Fluvial biotopes influence macroinvertebrate biodiversity in South-East Asian tropical streams

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Abstract. Given the widespread degradation of aquatic systems caused by land-use changes associated with palm oil production in South-East Asia, it is imperative to identify and study the remaining undisturbed rivers and streams. Stream macroinvertebrates are reliable indicators of environmental health. Linking the community structure of these organisms to natural hydraulic and geomorphic conditions (categorized as biotopes) is vital for the conservation and restoration of streams. This study characterizes the effects of biotopes on macroinvertebrate community structure in three streams within Ulu Temburong National Park in northern Borneo. Biotopes within these streams were categorized as either bedrock (waterfalls and cascades) or mixed substrate (riffles and pools). In total, 119 taxa were collected from all sampled biotopes, but not all taxa were collected from each stream. Biotopes were statistically distinct in terms of taxonomic richness, but not mean individual density or average community biomass. There were differences in community structure between waterfalls, cascades, pools, and riffles. The survey suggests that pool and riffle biotopes were more vulnerable to scouring flows and had similar community structure, while waterfalls and cascades likely experienced lower sheer stress during floods and had similar macroinvertebrate communities. This study has found that classification and mapping of macroinvertebrates with biotope theory in pristine, tropical streams is a useful framework for simplifying the many linkages between ecology, geomorphology, and hydrology. These natural patterns increase our understanding of tropical streams and can be used to assess the impacts of forest degradation.

Key words: biodiversity; biotopes; macroinvertebrates; palm oil plantations; tropical streams.

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Introduction

Human activities are increasing the urgency for investigating the basic tropical stream ecology (Dolný et al. 2011, Dudgeon 2015, Lewis et al. 2015, Ramírez et al. 2015). This is particularly apparent in South-East Asia, where rising world demand for palm oil is driving deforestation. In spite of this phenomenon, large areas of the South-East Asia tropics are not being actively studied (Ramírez et al. 2015). This includes Borneo, an island that is home to one of the oldest rain forests in the world. A recent study suggests that approximately 80% of Malaysian Borneo rain forests have been severely impacted by deforestation and conversion to palm oil plantations (Bryan et al. 2013). This land-use change and the subsequent loss of aquatic biodiversity limit the ability to study the properties of natural systems.

One approach to studying the tropical stream ecology is the classification and mapping of invertebrates associated with geomorphic and

Table 1. Flow type descriptions used to identify the physical biotopes present in the field (based on Newson and Newson 2000 and Parasiewicz 2007).

Associated biotope	Flow type	Description
Waterfall	Free fall	Water falls vertically and without obstruction from a distinct feature, generally more than 1 m high and often across the full channel width
Cascade	Chute	Fast flow with a smooth boundary and turbulent flow over boulders or bedrock. Flow is in contact with the substrate and exhibits upstream convergence and downstream divergence
Pool	Scarcely perceptible flow	Surface foam appears to be stationary and reflections are not distorted. A stick floated on the water's surface will remain still
Riffle	Unbroken standing waves	Undular standing waves in which the crest faces upstream without "breaking"

hydraulic conditions. This technique has provided a robust evaluation of the importance of hydraulics, sediment dynamics, and geomorphology on the temperate stream habitats (Bunn and Arthington 2002, McManamay et al. 2014, Villeneuve et al. 2015) and is operationally referred to as "biotope theory" (Dahl 1908, Townsend and Hildrew 1994, Newson and Newson 2000). At its core, biotope theory is based on observable environmental conditions (Jowett 1993, Wadeson 1995, Padmore 1998, Newson and Newson 2000, Clifford et al. 2006). As such, biotopes refer to the abiotic environment; in streams and rivers, these are typically observed as surface flow features (i.e., flow biotopes), such as riffles, pools, and waterfalls. These biotopes reflect the combinations of substrate type, depth, and velocity, which ultimately influence macroinvertebrate biodiversity (Newson and Newson 2000, Parasiewicz 2007; Table 1).

Few studies conducted in the tropics have strictly employed biotopes as a sampling framework (Furtado 1969, St Quentin 1973, Dudgeon 1994, Yule 1996, Ramírez et al. 1998, Principe 2008). However, other studies have modified the biotope theory to assess the longitudinal assemblage structure of tropical rivers (Bishop 1973, Rundle et al. 1993, Greathouse et al. 2005). Not surprisingly, there is still much to learn about the mechanisms by which the structure, compositions, and patterns of biotopes can affect the macroinvertebrate biodiversity in the tropics (Bisson et al. 1982, Ramírez and Pringle 1998, Cheshire et al. 2005, Md Rawi et al. 2014).

The configuration and hydraulic properties of biotopes are highly variable and depend on the process by which they were formed and position in the channel (Bisson et al. 1982). Many tropical headwaters experience flash floods and are categorized as relatively unpredictable systems (Boulton et al. 2008). This range in conditions can result in biotopes, especially those with mixed substrates (i.e., pools and riffles), exhibiting a continuum of conditions, which may result in two distinct environments. For example, during low flows, tropical streams are complex systems exhibiting a mix of flow biotopes (i.e., pools, riffles, and cascades) and functional habitats (i.e., wood debris, leaf litter, cobbles, and gravel; *sensu* Harper et al. 1995, Harvey et al. 2008); however, during a flood event, these streams become homogeneous as water rises to form a uniform flood biotope. For naturally disturbed systems, fixed habitat features create refuge space for macroinvertebrates during high flows (Bond and Downes 2000), suggesting that some biotopes and habitat features may have a disproportionate importance on the maintenance of biodiversity (Buendia et al. 2014).

It is vitally important to increase our understanding of tropical stream ecosystems in order to assess and mitigate the impacts of forest modification and destruction on biodiversity (Dolný et al. 2011). Streams flowing through Ulu Temburong National Park in northern Borneo are still surrounded by unlogged primary rain forest, with no roads (Sheldon 2011). This provides a unique opportunity to study the importance of biotopes in preserving the macroinvertebrate biodiversity. This study aimed to evaluate the macroinvertebrate biodiversity and community structure among three study streams in four
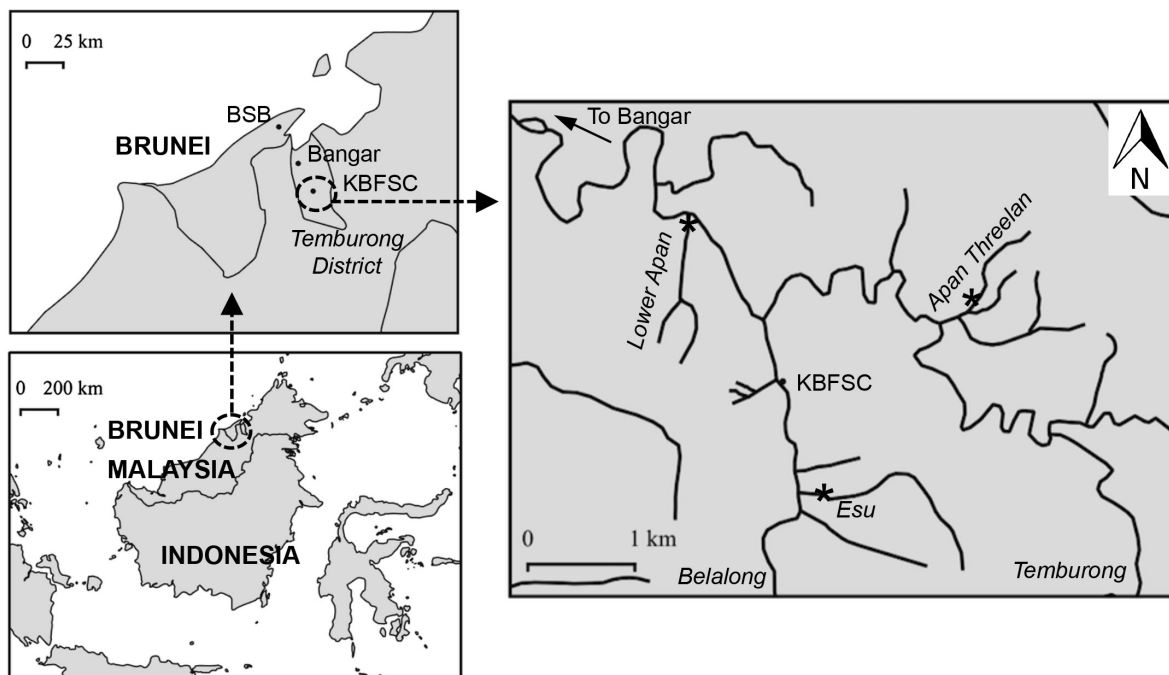
Fig. 1. Brunei is situated in the north of Borneo. The country is split into two contiguous regions, with Ulu Temburong National park located within the Temburong District. Kuala Belalong Field Study Centre (KBFSC) and the study reaches including Lower Apan, Esu, and Threelan (highlighted by asterisks) are all within the national park.

types of biotopes: pools, riffles, cascades, and waterfalls. This study specifically evaluated the importance of biotopes, rather than streams or reaches, for the operational scale of biodiversity.

METHODS

Study sites

This project was conducted in Ulu Temburong National Park in the Temburong District of Brunei, northern Borneo (Fig. 1). The national park has sharp topography; the elevation of Kuala Belalong is 30 m. a.s.l., but rises to mountain peaks of 1850 m. a.s.l. at Bukit Pagon and 913 m. a.s.l. at Bukit Belalong (Dykes 1994). The area is composed of deep V-shaped valleys with no floodplains, and many waterfalls occur along the tributaries that drain the mountains. The geology is characterized by sedimentary rocks with some sandstone pebbles that have been transported from the headwaters in the southeast. Brunei has a tropical climate, which is weakly influenced by the South-East Asia monsoon season (Dykes 1996). Despite the annual

climate pattern, daily weather in the Ulu Temburong National Park is very erratic. Most rain originates as convection cells; as the cells rise over Bukit Belalong and Bukit Pagon, they condense, producing heavy rainfall (Cranbrook and Edwards 1994). Dykes (1997) has argued that no month can be considered dry as every month of the year receives an average of over 200 mm of rainfall.

Three streams situated near the Kuala Belalong Field Study Centre (KBFSC) were the focus of this study: Sungai Lower Apan, Sungai Esu, and Sungai Apan Threelan (Fig. 1). All three streams are tributaries of Sungai Belalong or Sungai Temburong and were chosen because they each contain a mixture of biotopes. Further, these streams are uninfluenced by anthropogenic factors, and their natural water quality is high (Sheldon 2011), which is important because the variation in water quality impacts the biodiversity patterns (Everaert et al. 2014). Lower Apan has the longest reach (90 m), exceeding those of Esu (70 m) and Apan Threelan (75 m). For each stream, the survey locations started just before

the first waterfall upstream from each confluence with the main rivers (Belalong or Temburong). Esu and Apan Threelan had waterfalls higher (approximately 6 m high) than those of Lower Apan (approximately 3 m high). Sampling locations began 360 m upstream from the confluence of Apan Threelan and Temburong, 157 m upstream from the confluence of Esu and Belalong, and 60 m upstream from the confluence of Lower Apan and Temburong (Fig. 1). Sampling was conducted during April 2013.

Field methods

Biotopes (i.e., pools, riffles, cascades, and waterfalls) were mapped in each of the study reaches by observing river surface features at baseflows (Newson and Newson 2000, Parasiewicz 2007). For the Lower Apan reach, 14 biotopes were sampled: five pools, two riffles, five cascades, and two waterfalls. For the Esu reach, 10 biotopes were sampled: five pools, one riffle, two cascades, and two waterfalls. For the Threelan reach, 11 biotopes were sampled: six pools, two riffles, one cascade, and two waterfalls. Across the entire study 16 pools, five riffles, eight cascades, and six waterfalls were sampled.

Features of each biotope habitat were measured. Large habitat features can form biotopes, such as boulders and tree trunks that dam the water flow (Fig. 2). Conversely, habitat features, such as leaf litter, can occur within biotopes. Physical conditions of the biotopes were measured with surveying tapes and meter sticks and included wetted and bankfull width and channel

Fig. 2. Extensive debris dam at waterfall on Sungai Esu. A man is highlighted in white circle to indicate scale.

depth. Stream velocity was measured using an electromagnetic flowmeter (Valeport model 801; Valeport Ltd., Totnes, UK). Benthic substrates were assessed visually and categorized according to the percentage gravel, cobble, boulder, and bedrock. The presence or absence of functional habitats was recorded including wood debris (large and small), leaf litter, and moss; trailing roots in all biotopes were also recorded.

Benthic macroinvertebrates were sampled in each biotope using a Surber sample (0.10 m^2; 250-µm mesh). Decapods are not effectively sampled by Surber sampling (Jacobsen et al. 2008) and therefore were not included in this study. Because of low macroinvertebrate densities, three samples were composited for each biotope.

Laboratory methods

Owing to the requirements of specimen export permits, macroinvertebrate samples were processed under (10×) magnification at KBFSC and preserved in 70% ethanol. Once exported to the UK, macroinvertebrates were identified to the lowest practical taxonomic level and enumerated; the total body lengths were measured to the nearest 0.5 mm. The macroinvertebrate diversity of Borneo is still mostly undescribed; therefore, the identifications were made using the few keys available, including Dudgeon (1999) and Yule and Yong (2004) as well as open source identification methods. Most specimens were identified to the genus level or morphotyped to a similar level. However, some taxa, such as Coleoptera and Diptera specimens, could only be identified to the family level (Yule 2004; J. Manfred, *personal communication*).

Taxa-specific ash-free dry mass (AFDM) was calculated using length–mass regressions (Benke et al. 1999, Sabo et al. 2002, McNeely et al. 2007). When no taxon-specific equations were available, estimates were made using the equations from taxa with similar body shapes (Ramírez and Pringle 1998). Where only dry mass (DM) estimates were available, the values were converted to AFDM following Waters (1977).

Data analysis

Macroinvertebrate biodiversity, richness, density, and biomass (AFDM) were quantified for all of the biotopes in each of the tributaries. Comparisons among tributaries and biotopes

were carried out via a two-way ANOVA followed by Tukey's post hoc tests. Richness and density met the required statistical assumptions (i.e., normally distributed, homoscedastic residuals), but biomass was square-root-transformed in order to minimize the deviations from normality and homoscedasticity. Similarity percentage analysis (SIMPER) was used to identify the taxa that contributed most to the average dissimilarity among biotopes. Analysis of similarities (ANOSIM; Clarke 1993) was used to test for the differences in abundance and composition of macroinvertebrates among the biotopes. The global R statistic, which ranges from −1 to +1, measures the distinctiveness of the grouping according to ANOSIM. Values close to 1 indicate high similarity among groups, 0 indicates that there is no relationship in composition among the groups, and −1 indicates that the samples are distinct to each group. Abundance data were used for both SIMPER and ANOSIM, and both of these tests use the Bray–Curtis index, a popular dissimilarity index for ecological data (Borcard et al. 2012).

Macroinvertebrate assemblage structures were examined among biotopes using a hierarchical cluster analysis carried out using Bray–Curtis index values (Thomas et al. 2013). Bray–Curtis dissimilarity matrices were calculated, summarizing the compositional dissimilarity of sites based on the density of taxa at each site. Non-metric multidimensional scaling (NMDS) analysis was used to test the robustness of groups defined by the cluster analysis. NMDS is a flexible statistical tool with few statistical assumptions. The stress value was 0.16, which indicates a good ordination (Thomas et al. 2013). Environmental data were fitted to the ordination using the "envfit" function of the vegan package in the statistical computing environment R (R Core Team 2013). The "envfit" function uses the mixed environmental data including both continuous variables and categorical data (Oksanen 2016). Only the statistically significant environmental variables (i.e., $P < 0.05$) were fitted and are independent of the NMDS ordination.

RESULTS

Site description

Many biotopes in Lower Apan were unconstrained laterally, transitioning directly from the stream to the rain forest, whereas Esu and Apan Threelan were constrained by riparian bedrock, resulting in narrower bankfull widths. Thus, the Lower Apan had more trailing roots and terrestrial vegetation at the margins of the stream compared with the other study reaches. All of the study reaches exhibited evidence of landslides, and large wood debris was often found to be lodged between waterfalls, sometimes creating dams. Many of these dams were quite large; for example, Fig. 2 shows a large debris dam at a waterfall on Esu.

Esu had the highest baseflow discharge ($0.92 \, m^3/s$) compared with Lower Apan ($0.62 \, m^3/s$) and Apan Threelan ($0.18 \, m^3/s$; Table 2). However, bankfull width ($F_{2,29} = 1.84$, $P = 0.18$) and wetted width ($F_{2,29} = 1.23$, $P = 0.30$) did not differ among tributaries. Average depths differed significantly among tributaries ($F_{2,29} = 15.79$, $P < 0.001$) with Apan Threelan having the shallowest biotopes (0.16 m), followed by Lower Apan (0.25 m) and then Esu (0.37 m). Average velocities were higher along Lower Apan (0.39 m/s) than along Esu (0.37 m/s) and Apan Threelan (0.20 m/s; $F_{2,29} = 4.66$, $P < 0.05$).

Bankfull widths differed among biotopes ($F_{3,29} = 3.56$, $P < 0.05$), with waterfalls (7.07 m)

Table 2. Average physical conditions including depth, wetted and bankfull width, velocity, and discharge of the three study streams (pooled across all biotopes) and of the four biotopes (pooled across all study reaches).

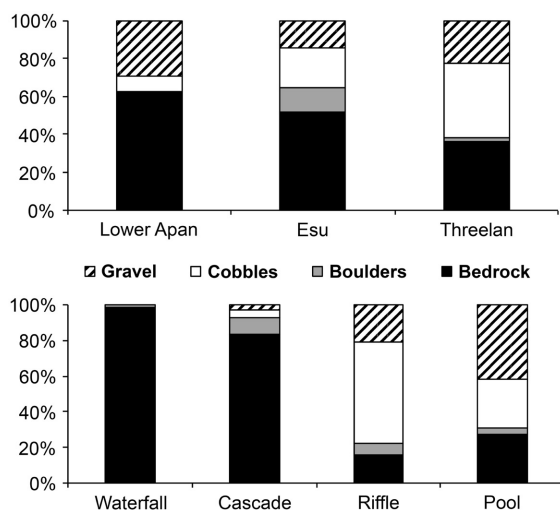| Sites	Average depth (m)	Wetted width (m)	Bankfull width (m)	Velocity (m/s)	Discharge (m^3/s)
Lower Apan	0.26	5.58	8.79	0.39	0.62
Esu	0.37	4.88	7.65	0.37	0.92
Threelan	0.16	3.76	6.78	0.20	0.18
Pool	0.47	5.47	7.15	−0.12	–
Riffle	0.14	3.42	11.89	0.48	–
Cascade	0.06	5.02	7.23	0.60	–
Waterfall	0.07	3.90	7.07	1.01	–

Fig. 3. Percentage substrate (gravel, cobbles, boulders, and bedrock) of the three study streams (pooled across all biotopes) and of the four biotopes (pooled across all study reaches).

having the lowest average values and riffles having the highest (11.89 m). Wetted widths also differed among biotopes ($F_{3,29}$ = 33.95, P < 0.05), with the lowest values occurring at riffles and waterfalls (<4 m) and the highest values at cascades and pools (>5 m). Biotope depths differed ($F_{3,29}$ = 55.14, P < 0.001), with average values lowest for the waterfalls and cascades (<0.10 m) and highest for the pools (>0.40 m). There was a difference in velocity among the biotopes ($F_{3,29}$ = 80.91, P < 0.001), with the lowest average velocity in the pools (−0.12 m/s) and the highest in the waterfalls (1.01 m/s). Pools and riffles contained a mix of gravel, cobbles, and boulders, while cascades and waterfalls were dominated by bedrock (<80% coverage; Fig. 3). Pools had the highest percentage presence of functional

habitats compared with the other biotopes with 88% of pools having leaf litter (Table 3). Cascades and waterfalls had the lowest percentage presence of functional habitats with moss occurring in the highest percentage (Table 3).

Biodiversity of the study reaches

In total, 119 taxa were collected in this study. After pooling all the biotopes in each study reach, total richness was lowest at Lower Apan (71 taxa), followed by Esu (77 taxa) and then Apan Threelan (81 taxa; $F_{2,29}$ = 9.02, P < 0.001; Fig. 4; Appendix S1). Average biomass was also lowest at Lower Apan (65 mg/m^2), followed by Esu (176 mg/m^2) and then Apan Threelan (65 mg/m^2; $F_{2,29}$ = 9.46, P < 0.001; Fig. 4). There was no difference in the macroinvertebrate density among the tributaries ($F_{2,29}$ = 2.59, P = 0.07). A Tukey post hoc test showed that richness and biomass at Lower Apan were significantly lower than at Apan Threelan and Esu. ANOSIM showed an overall difference in the macroinvertebrate community structure among the three tributaries (global R = 0.31; P = 0.03). These differences were illustrated by the SIMPER analysis, which revealed that the average similarity between taxa was highest for Apan Threelan (51%), followed by Esu (47%) and then Lower Apan (41%; Table 4).

Pooling together all benthic macroinvertebrates revealed that Diptera (38%) was the most abundant order, with the highest number of individuals sampled from the three streams. Other dominant orders included Coleoptera (21%), Ephemeroptera (20%), Trichoptera (9%), and Plecoptera (5%; Appendix S1). In addition to these biodiversity measurements, there were some first recordings of aquatic insects from Borneo including *Compsoneuriella* sp. (Ephemeroptera: Baetidae), (M. Sartori and J. C. Gattolliat, *personal communication*) and new

Table 3. Percentage presence of functional habitats of the three study streams (pooled across all biotopes) and of the four biotopes (pooled across all study reaches).

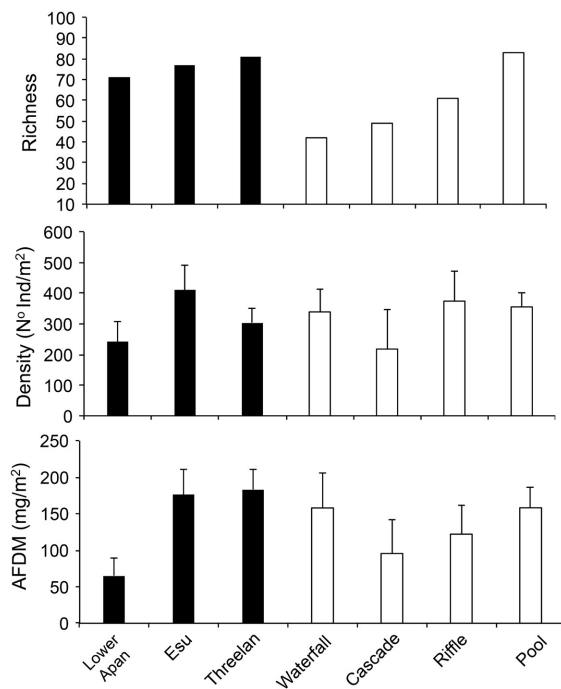| Sites	Large wood debris	Small wood debris	Leaf litter	Moss	Trailing roots
Lower Apan	25	38	63	44	44
Esu	44	56	50	38	6
Threelan	31	50	63	31	13
Pool	56	81	88	25	38
Riffle	19	31	31	19	13
Cascade	6	25	38	31	6
Waterfall	19	6	19	38	6

Fig. 4. Richness, density, and biomass (ash-free dry mass; AFDM) of macroinvertebrates for Sungai Apan Threelan, Sungai Esu, and Sungai Lower Apan as well as for each biotope (cascade, waterfall, riffle, and pool). Error bars represent standard deviations (Lower Apan, $n = 14$; Esu, $n = 10$; Apan Threelan, $n = 11$; waterfall, $n = 6$; cascade, $n = 8$; riffle, $n = 5$; and pool, $n = 16$). Taxa richness ($F_{2,29} = 9.02$, $P < 0.001$) and biomass ($F_{2,29} = 9.46$, $P < 0.001$) differed among tributaries. Taxa richness differed among biotopes ($F_{3,29} = 3.97$, $P < 0.05$).

recordings from Brunei with *Pelthydrus elongatulus* (Coleoptera: Hydrophilidae; Schonmann 1995), *Schinostethus* sp. (Coleoptera: Psephenidae), *Dryopomorphus memei* (Coleoptera: Elmidae; Čiampor et al. 2012; J. Manfred, *personal communication*).

Biodiversity among biotopes

There were differences in average richness among all biotopes (waterfalls, cascades, riffles, and pools; $F_{3,29} = 3.97$, $P < 0.05$). Post hoc tests revealed significant differences both between riffles and cascades ($P < 0.05$) and between riffles and waterfalls ($P < 0.05$). Based on the two-way ANOVAs (using stream and biotope as factors), waterfalls at Lower Apan had significantly lower richness than waterfalls at Esu and Apan Threelan ($F_{3,29} = 3.97$, $P < 0.05$). However, no difference in density ($F_{3,29} = 0.50$, $P = 0.69$) or biomass ($F_{3,29} = 2.54$, $P = 0.08$) was observed among the other biotopes. For the overall community structure, ANOSIM showed a strong difference among biotopes (global $R = 0.71$; $P = 0.01$). This result was supported by the SIMPER analysis, which showed that the average similarity between macroinvertebrates was highest in the pools (51%), followed by riffles (43%), waterfalls (44%), and cascades (19%; Table 5).

Community ordination analysis using individual taxon densities showed community structure among the biotopes (Fig. 5; stress = 0.16; Clarke and Warwick 2001). Ordination axis 1 likely represented a gradient of both substrate and velocity, in which higher velocities and increased bedrock substrate were associated with waterfalls and cascades. In addition to gradients in velocity and substrate, axis 2 strongly reflected the patterns in taxa richness. Specifically, sites AWF1, AWF2, and AC3 (each with less than six taxa) all clustered at the top of the plot. According to the analysis performed with envfit, the environmental factors that were most strongly correlated with biological variables were velocity, gravel, cobbles, and bedrock ($P < 0.001$), along with depth, small wood debris, and moss ($P < 0.05$). As expected, pools and riffles were associated with increased depths and areas of deposition, with a strong association with small wood debris, gravel, and cobbles. Bedrock and high flow velocities were associated with waterfalls and cascades.

The hierarchical cluster analysis supports the results of the ordination analysis. There was a Bray–Curtis dissimilarity of >0.8 between the rock biotopes (cascades and waterfalls) and mixed substrate (riffles and pools; Fig. 6). However, two waterfalls (TWF2 and EWF2) were separated from the rock biotopes, which may be explained by the higher richness of these waterfalls (25 individuals) compared with other rock biotopes.

Discussion

This study represents the first systematic study of aquatic macroinvertebrate community biodiversity in Ulu Temburong National Park; previous studies have focused on single orders, such as shrimp (Wowor and Choy 2001), dragonflies

Table 4. Similarity percentage analysis of the top taxa contributing to the study sites.

Taxa	Contribution %	Cumulative contribution %
Threelan: average similarity: 50.59		
ElmidaeGen1 (L)	13.85	13.85
Non-predacious Chironomidae	12.83	26.68
Predacious Chironomidae	12.39	39.07
Caenis	8.68	47.76
Anisocentropus	7.73	55.49
Esu: average similarity: 46.50		
ElmidaeGen1 (L)	16.76	16.76
Predacious Chironomidae	11.53	28.29
Euthraulus	9.77	38.06
Potamanthus	8.29	46.35
Caenis	7.68	54.03
Lower Apan: average similarity: 40.96		
Simuliidae	16.65	16.65
Euthraulus	14.33	30.98
ElmidaeGen1 (L)	13.84	44.83
Non-predacious Chironomidae	11.69	56.52
Neoperla	6.92	63.44

Notes: This method uses the Bray–Curtis dissimilarity index. The percentage contribution and the cumulative contribution (Cum.) of contributing taxa within each biotope are shown as percentages.

(Orr 2001), and Hemiptera (Zettel et al. 2008). Additionally, very few studies have evaluated the aquatic macroinvertebrate biodiversity of the few remaining pristine catchments in Borneo, although the Sungai Wain Protected Forest in East Kalimantan (Dolný et al. 2011) and Kubah National Park in Sarawak (Iwata et al. 2003) are exceptions. Although these national parks protect extensive pristine rain forest, this is not the norm in Borneo or South-East Asia (White and Klum 2008, Miettinen et al. 2011). Widespread land-use degradation associated with conversion to agriculture limits the potential for baseline research and creates urgent pressure to characterize the tropical stream biodiversity of South-East Asia. Our results indicated that the classification and mapping of macroinvertebrates based on the biotope theory is a highly useful framework to investigate the biodiversity and community structure of tropical streams. Furthermore, these results provide a more robust understanding of biotopes by considering the many linkages between the ecological, geomorphological, and hydrological properties that drive ecohydromorphic complexity.

Biodiversity of the study reaches

Our study reaches had higher total taxa richness (Lower Apan—71 taxa, Esu—77 taxa, and Apan Threelan—81 taxa) compared with similar-sized tropical streams (e.g., Sabalo stream, Costa Rica, with 53 taxa: Ramírez and Pringle 1998, Rio Camuri Grande stream, Venezuela, with 52 taxa: Cressa 1998). However, higher levels of richness have also been observed in Sungai Gombak (Peninsular Malaysia), where 204 morphospecies were identified (Bishop 1973); in Yuccabine Creek (northern Australia), where 267 morphospecies were recorded (Pearson et al.

Table 5. Similarity percentage analysis of the top taxa contributing to the observed similarities between the biotopes.

Taxa	Contribution %	Cumulative contribution %
Pool average similarity: 51.44		
ElmidaeGen1 (L)	15.95	15.95
Predacious Chironomidae	11.68	27.63
Euthraulus	11.46	39.09
Non-predacious Chironomidae	10.71	49.8
Caenis	7.70	57.51
Riffle average similarity: 42.54		
ElmidaeGen1 (L)	15.50	15.5
Simuliidae	13.51	29.02
ScirtidaeGen1 (L)	9.52	38.53
Neotelmatoscopus	8.41	46.95
Neoperla	7.95	54.9
Cascade average similarity: 19.06		
Simuliidae	28.91	28.91
Non-predacious Chironomidae	12.88	41.79
Hydromanicus	11.15	52.94
Neotelmatoscopus	10.66	63.6
Asiobaetodes	9.87	73.47
Waterfall average similarity: 44.43		
Simuliidae	43.62	43.62
Neotelmatoscopus	9.47	53.08
Potamyia	9.06	62.14
ElmidaeGen1 (L)	7.08	69.22
Non-predacious Chironomidae	5.51	74.73

Notes: This method uses the Bray–Curtis dissimilarity index. The percentage contribution and the cumulative contribution (Cum.) of contributing taxa within each biotope are shown as percentages.
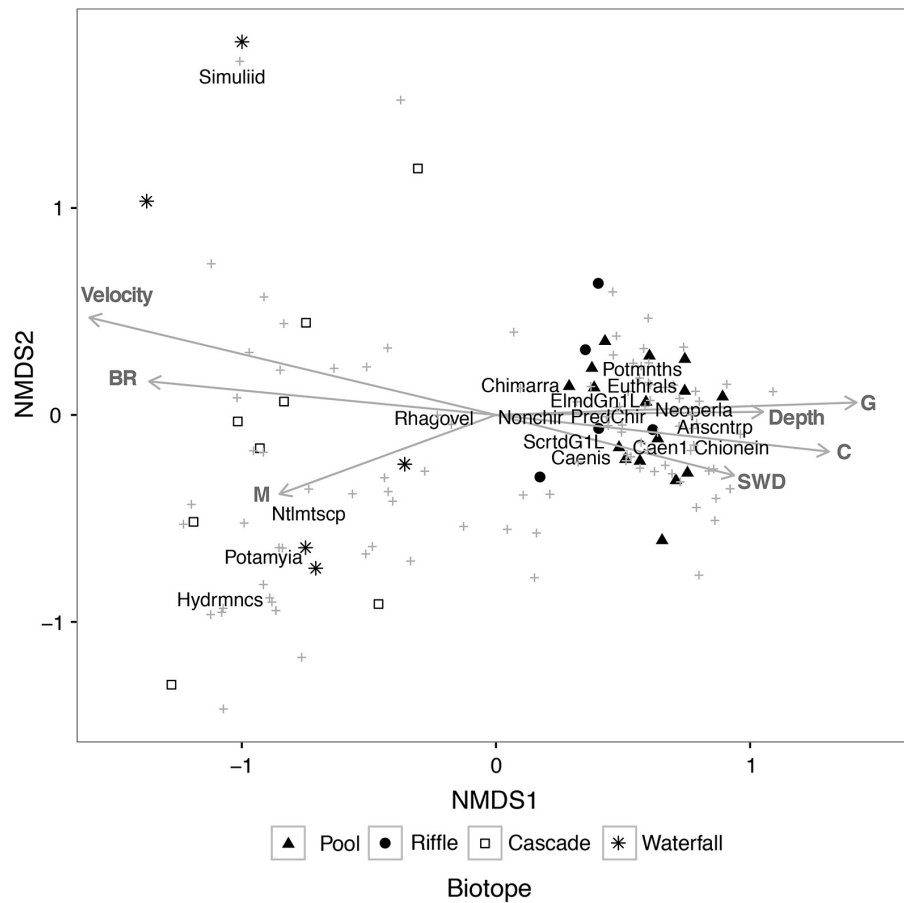
Fig. 5. Nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate density among the sampled biotopes. Environmental data were fitted to the ordination axis using the envfit function of the vegan package in R. The environmental factors displayed are those that are most strongly correlated with the taxa. This includes velocity, gravel (G), cobbles (C), and bedrock (BR; $P < 0.001$) as well as depth, small wood debris (SWD), and moss (M; $P < 0.05$). The biotopes are represented as symbols: pool, black triangle; riffle, black circle; cascade, white square; and waterfall, black star (stress = 0.16). Abbreviations of taxa are shown in Appendix S1.

1986); and in a mountainous stream (Papua New Guinea), where 182 morphospecies were sampled (Yule and Pearson 1996). Dudgeon (1988) even recorded 94 morphospecies from one riffle during one day of sampling in Tai Po Kau Forest stream (Hong Kong). These differences in taxa richness among the tropical streams could be caused by the differences in sampling, study intensity, and duration. However, Jacobsen et al. (2008) argued that these differences in taxon richness may not solely be the result of differences in sampling design and instead be due to natural regional and inter-regional patterns. Two separate studies, one conducted at a regional scale

(Ecuador; Bojsen and Jacobsen 2003) and the other at an inter-regional scale (Hong Kong and New Guinea; Dudgeon 1994), had substantial differences in taxon richness between streams despite having similar sampling design.

Variation in taxon richness was found among our study streams, with Lower Apan having the lowest richness and biomass compared with Esu and Apan Threelan (Fig. 4). Given the close proximity of all of our sites, the differences are likely explained by the biotope distributions and other geomorphological differences. For example, Lower Apan had the highest number of cascade biotopes, which had the lowest levels of richness
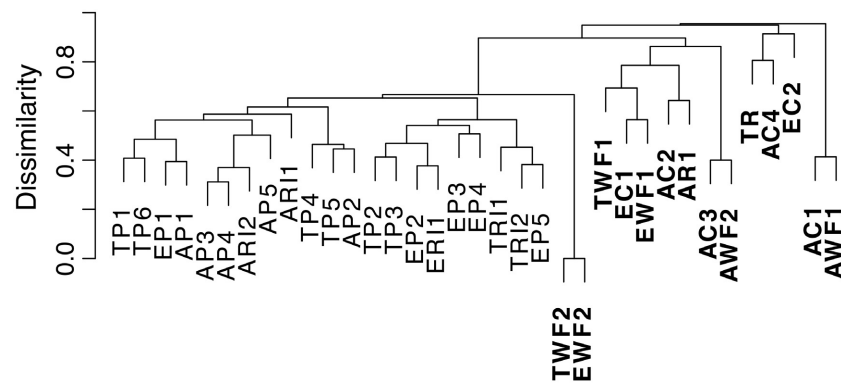
Fig. 6.   Hierarchical cluster analysis of macroinvertebrate density of the biotopes. The first letters represent the study site: E, Esu; T, Threelan; A, Lower Apan. The second letters represent biotope type: C or R, cascade; RI, riffle; WF, waterfall; and P, pool. The number represents the number of the biotope at that study reach. For example, TP1 is Threelan, pool 1. Bold text is used to highlight the fast-flowing biotopes (i.e., cascades and waterfalls).

and therefore decreased the sampling totals for the whole reach. Thus, this study, which assessed the biodiversity on a biotope scale, may have allowed for a more complete consideration of biodiversity among the study streams. Previous studies, which have just focused on single biotopes, usually riffles or pools (Dudgeon 1988, Ramírez and Pringle 1998), likely are underrepresenting aquatic biodiversity.

Differences in biotope stream richness can also be related to the wider stream network. For example, Lower Apan was nearer to the confluence of the main river (Sungai Belalong) relative to the other study sites. This could be associated with an increased hydraulic disturbance of the Lower Apan study reach, with scouring flows and the increased interaction between the main river and the tributary, which may reduce the macroinvertebrate biodiversity. The proximity to the confluence also places it close to a source of fish, which are known to use the tributaries as refuges during high river discharges (Lucas et al. 2001). Higher numbers of fish were present at Lower Apan compared with the other tributaries (K. Baker, *personal data*); therefore, there may have been higher levels of predation or competition for resources. These patterns reflect the processes that are affecting biotopes, but are not related to stream flows.

Biodiversity of the biotopes

Differences in richness and community structure among the biotopes were most distinct between the bedrock-based biotopes (cascades and waterfalls) and mixed-substrate biotopes (pools and riffles). As shown by other studies (e.g., Rabeni and Minshall 1977, Erman and Erman 1984, Pearson 2014), current velocity, substrate size, and leaf litter were the main environmental correlates of taxon richness and community structure. Cascades consistently had the lowest richness, density, and biomass (Fig. 4), and these were the least complex biotope, having few functional habitats. In addition, the substrate was smooth bedrock with little space for the macroinvertebrate refuge (e.g., holes or crevices). In contrast, the riffles and pools had complex substrates composed of a mix of cobbles, boulders, and gravel as well as many functional habitats that support a range of macroinvertebrates (e.g., leaf litter, small wood debris) and promote higher macroinvertebrate richness. The level of waterfall complexity also appeared to affect the biodiversity; some waterfalls were very simple, being composed mainly of smooth rock, and thus were only habitable for filter feeders such as Simuliidae (Lower Apan, waterfall one, AWF1). Other waterfalls were geomorphically complex, with many ridges and holes, enabling a mix of leaf litter and small wood debris to become caught and thus increasing possible habitats for animals and therefore boosting biodiversity (Apan Threelan, waterfall one, TWF1). Beisel et al. (2000) found that the highest levels of macroinvertebrate richness

occurred in heterogeneous environments that provide a range of habitats for a variety of invertebrates.

The similar macroinvertebrate communities found in pool and riffle biotopes may be attributed to the frequent, high stream flow events, which occur in Ulu Temburong National Park (Dykes 1997). During these events, both biotopes experience similar hydrological scouring events, which may have selected taxa that can withstand or require these conditions. For example, the abundance of rheophilic Simuliidae in pool biotopes reveals the importance of such flows, as these taxa require fast flows to deliver food (Giller and Malmqvist 1999). Evidence of scouring potential in these systems was clearly demonstrated at Esu, where the substrates composed of thick layers of imbricated small pebbles and gravel were frequently observed. These substrates visibly shifted after each storm event, and in spite of this high level of disturbance, Esu had among the highest levels of biodiversity. Our observation of the importance of scouring flows for promoting the macroinvertebrate biodiversity is also supported for the tropical streams that experience both aseasonal (Md Rawi et al. 2014) and seasonal floods (Dudgeon 1993, Leung and Dudgeon 2011, Pearson 2014).

In most stream ecology studies, floods and associated high flows are viewed as disturbance events, which are often described as "resetting" macroinvertebrate communities (Power et al. 1988, Resh et al. 1988). However, in systems that flood frequently, such as streams that drain tropical rain forests, these events may not be disturbances. Regardless, flash floods play an important role in structuring the resident aquatic communities, especially the biotopes with high shear stress (pools and riffles) that undergo a consistent abrasion. Sheldon (2011) studied the comparative habitat use by grazing fishes in rivers flowing through the Ulu Temburong National Park and found that biotic interactions were minimal, with the system being physically controlled by the frequent flood events. This observation and our findings may support theories that predation and competition can be less important in highly disturbance-prone streams (Bishop 1973, Peckarsky et al. 1990, Yang and Dudgeon 2010). However, much more work is needed to elucidate these patterns in these tropical streams.

Difficulties of sampling in tropical streams

Collecting representative samples in any natural environment is challenging, but it is especially difficult in the tropics because species diversity is high and many taxa are rare (Gotelli and Colwell 2011, Chao et al. 2014; T. C. Hsieh et al. 2016). In our study, we sampled more pools (16) than any other biotopes as these biotopes occurred between the faster-flowing biotopes of riffles (5), cascades (8), and waterfalls (6). Sample size-based rarefaction and extrapolation from the data show that from the 16 pools sampled, most present taxa were likely sampled (a total of 83) and that by doubling the number of pools surveyed to 30, the number of sampled taxa would be predicted to increase to approximately 100 (Fig. 7). Extrapolation from riffle data shows a predicted total number of approximately 100 taxa, but this can be reached by sampling approximately 20 riffles (Fig. 7). The taxa accumulation curve for cascades and waterfalls rises faster, showing that these biotopes have lower taxa diversity and require fewer replicates in order to sample all taxa.

These results show that our sampling efforts were sufficient to obtain an accurate representation of the benthic macroinvertebrate communities that live in the biotopes. Mixed-substrate biotopes are more difficult to sample, owing to their range of substrate and functional habitats; however, our sampling effort was sufficient to obtain a strong representation of the taxa present. In the tropics, it is common for biodiversity surveys to miss taxa because of the high number of rare taxa, thus creating a slowly rising species accumulation curve (Gotelli and Colwell 2011).

Conclusion

Recent land-use changes caused by the widespread growth of the palm oil industry in South-East Asia have hastened the need to identify and study the remaining pristine rivers and streams. The simplicity of biotopes, which are easily identifiable by their surface flow, combined with the reliability of macroinvertebrates as indicators of environmental health makes the approach of this research a useful one for future studies of tropical rivers and streams. This study has demonstrated that the bedrock biotopes (cascades and waterfalls) and mixed-substrate biotopes (pools and riffles) harbored different communities and levels
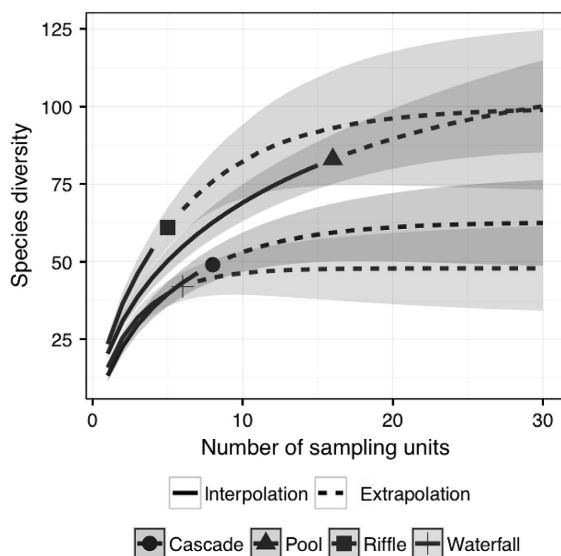
Fig. 7. Sample size-based rarefaction and extrapolation showing that sampling effort was sufficient for each of the biotopes: pool, $n = 16$; riffle, $n = 5$; cascade, $n = 8$; and waterfall, $n = 6$. At each of the individual biotopes, three Surber sampling replicates were taken.

of taxa richness. The more consistent environmental conditions of waterfalls and cascades, in comparison with the mixed-substrate biotopes (pools and riffles), appeared to have a strong influence on the macroinvertebrate communities. Macroinvertebrates inhabiting waterfalls and cascades form a community that differs from those of pools and riffles. This study shows that macroinvertebrate communities are associated with biotopes rather than with streams. Understanding how the different biotopes contribute to reach-scale biodiversity is therefore vitally important for the conservation of stream ecosystems.

Acknowledgments

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