Eco-hydromorphic Classification for Understanding Stream Macroinvertebrate Biodiversity in Brunei Darussalam, Northern Borneo

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Kate Baker, Michael A. Chadwick, and Zohrah Haji Sulaiman (2016) Linking ecology with river geomorphology and hydrology (geomorphic and hydraulic template) plays an important role in the study of macroinvertebrate biodiversity. This understanding and knowledge is crucial in implementing sensible conservation management for ecosystem health monitoring. However, most macroinvertebrate research has been conducted in temperate ecosystems. This study examines the eco-hydrogeomorphology and macroinvertebrate biodiversity of two remote tropical streams in northern Borneo (Bukit Pagon catchment, Brunei Darussalam's highest mountain - 1850 m) using temperate classification models, more specifically, biotopes. Fast flowing biotopes were defined as bedrock runs and cobble riffles whilst the slow flowing biotopes were deposition pools. Macroinvertebrate size structure associated with biotopes, which can influence overall ecological processes, was also investigated. Forty-three macroinvertebrate taxa were recorded during the study; biodiversity was similar between the study streams. There were differences among biotopes with the lowest diversity occurring in fast flowing biotopes ($p = 0.05^*$). Community structure also varied among the biotopes. Cluster analysis of macroinvertebrate abundance revealed an 0.8 dissimilarity between the fast and slow biotopes. Several taxa were found in multiple biotopes, which is likely linked to the occurrence of moss and leaf litter. Macroinvertebrate size structure distribution between the fast and slow biotopes was statistically different. Our findings suggest biotopes may be an appropriate scale to investigate macroinvertebrate biodiversity in tropical streams. Specifically, we found that biotopes had different macroinvertebrate communities and richness. Further research is required to understand the importance of habitat parameters that are not directly related to flow velocities such as moss. These habitats are important as places of refuge, allowing colonisation that would otherwise be inhospitable during flood periods.

Key words: Macroinvertebrates, Tropical streams, Biodiversity, Biotopes, Eco-hydrogeomorphology.

BACKGROUND

It is widely recognised that interactions between hydrology, sediment dynamics and river morphology controls the size, pattern and habitat structure of river channels (Brierley et al. 2013; Villeneuve et al. 2015). These linkages are responsible for making the river channel highly diverse, due to the different and specific composition of the patches, which support diverse macroinvertebrate communities (*i.e.* eco-hydromorphic complexity; *sensu* Townsend 1996,

Hannah et al. 2004). Consequently, eco-hydromorphology plays a crucial role in comprehending the spatial and temporal diversity of river habitats. Classification and mapping of eco-hydraulic patch complexity provides a robust technique for exploring how stream habitats are formed and maintained (Poff and Ward 1989; Hart and Finelli 1999; Bunn and Arthington 2002). In temperate streams, eco-hydrogeomorphology has become a cornerstone for investigating ecological patterns, with flow widely recognised as the master variable which regulates community structure of both

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vertebrates and invertebrates (Poff and Ward 1989; Hart and Finelli 1999; Stubbington et al. 2009). In contrast, few studies have examined eco-hydromorphic complexity in tropical streams (however see: Ramírez and Pringle 1998; Boyero 2003; Boulton et al. 2008; Principle 2008; Md Rawi et al. 2014).

Classification concepts organise information, providing a systematic and repeatable method to view the eco-hydrogeomorphic complexity of stream ecosystems (Brierley and Fryirs 2008). One approach to classifying stream habitats is to describe a set of biotopes (Jowett 1993; Wadeson 1995; Padmore 1998; Newson and Newson 2000; Clifford et al. 2006). A biotope is defined as a "habitat assemblage with a characteristic range of temporally variable hydraulic and substrate characteristics which can be associated with the morphological units" (Wadeson 1995, p7). As such, biotopes are a useful classification tool as they can be observed as river surface flow features (flow/hydraulic biotopes; Table 1) such as riffles and pools, which reflect combinations of sediment, depth and velocity associated with the organisation of the river bed (*i.e.*, physical biotope; Harvey et al. 2008).

In the tropics, biotopes have been used as a sampling framework for a few studies (Furtado 1969; Quentin 1973; Dudgeon 1994), while some studies have examined pools and riffles to assess longitudinal assemblage structure in tropical rivers (*e.g.*, Furtado 1969; Bishop 1973; Rundle et al. 1993; Greathouse and Pringle 2006). However, there has been little research on how the structure, composition and pattern of biotopes affect macroinvertebrate biodiversity (Ramírez and Pringle 1998; Boyero 2003; Cheshire et al. 2005; Md Rawi et al. 2014).

Along with biodiversity, macroinvertebrate size structure within biotopes is important because body size influences many ecological processes (Schoener 1986). For example, macroinvertebrate size structure affects the structure and dynamics at the community level as it influences potential resource use and impacts predation rates (Schmid et al. 2000; Woodward and Warren 2007). Differences in macroinvertebrate size structure have been found in runs and riffles in Costa Rica and these differences were suggested to indicate different ecological functions at the biotope scale (Principe 2008). Despite there being numerous studies on macroinvertebrate size structure in temperate streams (*e.g.*, Lafferty and Kuris 2002; Woodward et al. 2005; White et al. 2007; Dial et al. 2008) there have been few conducted in the tropics (however see Principe 2008).

Differences between temperate and tropical systems are important to understand in regards to the geomorphology and the ecology. Quantification of habitat use in tropical streams assist in the prediction of macroinvertebrate responses to changes in habitat availability (*sensu* Hawkins et al. 1993). Extrapolation of ecosystem models based on temperate streams may not apply to tropical systems and the management techniques used in temperate areas may not work or may even damage tropical systems (Boulton et al. 2008). In addition, the urgency of understanding basic tropical stream ecology is put under immense pressure with the increasingly strong influence of people on these ecosystems (Dudgeon et al. 2006). Therefore, the aim of this paper is to investigate patterns of macroinvertebrate biodiversity and size structure using the Biotope concept developed for temperate streams.

MATERIALS AND METHODS

Study Sites

This study was part of a larger project that gathered experts from around the world to conduct the first systematic study of the environment and

Table 1. Flow type descriptions used to identify the physical biotopes present in the field. From: Newson and Newson 2000 and Parasiewicz 2007

Associated biotope	Flow type	Description
Run	Chute	Surface turbulence does not produce waves, but symmetrical ripples that move in a general downstream direction
Pool	Scarcely perceptible flow	Surface foam appears to be stationary and reflections are not distorted; a stick placed on the water's surface will remain still
Riffle	Unbroken standing waves	Undular standing waves in which the crests face upstream without 'breaking'

biodiversity of high altitude primary rainforest to Bukit Pagon (1850 m), Brunei's highest mountain (Fig. 1A). Prior to this expedition, no previous scientific studies had been conducted. Base camp was situated on the slopes of Bukit Pagon (4°33'614"N, 115°26'153"E), set up at an elevation of 862 m.a.s.l. and 30 km away from the nearest road, only accessible by helicopter (Fig. 1A). The dominant vegetation type was sub-montane heath forest (Ahmad Sah et al. 2006). The study reaches were less than 10% in gradient and no waterfalls present. Two streams close to the base camp were the focus of this study (stream 61a and tributary of 61a; Fig. 1B). In each stream, three repeating fast/slow habitat units being approximately 50-meters in length defined the reach. Sampling took place from 4-6th July 2012. Stream 61a was a larger stream with its tributary entering it upstream of the designated study reach.

Field Methods

The fast/slow habitat units in each reach were mapped as biotopes (pools, riffles and runs) by observing river surface features (Newson and Newson 2000, Parasiewicz 2007; Table 1). For each biotope a formal cross-section of velocity and depth was taken every 0.5m following common methods described by Gorden et al. (2004). In addition both wetted width (defined by the area of stream channel filled with water) and bank-full width (defined by the width of the river during high discharge) was measured. Channel dimensions were measured with surveying tapes and meter sticks. Stream velocity was measured at 60% depth as suggested by Gordon et al. (2004), using an electromagnetic flowmeter (Valeport® model 801; Valeport Ltd., Totnes, UK). Discharge (Q) was calculated for each stream using the following equation:

$$\text{Discharge (Q)} = \text{Velocity (V)} \times \text{Cross sectional Area (A)}$$

For the whole biotope unit, the benthic substrate was assessed visually using a collapsed version of the Wentworth scale catagorising the percent coverage of gravel, cobble, boulder and bedrock (Gorden et al. 2004). The presence or absences of wood debris, leaf litter, and moss in all biotopes were also recorded. Benthic
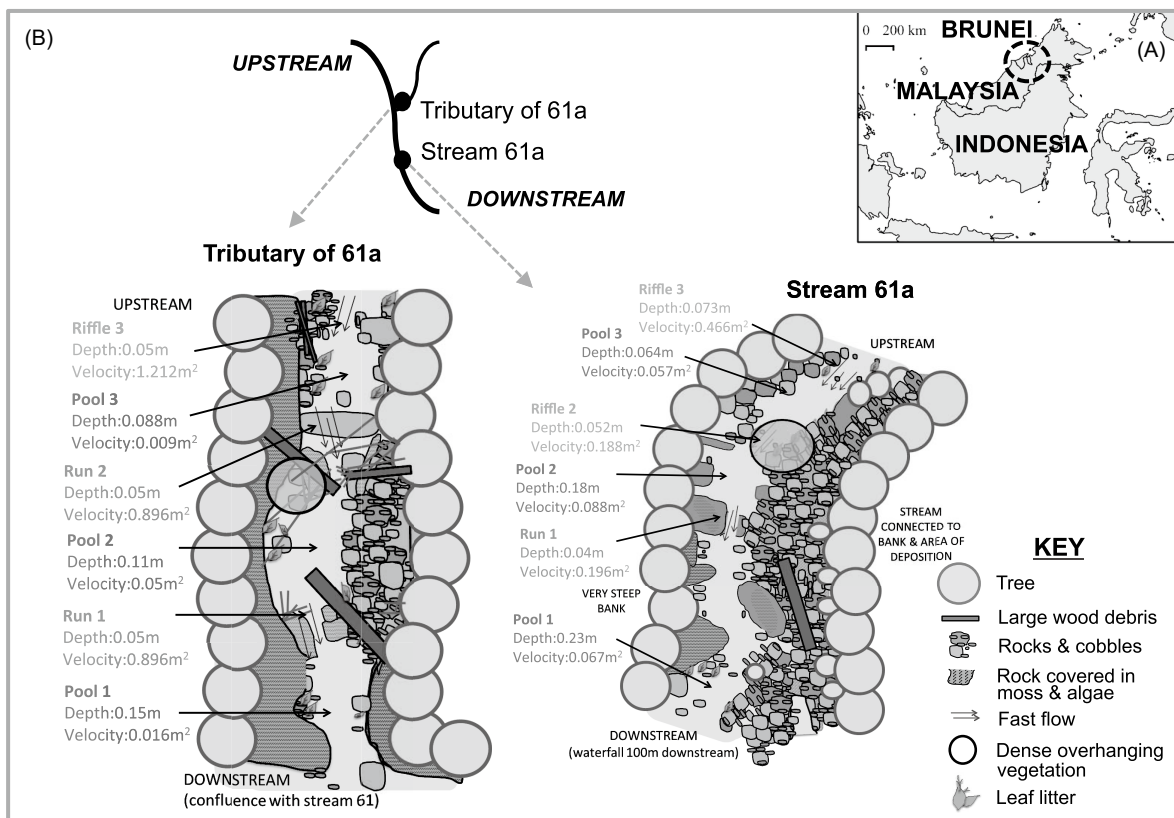
Fig. 1. Map and schematic of study sites A) Map of Borneo Island in S.E Asia with Brunei situated in the north. The dotted circle highlights Brunei. B) Plan view schematic of the two study sites, tributary of 61a (left) and stream 61a (right).

macroinvertebrates were sampled in each biotope using a Surber sample (0.10 m^2; 1 mm mesh) with three replicates taken randomly in each biotope. Due to low densities of macroinvertebrates, three samples in each biotope were composited to create one intact sample.

Laboratory Methods

Macroinvertebrate samples were processed in the field in 70% Ethanol. Once exported to the UK, collected individuals were identified to the lowest practical taxonomic level, enumerated and measured to the 0.5 mm under a microscope.

Identifications were conducted mainly using taxonomic keys from Dudgeon (1999) and Yule and Yong (2004b). However, given the paucity of macroinvertebrate taxonomic knowledge in Borneo, open source identification methods were used. Specifically, taxa were photographed, highlighting the distinguishing morphologies and uploaded onto the Flickr website (flickr.com/photos/tropical-streams/sets/) where interested experts could comment on specimens. This method was a useful tool to confirm identifications via input from appropriate research groups and taxonomists from around the world. Most taxa were identified to genera or morphotyped to similar level. Some taxa, particularly specimens in the Orders Coleoptera and Diptera, which are significantly under researched in northern Borneo, could only be identified to the family level (Manfred, personal communication, 2014; Yule 2004a).

Body lengths (not including appendages and setae) of sampled individuals were measured to the nearest 0.5 mm to estimate taxa-specific ash free dry mass (AFDM) using length- mass regressions (Benke et al. 1999; Sabo et al. 2002; McNeely et al. 2007). In cases where no taxa-specific equations exist, estimates were made using equations from taxa with similar body shape following Ramírez and Pringle (1998). Where only dry mass (DM) estimates are available, values were converted to AFDM following Waters (1977).

Individual body lengths were also used to investigate patterns of macroinvertebrate size structure between the biotopes. Macroinvertebrates were placed into 6 size classes: I = > 0-2 mm, II = 2.1-4 mm, III = 4.1-6 mm, IV = 6.1- 8 mm, V = 8.1-10 mm, VI = 10.1-20 mm.

Data Analysis

To assess macroinvertebrate biodiversity, richness, density and biomass were quantified in all the fast and slow biotopes in each study streams. T-tests were used in this paper to compare the physical variables (width, depth and velocity) and biodiversity (mean density and biomass per unit area, and richness) between the tributaries and fast/slow habitats. The statistical analysis of T tests was chosen based on the distribution of the data (Thomas et al. 2013).

Physical variable structure was examined within the biotopes using a hierarchical cluster analysis carried out based on Gower Coefficient, which can handle nominal, ordinal, and asymmetric binary data (Gower 1971). Macroinvertebrate assemblage structure was examined within the biotopes using a hierarchical cluster analysis carried out based on Bray Curtis Coefficient, a popular similarity index for ecological data (Borcard et al. 2012). Bray-Curtis similarity matrices calculated the compositional dissimilarity of sites based on the abundance and biomass of taxa at each site. Multi-dimensional scaling (MDS) analysis with the Bray-Curtis dissimilarity was used to test the robustness of groups defined by the cluster analysis. A BIO-ENV (Clarke and Ainsworth 2001) analysis was carried out to investigate which environmental variables best correlate with macroinvertebrate community structure. Then similarity percentage analysis (SIMPER) was used to identify taxa, which contributed most to the average dissimilarity between biotopes. Kolmogorov-Smirnov test was used to assess any differences in the taxa size structure among the biotopes by comparing the general shape of distributions (Thomas et al. 2013). Statistical analysis was carried out in the statistical computing environment R (R Core Team 2013) using the Vegan, Cluster, and Labdsv packages.

RESULTS

Site Description

In both study reaches, slow flow biotopes (pools) were interspersed with fast flow biotopes (riffles and runs; Fig. 1B). The tributary had three pools, two runs and one riffle while the stream 61a study reach had three pools, one run and two riffles. Overall, both study reaches had similar average wetted widths for all the biotopes (tributary - 2.1 m; stream 61a - 3.2 m; Table 2). However, average bankfull width for all the biotopes was twice as wide for stream 61a than the tributary

(stream 61a - 7.0 m vs. tributary - 3.8 m). Average biotope depths between the two study reaches were similar (tributary - 0.09 m vs. stream 61a - 0.10 m). Discharge was slightly higher at stream 61a (0.18 m^{-3} s^{-1}) compared to the tributary (0.12 m^{-3} s^{-1}). However, average velocities were faster in the tributary (0.54 m s^{-1}) compared to stream 61a (0.21 m s^{-1}).

Widths, depths and velocities of course varied among biotopes in each study reach. Slow flow biotope wetted widths were ~1 meter less in the tributary compared with the stream, while bankfull widths ranged from 6.70 m (stream 61a-pool 3) to 2.50 m (tributary- pool 1) as shown in table 2. Fast flow biotopes, including riffles and runs, had wetted widths ranging from 4.27 m (stream 61a-riffle 2) to 1.90 m (tributary-riffle 3), while bankfull widths ranged from 9.40 m (stream 61a-riffle 2) to 3.57 m (tributary-run 2). As expected, slow flow biotopes (0.06 m to 0.23 m) were deeper than fast flow biotopes (0.04 m to 0.06 m). Velocities in slow flow biotopes were mainly negative, while velocities in fast flow biotopes varied from 0.20 m s^{-1} (stream 61a-run 1) to 1.21 m s^{-1} (tributary-riffle 3). These physical measurements are summarised in Table 2.

The tributary was constrained by the riparian bedrock, resulting in narrower bankfull widths and a smaller canopy gap with less sunlight reaching the channel (Fig. 1B). This constrained reach also contained more wood debris (large and small), leaf litter packs and the associated buildup of fine sediments and organic debris. In contrast, the wider reach at stream 61a had more sunlight reaching the channel that promoted filamentous algae and moss in fast flow biotopes. Further, woody debris accumulated in one fast flow biotope (stream 61a-riffle 2; Fig. 1B).

The dominant substrate types in both study reaches were similar among slow flow biotopes with a mix of cobbles, gravel and boulders (Table 2). However, tributary-pool 2 and stream 61a-pool 2 also had large amounts of bedrock. Substrate at the fast flowing biotopes varied with runs being primarily bedrock (> 80% coverage) and riffles being comprised of a mix of cobbles, gravel and boulders (Table 2).

Cluster analysis of the physical variables among biotope habitats (*i.e.*, Table 2) shows 0.7 dissimilarity between the runs compared to other biotopes (Fig. 2A). Variation in substrate type separated runs from the other habitats (*i.e.*, runs being mainly composed of bedrock). As such, some pools and riffles clustered together due to similarities in their physical conditions. However, tributary-pool 2 shows 0.3 dissimilarity from all other pools and riffles and is explained by the large amount of bedrock present (*e.g.*, 50%).

Taxa distribution in the biotopes

The two reaches were similar in terms of their overall macroinvertebrates biodiversity (Fig. 3

Table 2. Channel characteristics and physical conditions of the biotopes at stream 61a (S) and at the tributary (T). Type C = cobbles, G = gravel, B = boulders and BR = bed rock

|	Bankfull width (max) m	Wetted width (max) m	Depth (max/avg) m	Velocity (average) m s^{-1}	Dominant substrate type			
Slow flows					C	G	B	BR
S.Pool 1	6.20	3.47	0.37/ 0.23	-0.07	70	20	10	0
S.Pool 2	6.40	2.90	0.38/ 0.18	-0.09	60	10	0	30
S.Pool 3	6.70	2.65	0.13/ 0.06	-0.06	80	10	10	0
T.Pool 1	2.50	2.50	0.22/ 0.15	-0.02	50	40	0	10
T.Pool 2	4.70	2.50	0.21/ 0.10	-0.05	20	30	0	50
T.Pool 3	3.16	2.60	0.16/ 0.11	-0.01	80	15	5	0
Average	4.94	2.77	0.138	-0.05	60	21	4	15
Fast flows								
S.Run 1	6.10	1.02	0.05/ 0.04	0.20	5	0	0	95
S.Riffle 2	9.40	4.27	0.07/ 0.04	0.79	30	20	50	0
S.Riffle 3	7.30	2.47	0.15/ 0.05	0.47	85	15	0	0
T.Run 1	3.90	0.87	0.07/ 0.04	1.20	5	5	5	85
T.Run 2	3.57	2.04	0.05/ 0.05	0.90	0	5	0	95
T.Riffle 3	4.70	1.90	0.04/ 0.06	1.21	65	15	20	0
Average	5.83	2.10	0.047	0.79	32	10	12	46

and see Additional file 1). Taxon richness was the same at both sites ($p = 1$). Average density was not significantly different ($p = 0.09$), with stream 61a having 85 ± 18 individuals per m^2 compared to 60 ± 8 individuals per m^2 in the tributary. Average biomass (AFDM) was ~80% less in the tributary when compared to stream 61a (tributary: 38 ± 10 mg m^{-2}; stream 61a: 167 ± 102 mg m^{-2}), but no statistical differences were found between the two reaches ($p = 0.25$). The high average biomass at stream 61a is explained by the large Nepidae (*Cercotmetus*) found at SP3, without the water scorpion average biomass at stream 61a would be ~ 68 mg m^{-2}.

Differences in macroinvertebrate biodiversity were found among habitat types in the two study reaches (Fig. 3). Slow flowing biotopes had significantly higher average richness (11) compared to the faster flowing biotopes (8) ($p = 0.05*$) and riffles had 38% more taxa than runs (11 versus 5). Macroinvertebrate densities were similar ($p = 0.86$) among fast flow biotopes (average all fast habitats - 71 ± 18 individuals per m^2; runs - 75 ± 31 individuals per m^2; riffles - 66 ± 25 individuals per m^2) and slow biotopes (74 ± 8 individuals per m^2; Fig. 3). On average, macroinvertebrate biomass was lower in fast flowing biotopes (55 ± 21 mg AFDM m^{-2}) than slow flow biotopes (149 ± 104 mg AFDM m^2). However, there was no statistical difference between the fast and slow biotopes ($p = 0.45$). Pool biomass was 50% higher than the runs and 24% higher than the riffles.

Cluster analysis of taxa abundances showed a 0.9 dissimilarity between the 2 run biotopes (SR1 and TR1) and 1 riffle (SRIF3) with the rest of the biotopes. It also showed a 0.8 dissimilarity between the other 2 riffles (SRIF2 and TRIF3) and all the pool biotopes (Fig. 2B). MDS ordination of taxon abundances (Fig. 4) showed distinct community structure among the biotopes (stress = 0.01; Clarke and Warwick, 2001). The ordination identified three main groups of taxa, associated with the 3 biotopes: pools, runs, and riffles. Taxa found in pools were associated with wider wetted widths, gravel, cobbles, and deeper depths. The taxa found in runs were associated with moss, higher percentage of bedrock, and faster velocities. While the taxa found in riffles were associated with wider bankful widths, wood debris, leaf litter, and faster velocities. BIO-ENV shows the best single environmental factor that correlates to the taxa was cobble substrate (rank correlation = 0.65), whilst the best 3 environmental factors combined were velocity, cobbles and gravel (rank correlation = 0.70). As expected, pools had a strong association with depth and a negative association with velocity, whilst riffles were least associated with depth and most related to high velocities (Fig. 4). Cobbles, gravel, and leaf litter were associated with both riffles and pools. Bedrock and moss were most strongly associated with runs.

SIMPER analysis showed average similarity between taxa was highest in the pools at 44% and lowest in the riffles at 27% (Table 3). In pools, *Thalerosphyrus* species (Ephemeroptera: Heptageniidae) contributed about 30% to the total similarity, followed by *Eubrianax* species (Coleoptera: Psephenidae) at nearly 20%. In
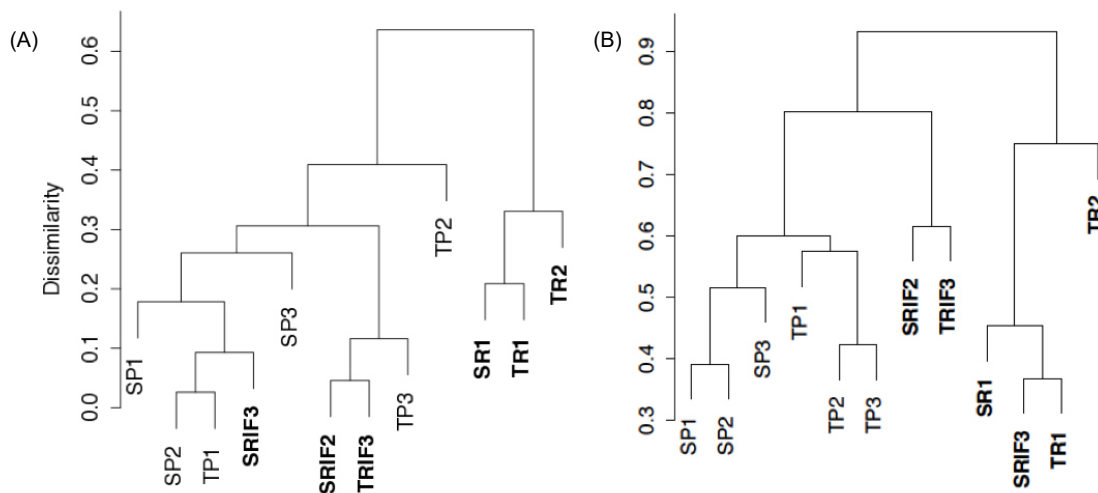

Fig. 2. Dendrogram of A) biotope physical conditions and B) biotope taxa abundance. The first letters represents the study site: S = stream 61a, T = tributary. The second letter and the number represents the biotope sampling unit: R = run, RIF = riffle, P = pool. Letters in bold represent the fast flowing biotopes.

the riffles average similarity was only 27%, with Gomphidae contributing 40% to the total. In the runs average similarity was 37%, *Grouvellinus* species (Coleoptera*:* Elmidae) contributed 78% to the total.

Macroinvertebrate size structure in the biotopes

Average taxon lengths in the two reaches showed a similar pattern, with most taxa occurring in size class II (Fig. 5). There was a significant difference ($p = 0.04*$) between the taxon lengths found in fast and slow flow biotopes. A larger proportion of taxa present in fast flow biotopes were found in the smallest size class. Differences in taxa length between the biotopes were also evident; significant difference between pools and runs ($p = 0.01**$) and between riffles and runs ($p = 0.01**$). Taxa present in runs were only found in the smallest three size classes, with the highest number of taxa in size class I. Pools and riffles had
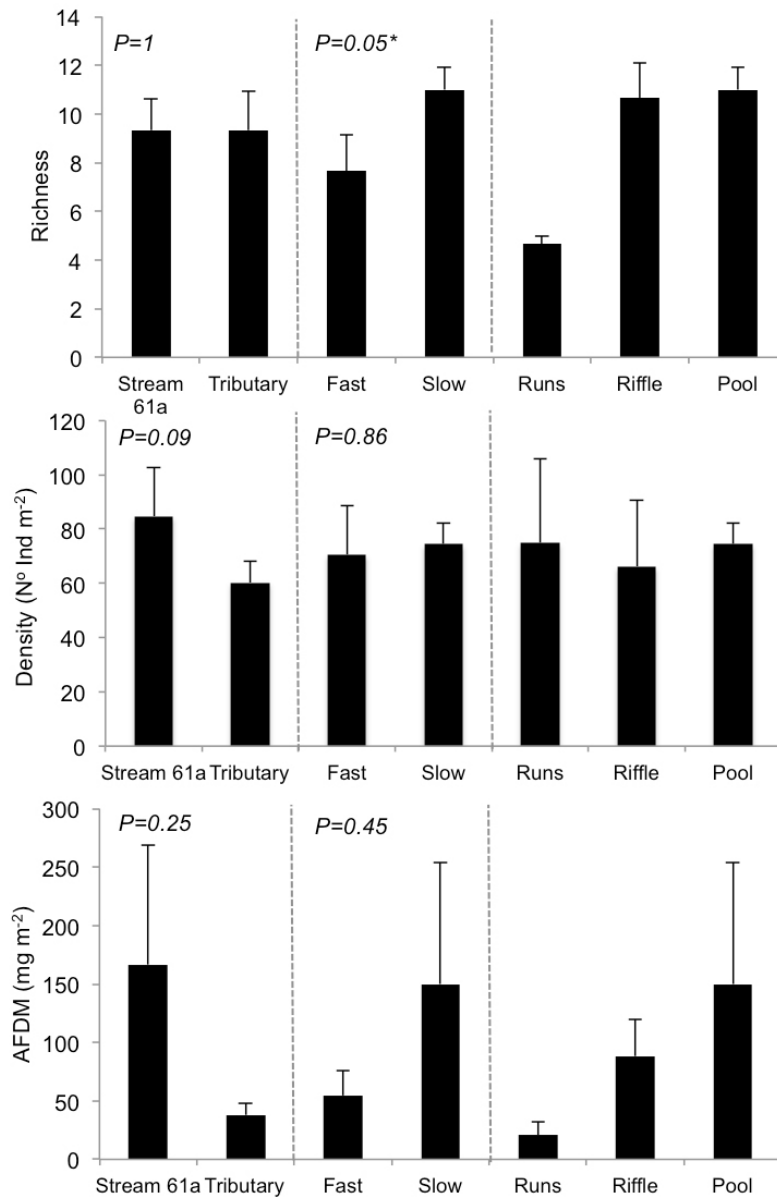
Fig. 3. Bar plots with richness, density, and biomass of macroinvertebrates at the two study sites. Includes bar plots of stream 61a and tributary, the fast and slow flowing habitats, and the three biotopes (runs, riffles and pools). Error bars represent standard deviation (Stream 61a $n = 6$, tributary $n = 6$, both fast and slow flowing habitats $n = 6$, runs $n = 3$, riffle $n = 3$ and pool $n = 6$). Significant differences between the fast and slow sites with richness ($p = 0.05*$).

a similar distribution among size classes (p = 0.10); the only difference being that taxa in riffles had a higher average number of individuals in size range I and size range VI.

DISCUSSION

This project used the eco-hydrogeomorphic concept of biotope as a framework to investigate the biological and physical relationships of two streams draining Bukit Pagon. The sites were less than 100m apart, under the same environmental conditions of discharge regime, geology and climate and as a result had very similar physical

conditions. These similarities allowed for a critical examination of fast and slow flow biotopes and the associated macroinvertebrate biodiversity (Table 2).

At both study streams macroinvertebrate diversity was lower compared to a similar system in Malaysia (204 taxa; Bishop 1973). However, there are examples of tropical lotic ecosystems with values of richness close to those measures in our system, for example 53 taxa were found in Sabalo stream, Costa Rica (Ramírez and Pringle 1998) and 52 taxa in the Rio Camuri Grande, Venezuela (Cressa 1998). However, comparing richness among all of these datasets should come with caution due to the incomplete knowledge of
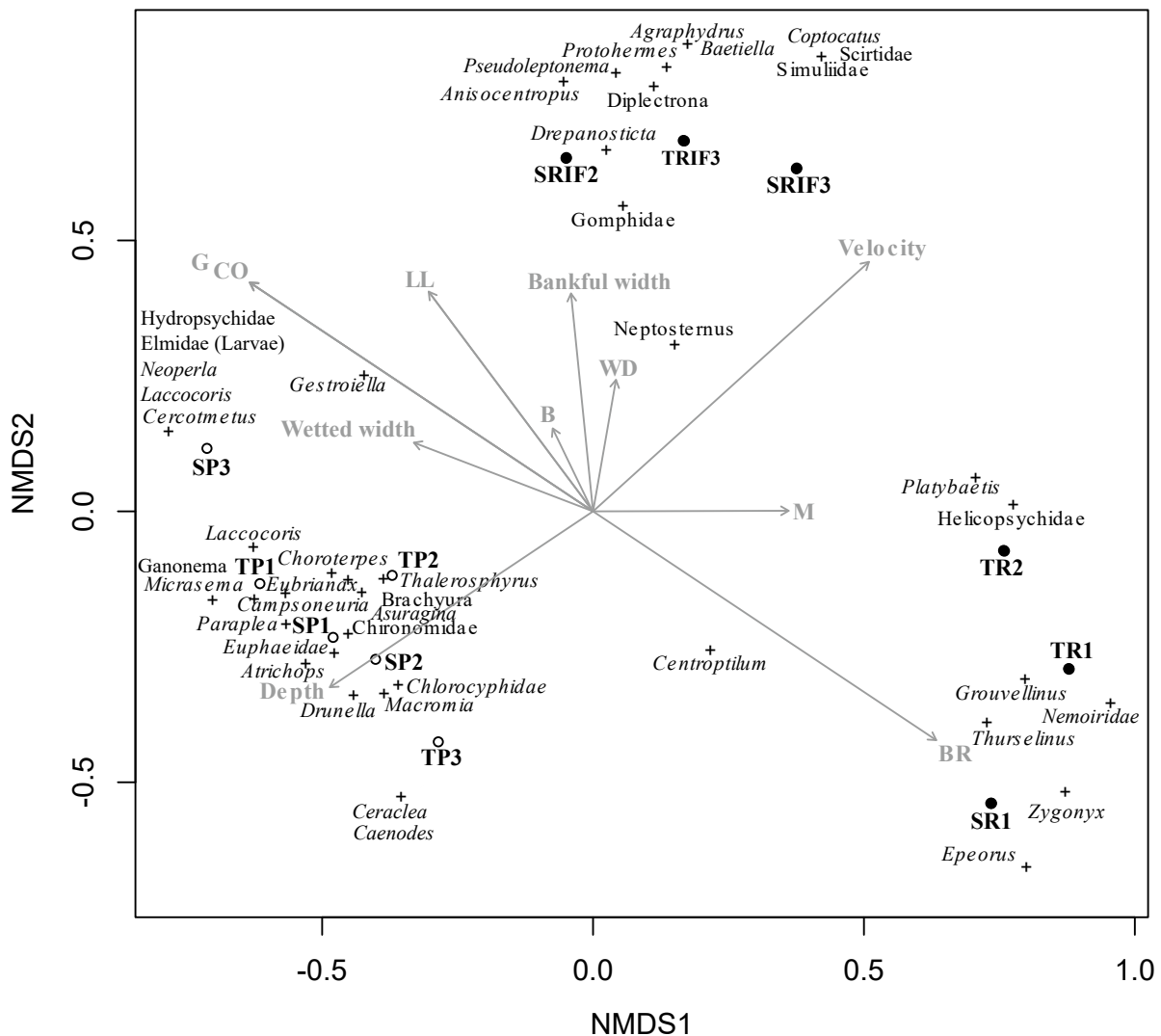
Fig. 4. MDS ordination with a BIO-ENV that shows the environmental variables that best correlate with macroinvertebrate community structure. The biotope names have been abbreviated with the first letter representing the study site: S = stream 61a, T = tributary. The second letters represent the biotopes: R = run, RIF = riffle, P = pool. The environmental data in grey with G = gravel, CO = cobbles, B = Boulders, LL = leaf litter, BR = bedrock and WD = wood debris, M = moss. Stress: 0.01.

tropical macroinvertebrates and different sampling techniques (Jacobsen et al. 2008). For example, we used a large mesh size (*i.e.*, 1 mm) which may have resulted in a loss of small taxa. However, these "missing taxa" would likely be chironomid taxa (Insecta: Diptera: Chironomidae) taxa, which are underrepresented in many stream ecology studies (Armitage et al. 2012; Ferrington 2008).

Macroinvertebrate density and biomass were also low at the two study reaches, with average density of 72 individuals per m^2 and average biomass of 102 mg AFDM m^{-2}. Graça et al. (2015) found an average of 150 to 300 individuals per m^2 in eight headwater streams in Brazil, whilst Boyero and Bailey (2001) study on riffle habitats in Panama found an average density of 905 individuals per m^2. The low densities in our study reaches may be explained by abiotic factors, with disturbance caused by flooding spates having a strong influence on macroinvertebrate diversity (Power et al. 1988; Resh et al. 1988; Death 2002). The study streams draining Bukit Pagon are similar to many tropical headwaters, characterised by frequent flashy storm hydrographs and spates which tend to lead to significant scouring of

individuals that lack refugia from elevated flows (Boulton et al. 2008). Another reason for low densities in the tropics could be due to the higher levels of predation by both macroinvertebrates and fish (Fox 1977; Flowers and Pringle 1995).

Padmore (1998) highlighted that biotopes are not static units with most turning into deep runs under flood conditions. In Bruneian streams, this continuum of conditions can occur frequently, with daily storms during most months, creating two distinct stream environments. During low flows, Bruneian streams are complex systems with a mix of flow biotopes (pools, riffles, waterfalls) and other habitats (wood debris, leaf litter, cobbles, gravel). Conversely during flood events, these streams become homogeneous forming one flood biotope. As many tropical systems have this natural and consistent flow disturbance, other types of habitats become vital areas of refuge. This is especially true of habitats that can withstand scour, such as bedrock. Bank irregularities and flow obstructions such as large rocks are also important in creating heterogeneous hydraulic conditions throughout a range of flow stages, thereby providing another refuge (Harvey and Clifford 2009).

Table 3. SIMPER analysis of the top taxa contributing to the observed similarities between the biotopes. The method uses the Bray-Curtis measure of similarity. Summary results show the contribution and the cumulative contributing taxa to each biotope with percentages

	Contribution (%)	Cumulative contribution (%)
Pool: Average similarity: 44.09		
Thalerosphyrus	29.6	29.6
Eubrianax	19.6	49.2
Choroterpes	17.2	66.4
Campsoneuria	9.5	75.9
Chironomidae	5.8	81.7
Euphaeid	4.3	86.0
Centroptilum	4.3	90.3
Run: Average similarity: 37.60		
Grouvellinus	78.3	78.3
Platybaetis	6.1	84.4
Helicopsychidae	6.1	90.5
Riffle: Average similarity: 26.76		
Gomphidae	40.0	40.0
Protohermes	20.0	60.0
Campsoneuria	9.6	69.6
Macronematini	9.6	79.2
Thalerosphyrus	5.5	84.7
Diplectrona	5.5	90.2

Interestingly the two Bray Curtis dendrograms, one with physical (Fig. 2A) and the other with the taxa data (Fig. 2B), show taxa fitting the biotopes more strongly than the physical data. The flashy flows in tropical streams create a very dynamic geomorphic template, making it difficult to find patterns with the physical data during a one off survey. In comparison, this study suggests that the taxa reflect the biotopes more accurately than single physical measurements. This is not surprising given that the communities often tell the 'longer story' (*e.g.*, macroinvertebrates being used as indicators for water quality; Giller and Malmqvist 1999).

Despite the broader pattern of macroinvertebrates reflecting the biotope framework, there is a hierarchy of factors that affect the distribution of each taxon, which would explain why few taxa were uniquely associated with certain biotopes. These findings are similar to results from temperate streams, which concluded that due to the range of habitats and life stages,
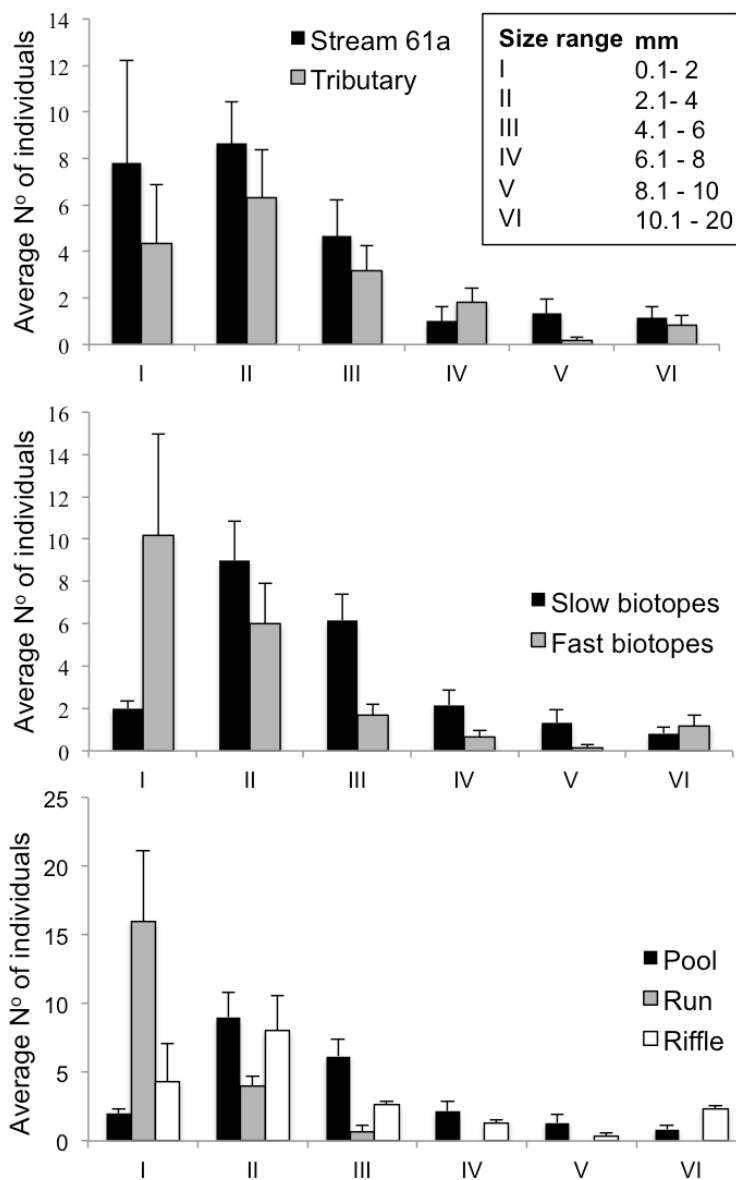
Fig. 5. Length- frequency distributions of macroinvertebrates among stream 61a and its tributary, fast and slow biotopes, and among the three biotopes (runs, riffles and pools). Error bars represent standard deviation (stream 61a *n* = 6, tributary *n* = 6, both fast and slow flowing habitats *n* = 6, runs *n* = 3, riffle *n* = 3 and pool *n* = 6). Significant differences found between the fast and slow sites (*p* = 0.04*), pool and runs (*p* = 0.01**) and riffles and runs (*p* = 0.01**) using Kolmogorov-Smirnov test.

along with synecological factors (such as competition and predation), it is difficult to find distinct macroinvertebrate communities within individual flow biotopes (Newson and Newson 2000). Macroinvertebrate communities may also be affected by the configuration and hydraulic properties of biotopes, with biotopes in the same class being highly variable depending on how they are formed and their position in the channel (Bisson et al. 1982). Other habitat parameters (*i.e.*, leaf litter and moss) can be flow independent. As a result, these factors can be found in all flow biotopes influencing macroinvertebrate distribution and biodiversity regardless of the dominate flow types. In this study, the pools and riffles had more leaf litter and wood debris than the runs.

Runs had swift current velocity, but limited leaf litter and wood debris. Water flowing over the runs was smooth with little turbulence or spray resulting in low hydraulic heterogeneity. This could be a reason for the lowest biomass (AFDM) and richness at both study reaches (Fig. 3). However, these conditions appear to be particularly good for *Grouvellinus* species (Coleoptera: Elmidae) based on the high densities in runs, especially at SR1. These elmids were very small, few were > 1.5 mm therefore not increasing overall biomass.

Other habitat parameters appear to be important in the faster flowing biotopes. For example, *Grouvellinus* species and *Zygonyx* species (Odonata: Libellulidae) are known to cling to hard substrates covered by moss, to help them withstand fast flows (personal observations). Furtado's (1969) analysis of Odonates in a Malaysian stream found that *Zygonyx* species managed to inhabit trailing plants and accumulated debris irrespective of water velocity. The morphology of *Zygonyx* species with spines covering the whole body aid attachment, enabling the animal to use moss as refuge from a range of flow velocities. It is clear that moss and other habitats (*i.e.*, leaf litter) can have strong influences on both body size and biomass in fast flowing biotopes. In support of this, Rackemann et al. (2013) emphasised the need for further investigation into the role of moss in protecting insects and therefore maintaining higher diversity in another fast flow biotope - waterfalls.

Body size can influence an organism's ability to withstand fast flows. Results from this study show that taxa in pools are generally larger, and that communities were composed of smaller number of taxa, in fast flow biotopes. This is particularly evident in the runs, with communities dominated by elmids and simulids. For example, 75% of organisms present at run 1 (stream 61a) was attributed to the family Elmidae. Their small body size enables them to take refuge from fast flows within the crevasse of the bedrock, moss or algal-covered patches. In pools average size of taxa was slightly larger, animals such as chironomids and oligochaetes, were able to avoid high flows by burrowing into the fine sediments (Stubbington 2009). These refuges evidently provide protection for a wider range of body sizes than habitats available in runs. The increased range of macroinvertebrate body sizes found in the pools and riffles potentially reflects the diverse mix of habitats.

Collecting representative samples in any environment is difficult but it is especially problematic in the tropics because species diversity is high but many species are rare (Gotelli and Colwell 2011; Chao et al. 2014; Hsieh et al. in press). In our study we found that with 6 replicates of the fast and slow biotopes species diversity is ~ 25 (Fig. 6A). If we double our sampling effort to 12 replicates, species diversity is expected to increase to ~30-35 taxa (Fig. 6A). However, if we eliminate the rare taxa (classed in this study as taxa occurring only once), it shows that we have colle-cted the common taxa (Fig. 6B). In the tropics it is not uncommon for biodiversity surveys to miss taxa due to the high number of rare taxa, creating a slowly rising species accumulation curve (Gotelli and Colwell 2011). In this study the main aim was to make comparisons of the biotopes during one time period, when comparing community structure between the biotopes this will be dictated mainly by the common taxa.

CONCLUSIONS

Streams are heterogeneous and extremely dynamic in nature. Biotopes are a logical place to start understanding this complexity as they can be easily observed as river surface flow features, which reflect hydraulic and sediment characteristics. This study has shown that biotopes are useful for examining macroinvertebrate biodiversity in streams, with richness and community structure reflecting conditions at the biotope scale rather than at the reach level. Cluster analysis also showed distinct community structure among the pools, runs, and riffles. Macroinverterbate size structure among biotopes was distinct between fast and slow flows, with the

smallest taxa being most abundant in runs. This study suggests that further research is required to understand the importance of a range of habitat parameters, which are not directly related to flow velocities. These habitat parameters are important as refuge and allowing the colonisation of habitats that would otherwise be inhospitable during flood periods.

The timeframe to investigate and understand basic tropical stream ecology is put under pressure due to the strong influence of man on these ecosystems (Dudgeon et al. 2006). Given environmental changes and associated loss of biodiversity, it is imperative to collect baseline data and understand the processes and roles of natural pristine tropical systems. This will enable understanding of the potential consequences of extinction and declining biodiversity (Dudgeon et al. 2006; Corlett 2009).
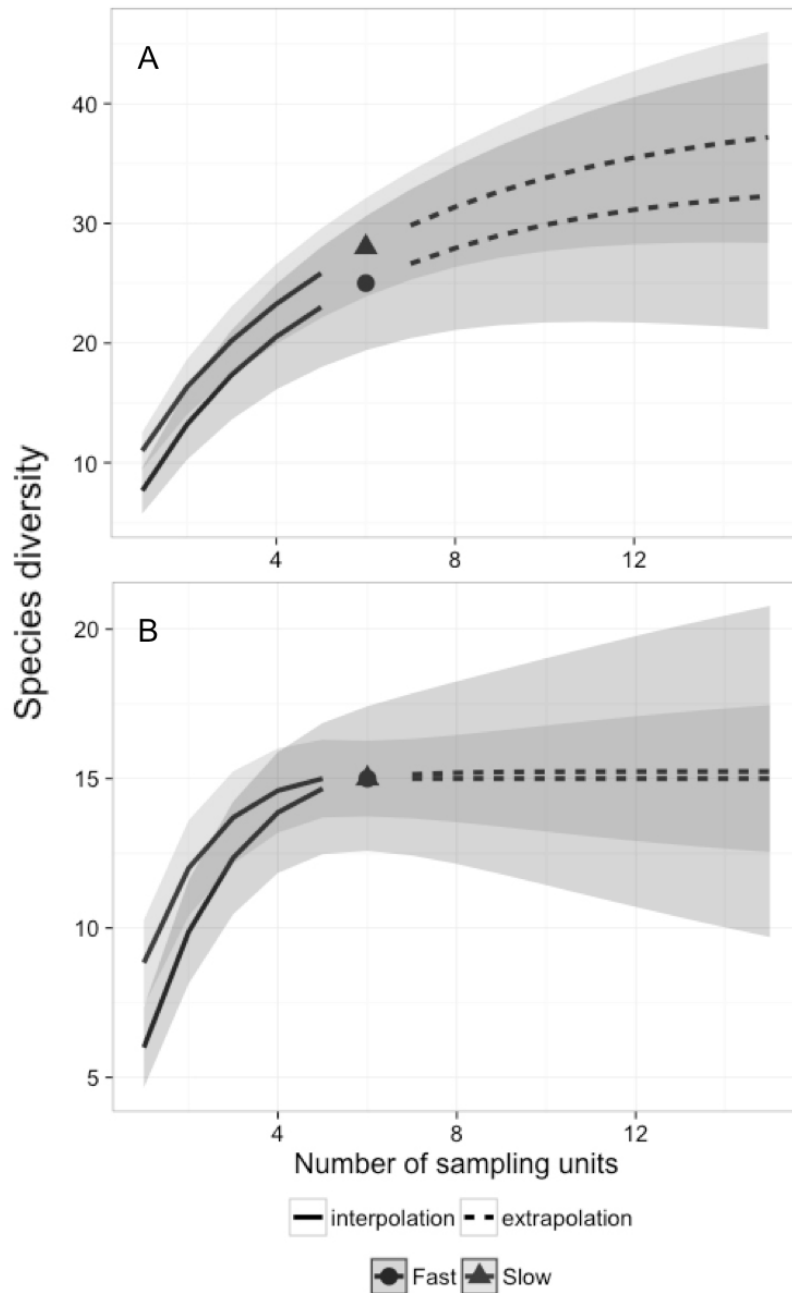
Fig. 6. Sample-size-based rarefaction and extrapolation for fast and slow biotopes. Graph (A) includes all sampled taxa and (B) includes the common taxa which is defined as any taxa that is found more than once.

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Appendix 1. Density (individual per m^2) and Biomass (AFDM mg m^{-2}) at the two study sites and at all the biotopes. Density and biomass has been calculated by compositing X 3 Surber samples with a combined area of 0.3069 m^2. NB: L = larvae, S = stream and T = tributary.

		SP1	SP2	SP3	SR1	SRif2	SRif3
Brachyura							
	Brachyura						
Ephemeroptera							
Leptophlebiidae	*Choroterpes*	6.52/2.43	6.52/1.41	6.52/2.00		3.26/0.71	
Baetidae	*Centroptilum*	3.26/0.36	13.03/2.38		6.52/0.62		
	Baetiella						
	Platybaetis						
Heptageniidae	*Campsoneuria*	3.26/0.64		9.78/7.29		3.26/2.04	
	Epeorus				6.52/7.98		
	Thalerosphyrus	13.03/11.16	29.33/15.06	19.55/2.87		6.52/1.40	3.26/14.26
Caenidae	*Caenodes*						
Ephemerellidae			3.26/0.77				
Odonata							
Libellulidae	*Zygonyx*				13.03/4.75		
Gomphidae	Gomphidae					6.52/1.48	9.78/4.57
Platystictidae	*Drepanosticta*			3.26/3.16			3.26/8.09
	Euphaeid.sp	3.26/5.18	3.26/16.62				
Macromiidae	*Macromia*						
	Chlorocyphidae						
Perlidae							
Perlidae	*Neoperla*			3.26/0.64			
Heteroptera							
Nemoiridae	Nemoiridae						
Pleidae	*Paraplea*	6.52/0.03		3.26/0.02			
Naucoridae	*Coptocatus*						3.26/23.54
	Thurselinus				6.52/5.02		3.26/49.75
	Gestroiella			3.26/5.16			
	Laccocoris		3.26/3.91	6.52/45.50			
	Coptocatus	6.52/0.46					
Nepidae	*Cercotmetus*			3.26/593.94			
Megaloptera							
Corydalidae	*Protohermes*					3.26/20.48	3.26/5.29
Trichoptera							
Brachycentridae	*Micrasema*						
Calamoceratidae	*Ganonema*						
Hydropsychidae	Hydropsychidae			3.26/2.95			
	Pseudoleptonema					3.26/13.05	
	Diplectrona					3.26/13.05	3.26/4.59
Helicopsychidae	Helicopsychidae						13.03/1.53
Leptoceridae	*Athripsodini*						
Calamoceratidae	*Anisocentropus*					3.26/5.72	
Coleoptera							
Elmidae	*Grouvellinus*		3.26/0.79		97.75/23.69		55.39/30.6
Elmidae	Elmidae (L)			3.26/0.48			
Psephenidae	Eubrianax	13.03/7.80	26.07/9.43	3.26/2.75			3.26/0.72
Hydrophilidae	*Agraphydrus* (L)						
Dytiscidae	*Neptosternus*						6.52/6.76
Eulichadidae	Eulichadidae (L)						
Scirtidae	Scirtidae (L)						3.26/0.14
Diptera							
Athericidae	*Asuragina*						
	Atrichops						
Simuliidae	Simuliidae						3.26/0.45
Chironomidae	Chironomidae	6.52/0.30	6.52/1.05	13.03/2.85			

Appendix 1. (continued)

		TP1	TP2	TP3	TR1	TR2	TRif3
Brachyura							
	Brachyura		3.26/8.67				
Ephemeroptera							
Leptophlebiidae	*Choroterpes*	6.52/1.18	6.52/1.31	3.26/0.22			
Baetidae	*Centroptilum*		3.26/0.48	6.52/3.97		3.26/0.29	3.26/13.16
	Baetiella						3.26/0.29
	Platybaetis				3.26/0.62	3.26/0.29	9.78/4.97
Heptageniidae	*Campsoneuria*	3.26/0.41	6.52/2.99	22.81/3.08			3.26/0.14
	Epeorus						
	Thalerosphyrus	6.52/2.27	9.78/3.55	9.78/0.46			
Caenidae	*Caenodes*			3.26/0.46			
Ephemerellidae							
Odonata							
Libellulidae	*Zygonyx*				6.52/1.41		
Gomphidae	Gomphidae		3.26/5.45	3.26/15.40			6.52/19.40
Platystictidae	*Drepanosticta*						6.52/1.52
	Euphaeid.sp.	6.52/9.23		3.26/0.75			
Macromiidae	*Macromia*	3.26/3.86	13.03/25.15	19.55/7.21			
	Chlorocyphidae		3.26/2.28	3.26/3.16			
Perlidae							
Perlidae	*Neoperla*						
Heteroptera							
Nemoiridae	Nemoiridae				3.26/0.13		
Pleidae	*Paraplea*						
Naucoridae	*Coptocatus*						
	Thurselinus						
	Gestroiella	3.26/7.19					3.26/5.39
	Laccocoris						
	Coptocatus	3.26/0.04					
Nepidae	*Cercotmetus*						
Megaloptera							
Corydalidae	*Protohermes*						3.26/2.41
Trichoptera							
Brachycentridae	*Micrasema*	3.26/1.59					
Calamoceratidae	*Ganonema*	3.26/4.01					
Hydropsychidae	Hydropsychidae						
	Pseudoleptonema						3.26/5.50
	Diplectrona						
Helicopsychidae	Helicopsychidae				3.26/0.29	6.52/0.56	
Leptoceridae	*Athripsodini*			3.26/0.14			
Calamoceratidae	*Anisocentropus*						
Coleoptera							
Elmidae	*Grouvellinus*		3.26/0.59		55.39/14.7	9.78/2.58	3.26/1.03
Elmidae	Elmidae (L)						
Psephenidae	*Eubrianax*	6.52/2.66	19.55/6.99	3.26/2.91			
Hydrophilidae	*Agraphydrus* (L)						6.52/2.92
Dytiscidae	*Neptosternus*			3.26/13.50			
Eulichadidae	Eulichadidae (L)						
Scirtidae	Scirtidae (L)						
Diptera							
Athericidae	*Asuragina*		3.26/6.25				
	Atrichops	3.26/1.90	3.26/0.54	3.26/0.45			
Simuliidae	Simuliidae						
Chironomidae	Chironomidae			3.26/0.07			