence of soil/sand. Stream depth can be translated to

occurrence of stream-side pools. The edges of a pool might be used by frogs as oviposition sites. *Hylarana baramica* and *Ingerophrynus divergens* showed preference for pool areas. *I. divergens* is known to use stream-side pools as breeding sites.² In contrast, there have been no reports of *H. baramica* using stream-side pools as oviposition sites. The assemblage of *H. glandulosa*, *H. megalonesa*, *H. signata*, *A. baluensis* and *L. aff. kuhlii* were clustered in the centre of the CCA biplot suggesting that these species had no habitat preference and are thus likely to be habitat generalists within streams. This is in contrast to the previous study by Keller et al.²⁷ in the UTNP. For instance, *Hylarana signata* was found to be associated with large to mid-sized streams. However, in Teraja, *H. signata* was also encountered at Anai which was the narrowest studied stream. *Limnonectes. aff. kuhlii* was previously found to be associated with the presence of riffles and runs²⁷ and thus did show microhabitat specificity. *Limnonectes ingeri* is a pond breeder but was not grouped together with *H. baramica* and *I. divergens*. *Staurois guttatus* is known to be associated with rocky streams and the presence of waterfalls. Thus, it showed preference for less sandy or muddy areas. On the other hand, *Phrynoides asper*, which is a forest litter toad, preferred sandy or muddy areas.

The results of this study are different from that of Parris¹⁴ in Queensland, Australia and Keller et al.²⁷ in UTNP. Both studies revealed that anuran assemblages in streams were affected by three stream characteristics and their environment including the density of understorey vegetation, stream size and the presence of waterfalls or slope. Riparian vegetation is an important structural component used by frogs as calling or resting sites.¹⁴ However, the density of vegetation among the streams in Teraja showed little variation and thus no significant correlation with species assemblage although several species such as *A. baluensis*, *I. divergens* and *S. guttatus* were often found sitting on the leaves of understorey vegetation. Moreover, stream size was also

important in explaining the differential species composition in other studies.²⁷ Many frogs prefer large streams due to their ability to retain water for a very long period of time for tadpoles to metamorphose.⁴⁸ In contrast, stream size was not a determinant of anuran assemblages in the BTPF probably because streams were not variable enough. There was no large stream sampled in the BTPF. Furthermore, the presence of waterfalls, riffles, and runs as well as the general steepness of streams also influenced frog assemblage composition in the UTNP.²⁷ Although the BTPF had a lot of waterfalls, this factor showed no influence on species composition.

4.5 Complementarity between Teraja and Ulu Temburong

Complementarity analysis showed that there was a low complementarity or resemblance in anuran species richness between BTPF and UTNP. This is due to the low number of species overlap between both regions. Species occurring in the BTPF not found in the UTNP include all of the new records (*H. nicobariensis*, *K. baleata*, *L. malesianus*, *M. perparva*). Conversely, many of the litter frogs (Megophryidae) and all of the species in the genera *Ansonia*, *Kalophrynus* and *Meristogenys* did not occur in BTPF. Low complementarity between the two regions might be due to the differences in topography, differences in habitat structure, biogeographical distance or a combination of these factors. For example, high complementarity was found between UTNP and lowland forests in Mulu, as they are much closer in terms of biogeographic distance (CBR = 0.636, based on⁷ and pers. observations).

It is important to conserve areas with high biodiversity, but areas with complementary fauna must also be considered for conservation.⁴⁹ Although the BTPF has a lower frog diversity than the UTNP, the low species overlap between the regions suggests that the proposed extension of the Bukit Teraja Protection Forest harbours a distinctive fauna that should be conserved. It is thus lauded that the Forestry Department of Brunei

Darussalam has been tasked to gazette the proposed area, following the proposal to take action passed by the Heart of Borneo National Council.

On a larger regional scale, the diversity of stream-associated frogs within lowland mixed-dipterocarp rainforest sites in northern Borneo shows significant turnover in species richness and composition with stream width a good predictor of frog assemblages both locally and regionally.^{7,28} Thus, beta diversity plays a significant role in maintaining regional diversity of stream-associated frogs in Brunei and neighbouring Malaysia.¹⁹ In regard to its high beta diversity, and in order to protect the diversity of riparian anurans of northwestern Borneo, it is necessary not only to focus on a few hotspots, such as the Ulu Temburong National Park, but to put conservation efforts on other, less diverse, sites as well. The rate of species turnover in north-western Borneo is comparable to that of New Guinea and Bolivia and this calls for a network of protected forests.²⁸

5. Conclusion

In conclusion, this study confirms the presence of a substantial amount of anuran diversity in the BTPF, providing a baseline inventory for future amphibian research in this area. The four new records increase the anuran diversity in Brunei and extend the range of frog distributions in Borneo. Spatial and environmental effects both had an effect on the species assemblage of riparian frogs in the BTPF. The low species complementarity detected between the BTPF and the UTNP emphasizes the importance of conserving areas with not only high species richness but also areas with unique fauna. Since the forest is under threat of development, upgrading the proposed extension of the Bukit Teraja Protection Forest to a protection forest is strongly recommended.

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References

- [1] C.N. Jenkins, S.L. Pimm, L.N. Joppa, *Proceedings National Academy Sciences*, E2602-E2610, 2013.
- [2] R.F. Inger, R.B. Stuebing, T.U. Grafe, J.M. Dehling, *A Field Guide to the Frogs of Borneo*, 3rd Edition, 2017.
- [3] N.S. Sodhi, L.P. Koh, B.W. Brook, P.K.L. Ng, Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution*, 19, 654-660, 2004.
- [4] M. Pfeifer, V. Lefebvre, C.A. Peres, C. Banks-Leite, O.R. Wearn, C.J. Marsh, S.H.M. Butchart, V. Arroyo-Rodríguez, J. Barlow, A. Cerezo, L. Cisneros, N. D'cruze, D. Faria, A. Hadley, S.M. Harris, B.T. Klingbeil, U. Kormann, L. Lens, G.F. Medina-Rangel, J.C. Morante-Filho, P. Olivier, S.L. Peters, A. Pidgeon, D.B. Ribeiro, C. Scherber, L. Schneider-Maunoury, M. Struebig, N. Urbina-Cardona, J.I. Watling, M.R. Willig, E.M. Wood, R.M. Ewers, *Nature*, 551, 187-191, 2017.
- [5] D.K. Skelly, *Ecology*, 76, 150-164, 1995.
- [6] J.M. Hero, C. Gascon, W.E. Magnusson, *Australian Journal of Ecology*, 23, 474-482, 1998.

- [7] Y.M. Pui, I Das, *Naturalists, Explorers and Field Scientists in South-east Asia and Australasia, Topics in Biodiversity and Conservation 15*, Ed, I. Das, A.A. Tuen, Springer International Publishing Switzerland, 143-155, 2016.
- [8] A. Haas, B.H. Kueh, A. Joseph, M. bin Asri, I. Das, R. Hagmann, L. Schwander, S. Hertwig, *Evolutionary Systematics*, 2, 89-114, 2018.
- [9] G. Caughley, A. Gunn, *Conservation Biology in Theory and Practice*, 1996.
- [10] G.C. Daily, G. Ceballos, J. Pacheco, G. Suzán, A. Sánchez-Azofeifa, *Conservation Biology*, 17, 1-11, 2003.
- [11] E. Pineda, G. Halffter, *Biological Conservation*, 117, 499-508, 2004.
- [12] G. Santos-Barrera, J. Pacheco, F. Mendoza-Quijano, F. Bolaños, G. Chaves, G.C. Daily, P.R. Ehrlich, G. Ceballos, *Revista de Biología Tropical*, 56, 755-778, 2008.
- [13] J.N. Urbina-Cardona, M. Olivares-Pérez, V.H. Reynoso, *Biological Conservation*, 132, 61-75, 2006.
- [14] K.M. Parris, *Ecography*, 27, 392-400, 2004.
- [15] R. Ernst, M-O. Rödel, *Ecotropica*, 12, 113-129, 2006.
- [16] R. Ernst, M-O. Rödel, *Journal of Tropical Ecology*, 24, 111-120, 2008.
- [17] R. Ernst, M-O. Rödel, *Ecology*, 86, 3111-3118, 2005.
- [18] M. Menin, A.P. Lima, W.E. Magnusson, F. Waldez, *Journal of Tropical Ecology*, 23, 539-547, 2007.
- [19] T.U. Grafe, I. Das, *Conservation Biology of Amphibians of Asia. Status of Conservation and Decline of Amphibians: Eastern Hemisphere*, Ed, H. Heatwole, I. Das, Natural History Publications (Borneo), Kota Kinabalu, 300-309, 2014.
- [20] J. Davies, K. Abu Salim, *Forests and Trees of Brunei Darussalam*, Ed, K.M. Wong, K. Abu Salim, Universiti Brunei Darussalam, 15-34, 1999.
- [21] K. Abu Salim, K.M. Wong, *Forests and Trees of Brunei Darussalam*, Ed, K.M. Wong, K. Abu Salim, Universiti Brunei Darussalam, Gadong, 1-14, 1999.
- [22] P. Engbers, PNHS Teraja Survey highlights 2010-2011, 2011.
- [23] R. Malkmus, U. Manthey, G. Vogel, P. Hoffmann, J. Kosuch, J. *Amphibians and Reptiles of Mount Kinabalu (North Borneo)*. A.R.G. Gantner Verlag, Ruggell, Lichtenstein, 2002.
- [24] I. Das, *Amphibians and Reptiles of Brunei*, Natural History Publications (Borneo), Kota Kinabalu, 2007.
- [25] D.R. Frost, *Amphibian Species of the World: an Online Reference*, Version 6.0, American Museum of Natural History, New York, 2019. <http://research.amnh.org/herpetology/amphibia/index.html>. [Accessed 13 July 2019]
- [26] K.M. Parris, M.A. McCarthy, *Journal of Ecology*, 24, 495-502, 1999.
- [27] A. Keller, M-O. Rödel, K.E. Linsenmair, T.U. Grafe, *Journal of Animal Ecology*, 78, 305-314, 2009.
- [28] S. Goutte, H.H. Ahmad Sah, T.U. Grafe, *Herpetological Journal*, 27, 25-32, 2017.
- [29] J.W. Ribeiro, T. Siqueira, G.L. Brejão, E.F. Zipkin, *Ecological Applications*, 28, 1554-1564, 2018.
- [30] R.K. Colwell, *EstimateS 8.2 Users Guide. Statistical estimation of species richness and shared species from samples*, University of Connecticut, Connecticut, 2009.
- [31] C.J. Krebs, *Ecological Methodology*. 2nd ed. Addison Welsey Longman, Inc. Menlo Park, California, 1999.
- [32] C.J.F. ter Braak, P. Šmilauer, *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination* (version 4.5). Ithaca, New York, 2002.
- [33] A. Guisan, S.B. Weiss, A.D. Weiss, *Plant Ecology*, 143, 107-122, 1999.

- [34] K. Sasaki, M.W. Palmer, T. Hayashi, *Community Ecology*, 6, 219-227, 2005.
- [35] G.V. Ryckegem, A. Verbeken, *Fungal Diversity*, 20, 209-233, 2005.
- [36] M.W. Palmer, *Ecology*, 74, 2215-2230, 1993.
- [37] J. Leps, P. Smilauer, *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University, Cambridge, UK. 2003.
- [38] H. Wolda, *Oecologia*, 50, 296-302, 1981.
- [39] A. Adite, R. Van Thielen, *Environmental Biology of Fishes*, 43, 381-381, 1995.
- [40] L.D. Wilson, J.R. McCranie, *Amphibian and Reptile Conservation*, 3, 34-48, 2003.
- [41] Global Amphibian Assessment, 2019. <https://www.iucn-amphibians.org/> [Accessed 19 July 2019]
- [42] T.U. Grafe, A. Keller, *Salamandra*, 45, 25-38, 2009.
- [43] I. Das, S. Nyawa, J.K. Charles, *A Guide to the Amphibians and Reptiles of Tasek Merimbun Heritage Park Brunei Darussalam*. Brunei Museums Department, Bandar Seri Begawan, 2008.
- [44] R.F. Inger, *The Natural History Journal of Chulalongkorn University*, 3, 9-15, 2004.
- [45] I. Das, *Amphibian and Reptile Conservation*, 4, 3-11, 2006.
- [46] J.A. Sheridan, S.D. Howard, P. Yambun, J.L. Rice, R. Cadwallader-Staub, A. Karoulus, D. Bickford, *Tropical Natural History*, 12, 1-8, 2012.
- [47] A. Haas, I. Das, *Frogs of Borneo*, 2019. www.frogsofborneo.org [Accessed 19 July 2019]
- [48] R. Phochayavanich, H.K. Voris, W. Khonsue, S. Thunhikorn, K. Thirakhupt, *Zoological Studies*, 49, 632-639, 2010.
- [49] C. Azevedo-Ramos, U. Galatti, *Biological Conservation*, 103, 103-111, 2002.

Table 1. Anuran amphibian species recorded from the proposed extension of the Bukit Teraja Protection Forest. Data sources (P = encountered in plots, O = encountered outside of plots). Conservation status (Con. status) follows the Global Amphibian Assessment listings of IUCN 2004 Red List Categories (LC = Least Concern, NT = Near Threatened, VU = Vulnerable). New records are underlined.

Species	Data source	Habitat	Con. status	Total abundance at streams	Rank abundance at streams
Bufonidae					
<i>Ansonia</i> sp.	O	Pond behind Teraja Longhouse	-	-	-
<i>Ingerophrynus divergens</i>	P	On leaves and branches	LC	3	8.5
<i>Phrynoidis asper</i>	P	On rock at Cicak	LC	3	8.5
<i>Phrynoidis juxtasper</i>	O	Near Wong Kadir Waterfall	LC	-	-
Ceratobatrachidae					
<i>Alcalus baluensis</i>	P	Mostly on rocks and small plants	LC	12	4
Dicroglossidae					
<i>Fejervarya limnocharis</i>	O	On forest road	LC	-	-
<i>Limnonectes ibanorum</i>	O	On sand in front of Teraja Waterfall	NT	-	-
<i>Limnonectes ingeri</i>	P	On rocks at Burung	NT	2	10.5
<i>Limnonectes</i> aff. <i>kuhlii</i>	P	Mostly in water, on rocks and ground	LC	38	1
<i>Limnonectes laticeps</i>	O	Waterfall	LC	-	-

<i>Limnonectes leporinus</i>	P	In water, on ground and rocks	LC	6	6
<i>Limnonectes malesianus</i>	O	On forest trail to Teraja Waterfall	NT	-	-
<i>Limnonectes paramacrodon</i>	O	On forest trail to Teraja Waterfall	NT	-	-
<i>Occidozyga baluensis</i>	O	In puddle on trail to Teraja Waterfall	NT	-	-
<i>Occidozyga sumatrana</i>	O	In pond behind Teraja Longhouse	LC	-	-

Megophryidae

<i>Leptobrachium abbotti</i>	O	Tadpoles above Teraja Waterfall	LC	-	-
<i>Leptolalax gracilis</i>	O	Forest above the Teraja Waterfall	NT	-	-

Microhylidae

<i>Chaperina fusca</i>	P	On ground in Kancil	LC	1	13
<i>Kaloula baleata</i>	O	Rain pool behind Teraja Longhouse	LC	-	-
<i>Metaphrynella sundana</i>	O	In a tree hole near Teraja Waterfall	LC	-	-
<i>Microhyla borneensis</i>	O	Pond behind Teraja Longhouse	LC	-	-
<i>Microhyla perparva</i>	O	Pond behind Teraja Longhouse	NT	-	-
<i>Microhyla petrigena</i>	O	Pond behind Teraja Longhouse	NT	-	-

Ranidae

<i>Hylarana baramica</i>	P	On rocks, leaves in Kupu and Burung	LC	2	10.5
<i>Hylarana erythraea</i>	O	Road side near ditch	LC	-	-
<i>Hylarana glandulosa</i>	P	On ground, rocks, leaves and branches	LC	16	3
<i>Hylarana megalonesa</i>	P	Mostly on roots and rocks	LC	4	7
<i>Hylarana nicobariensis</i>	O	Forest up Teraja Waterfall	LC	-	-
<i>Hylarana signata</i>	P	On roots, branches, rocks and ground	LC	8	5
<i>Staurois guttatus</i>	P	Mostly on leaves, branches and rocks	LC	34	2
<i>Staurois latopalatus</i>	O	On rock near Teraja Waterfall	LC	-	-

Rhacophoridae

<i>Kurixalus</i>					
<i>appendiculatus</i>	O	Forest behind Teraja Longhouse	LC	0	13
<i>Nyctixalus pictus</i>	O	Vegetation behind Teraja Longhouse	NT	-	-
<i>Philautus tectus</i>	P	On leaves of low vegetation, Cicak	VU	1	13
<i>Polypedates leucomystax</i>	O	Vegetation behind Teraja Longhouse	LC	-	-
<i>Polypedates macrotis</i>	O	Vegetation behind Teraja Longhouse	LC	0	-
<i>Rhacophorus</i>					
<i>nigropalmatus</i>	P	Above pool in Burung	LC	1	13
<i>Rhacophorus pardalis</i>	O	Vegetation behind Teraja Longhouse	LC	0	-
<i>Zhangixalus dulitensis</i>	O	Vegetation behind Teraja Longhouse	NT	0	-