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Functional and trophic diversity of tropical headwater stream communities inferred from carbon, nitrogen and hydrogen stable isotope ratios

Hayden B.[1]*, Tongnunui, S.[2,3], Beamish, F.W.H.[2], Nithirojpakdee, P.[4], Soto, D.X.[5], and Cunjak R.A.[1]

[1]Canadian Rivers Institute and Biology Department, University of New Brunswick, Fredericton, NB, Canada

[2]Environmental Science, Faculty of Science, Burapha University, Bangsaen, Chon Buri, 20131, Thailand.

[3]Department of Conservation Biology, Mahidol University, Kanchanaburi Campus, 71150, Thailand

[4]Faculty of Argo-Industrial Technology, Rajamangala University of Technology, Tawan-Ok Chanthaburi Campus, Chanthaburi, 22210, Thailand

[5]UK Centre for Ecology and Hydrology, Lancaster Environment Centre, Lancaster LA1 4AP, UK

Abstract

Tropical freshwaters support an immense diversity of fishes and invertebrates but are understudied in comparison to temperate systems. This is especially true of headwater streams, as only a small number of studies has assessed the trophic dynamics underpinning food web structure in these streams. We used stable isotopes of carbon, nitrogen and hydrogen to determine the resource use of dominant invertebrate guild and fishes in seven headwater streams in Eastern and Western Thailand, and assessed the functional and trophic diversity of each community using isotope food web metrics. Benthic invertebrates (95% credibility interval: 37-85%) and fishes (39 - 79%) obtained most of their resources from autochthonous sources in each stream but allochthonous and autochthonous specialists were evident in each community. We observed an increase in isotopic diversity of fishes associated with increasing stream size, but this was primarily driven by increase in the range of isotope ratios of allochthonous and autochthonous food web endmembers rather than an increase in functional diversity. Maximum trophic position did increase with stream size. The snakehead, *Channa gachua*, was enriched in ^{2}H relative to all other fishes, possibly reflecting facultative air breathing by this species. Fish communities in the headwater streams analysed filled a variety of trophic niches, predominantly fuelled by autochthonous primary production.

Keywords: Channidae, Thailand, niche, trophic position, allochthony, biofilm

Declaration of interest: none

Introduction

Tropical streams are amongst the most species rich habitats on the planet (Tisseuil et al., 2013). However, these biodiversity hotspots are threatened by a wide range of factors including habitat degradation (Dudgeon, 2000), impoundments (Winemiller et al., 2016) and climate change (Magurran et al., 2011), all of which are increasing throughout the tropical biomes (IPCC, 2015). This creates an urgency to understand and protect the ecological mechanisms which support this great diversity of species (Dudgeon et al., 2006; Magurran et al., 2011).

Biodiversity is inherently linked to functional diversity (Stuart-Smith et al., 2013). To minimise direct competition with sympatric species, fishes occupy distinct trophic niches and foraging ecologies. Consequently, tropical fishes can often be assigned to distinct functional feeding guilds as species specialise on a specific prey or set of preys (Ward-Campbell et al., 2005). This approach provides a tool with which to determine how fishes compartmentalise food resources (Montaña et al., 2014; Tongnunui and Beamish, 2009) but, in the context of food web or ecosystem function, does not sufficiently account for the energy pathways supporting entire consumer communities. Streams in temperate biomes are predominantly fuelled by allochthonous and autochthonous primary producers, with consumer communities in headwater streams primarily reliant on terrestrial derived nutrients (Vannote et al., 1980). This diversity of resources underpins functionally diverse assemblages of primary consumers, although both production pathways are rapidly integrated in subsequent trophic levels (Hayden et al., 2016). Tropical streams in contrast, are primarily fuelled by autochthonous production throughout their length

(Dudgeon et al., 2010). The majority of research regarding these systems has taken place in lower reaches (Winemiller et al., 2011) but work on headwaters of streams in Hong Kong (Dudgeon et al., 2010; Lau et al., 2009) and French Guiana (Coat et al., 2009) and Brazil (Reis et al., 2020) indicated that fishes and invertebrates obtain the majority of their resources from autochthonous production.

Consumers' stable isotope ratios are an effective tool with which to infer the source of primary production which is fuelling a single species or entire community (Boecklen et al., 2011). This information is complementary to diet assessments which, although showing what a consumer has fed on do not readily account for the underlying energy pathways (Hayden et al., 2019). Stable isotope ratios of carbon, in particular, varies minimally between consumers and their prey. Therefore, provided allochthonous and autochthonous prey have distinct carbon isotope ratios, the relative importance of each to consumers can readily be assessed (Rasmussen, 2010). However, as the carbon stable isotope ratios of primary producers vary both spatially and temporally, it is not uncommon for allochthonous and autochthonous components of the food web to have similar values (Doucett et al., 2007). In these instances it is not possible to estimate resource use from carbon isotopes alone and additional tracers are necessary (Phillips et al., 2014). Stable isotopes of hydrogen (^{2}H) are useful in this regard, due to differential fractionation by terrestrial and aquatic plants, the δ^2H stable isotope ratios of allochthonous and autochthonous food web end members can differ by up to 200‰ (Vander Zanden et al., 2016). Hydrogen isotope techniques are more complex than carbon or nitrogen however, as values and analyses must be corrected for the contribution of environmental water (Solomon et al., 2011; Soto et al., 2013b), hydrogen exchangeability in organic materials (Soto et al., 2017; Wassenaar and Hobson, 2003) and the possible effect of lipids (Soto et al., 2011) prior to analysis. Despite these challenges, hydrogen isotopes are an increasingly common and useful tool to decipher the resource use of consumers in stream food webs, though their use in tropical environments is limited in comparison to carbon and nitrogen (Soto et al., 2019; Vander Zanden et al., 2016). In addition to estimates of resource use, the carbon, nitrogen and hydrogen stable isotope ratios of multiple consumers can be used to estimate food web breadth, i.e., diversity of resources integrated into the food web (Layman et al., 2012), and maximum trophic position, a proxy for food chain length (Vander Zanden and Rasmussen, 1999).

In order to develop a more complete understanding of the food web structure and energy pathways supporting diverse species assemblages in tropical headwater steams we used carbon, nitrogen and hydrogen stable isotope ratios to estimate the resource use of benthic macroinvertebrates and fishes in addition to calculating isotopic food web breadth and maximum trophic position. We tested two hypotheses: 1) That tropical headwater stream invertebrate and fish communities are primarily fuelled by autochthonous resources, and 2) that larger headwater streams would support a larger and more functionally diverse food web as evidenced by increased food web breadth and food chain length.

Methods

Study sites

Fish, aquatic benthic macroinvertebrates (hereafter BMI) and primary producers were sampled from seven headwater streams in eastern and western regions of Thailand (Figure 1). All sample sites were in stream sections considered as pristine or marginally impacted by agriculture and were considered to be representative of these stream sections (Tongnunui and Beamish, 2009). In eastern Thailand, near the border with Cambodia, sites were selected in three headwater streams (Sato, Stornoi and Nong Mai Khom, hereafter Nong) of the Trat River system. In western Thailand, within 27 km of the border with Myanmar (Figure 1), study sites were chosen in four (Pakkok, Pilok, Lichia and Kayeng) tributary streams of the Kwae Noi River. Sample sites in both regions were road-accessible but sampling was conducted >150 m of the nearest road or bridge. Eastern streams were sampled in January 2015 and western streams were sampled in March 2016. Habitat characteristics; stream width (± 0.1 cm), depth (± 1 cm), and water velocity (±1 cm s^{-1}) were measured and used to estimate the water discharge (L s^{-1}) as the product of the mean width, depth and velocity. The depth and velocity measurements were the average of 3 to 5 measurements made at approximately equal intervals along a single transect of each stream site. Velocity was measured with a calibrated propeller current meter (Model 2C; Ott; Kempten, Germany) placed at the surface and adjusted to represent the mean flow rate (Gillner and Malmqvist 1998). The length of the site was measured from upstream to downstream as an area for collecting fish, BMI, biofilm, leaf litter, macrophytes and filamentous algae. We measured a suite of habitat and physiochemical variables at each site (Supporting Table 1): canopy cover (%), turbidity (national turbidity units or NTU), velocity (cm s^{-1}), water temperature (ºC), discharge (l s^{-1}) and conductivity (µS.cm^{-1}). Dissolved oxygen, temperature, pH and conductivity were measured with regularly calibrated probes (models HI9147, HI98127 and HI9835, respectively; Hanna; Bangkok, Thailand). Ambient ammonia, nitrite, nitrate and silica were measured as described in American Public Health Association (2017). Elevation was measured using a calibrated global positioning meter (±10 m, model 60CSx; Garmin International; Kansas City, KS, USA). Due to high collinearity between canopy cover, mean depth, turbidity and velocity (VIF scores >15) we used principal component analysis (PCA) to summarize these four variables into a single composite variable (Supporting Fig. 1). The first principal component of this PCA, accounting for 85.1% of variation in these variables, with increasing PC1 values reflecting depth and turbidity and decreasing velocity and canopy cover. This principal component, hereafter 'Stream size', was included in subsequent models to reflect changes in these four closely associated variables among sites.

Sample collection

Water samples were collected from each site and sealed in air tight tubes for hydrogen stable isotope analysis. Leaf litter, macrophytes, filamentous algae and biofilm scrapings from rock were collected at each site. Biofilm scrapings from leaf litter were also collected from western streams in 2016. BMI were collected using qualitative kick net sampling at each site. BMI were identified to order level in the field and all individuals within each order (n = 3- 15) were pooled into a single sample representing that order. We did not identify invertebrate samples below order level and it is likely that the taxonomic composition of each order sample differed between streams. Invertebrate samples were preserved chilled during transport to the laboratory. Fish were captured using a back-pack electro-fisher (model LR24, Smith-Root, Vancouver, WA, USA). Output voltage was varied inversely with water conductivity and was mostly between 200 and 600 V in combination with a 30-60Hz wave width and frequencies of 1–4 m s^{-1}. Each site was electro-fished by moving upstream in a zigzag pattern from one bank to the other. After capture, fish were euthanized by the application of a lethal dose of tricaine methane sulfonate (>150 mg L^{-1}), which has minimal influence on the stable isotope ratios of ectotherms (Atwood, 2013). Total length (TL, 0.1cm) and wet mass (0.1g) of each individual was recorded and fish were identified to species level following Tongnunui and Beamish (2009; Tongnunui et al., 2016). A sample of dorsal muscle was dissected from each fish. All solid samples were oven-dried (24-48 hours at 60°C) and shipped to the Stable Isotopes in Nature Laboratory (University of New Brunswick, Canada) for stable isotope analysis.

Laboratory analysis

Fish and BMI samples were immersed in a 2:1 chloroform:methanol solution for 6 hours followed by two 60 minute immersions to remove lipids (Bligh and Dyer, 1959). All animal samples were uniformly treated to standardize the possible effects of lipid extraction on the δ^{15}N values (Logan and Lutcavage, 2008). Samples were then dried (24 hours at 60°C) and ground to a fine powder. For carbon and nitrogen stable isotope analysis, 1.0 ± 0.1mg subsamples were placed in tin-foil cups. Samples were combusted and analyzed in a Delta Plus continuous-flow isotope-ratio mass spectrometer (Thermo Finnigan GmbH, Bremen, Germany) connected to a Carlo Erba NC2500 elemental analyzer (ThermQuest S.p.A., Milan, Italy). Carbon and nitrogen isotope ratios are reported relative to international standards Vienna PeeDee Belemnite carbonate and atmospheric nitrogen respectively. Analytical precision, calculated as the standard deviation of repeat analyses of in-house standards muskellunge muscle and bovine liver, was estimated as 0.1 ‰ for both δ^{13}C and δ^{15}N. For hydrogen isotope analysis, 0.2 ± 0.05 mg subsamples of each sample were placed in silver foil cups. Stable hydrogen isotope measurements for animal tissues were normalized to the international standard VSMOW (Vienna Standard Mean Ocean Water) using keratin reference materials EC1 (CBS, δ^2H = -157.0 ‰) and EC2 (KHS, δ^2H = -35.3 ‰) (Soto et al., 2017). We determined the non-exchangeable δ^2H of samples using the comparative equilibration approach (Wassenaar and Hobson, 2003) with these two keratin reference materials (EC1 and EC2) by allowing that samples and standards to exchange with local atmospheric moisture for a minimum of 72 hours prior to analysis. Samples were pyrolysed at 1450°C and analysed using a High Temperature Conversion Elemental Analyser (TCEA; Thermo Scientific GmbH, Bremen, Germany) connected to a Delta *Plus* XP continuous flow isotope-ratio mass spectrometer (Thermo Scientific GmbH, Bremen, Germany). Within-run standard deviation of repeated measurements of δ^2H in an in-house standard, keratin (Spectrum-Porcine #SJ1400), indicated that analytical precision was below 2 ‰.

Data analysis

In order to obtain dietary δ^2H values, consumer δ^2H isotope ratios were corrected to account for the contribution of environmental water (Brett et al., 2018). Stable hydrogen isotope ratio of water was measured for the Khayeng (-31 ± 2‰), Lichia (-33 ± 2‰), Pakkok (-28 ± 2‰) and Pilok (-25 ±2‰) streams, and estimated to be -30‰, on average, in all other streams. We assumed that fish and aquatic macroinvertebrates respectively obtain 28% and 40% of their hydrogen from environmental water (Soto et al., 2013a, 2019) and calculated dietary δ^2H using the model outlined in Soto et al (2019). Corrected, dietary δ^2H values are used in all subsequent data analyses.

We used permutational multivariate analysis of variance, PERMANOVA (Anderson, 2001), to assess the degree to variation in isotope ratios (δ^{13}C, dietary δ^2H & δ^{15}N) between Region (East / West, fixed), Stream (7 levels, nested in Region), and fish species (16 levels, nested in Stream). We use the betadisp function in the R package vegan to test homogeneity among sites in the dataset prior to analysis. PERMANOVA analysis (9,999 permutations) was performed using the vegan (Oksanen et al., 2015) package in R (R Core Team, 2017).

We used the stable isotope mixing model MixSIAR (Stock et al., 2018) to estimate the relative contribution of allochthonous and autochthonous resources to each invertebrate order and fish species at each stream based on their carbon and hydrogen isotope ratios (Soto et al., 2019). Biofilm scraped from rocks and filamentous algae collected at each stream represented the autochthonous food web endmembers at that stream. Conditioned leaf litter collected at each stream was used as the allochthonous food web endmember for that stream. Where only a single composite allochthonous or autochthonous sample was available we treated that sample as a mean endmember value and estimated variance as 1‰ and 10‰ for $\delta^{13}C$ and $\delta^{2}H$ respectively. We assumed a trophic discrimination of 0.4 ‰ (±1.2) per trophic level for $\delta^{13}C$ (Post, 2002). No discrimination was considered for $\delta^{2}H$ as these values had previously been corrected for the influence of environmental water (Solomon et al., 2011; Soto et al., 2019). Uninformative (i.e. null) priors were included in all mixing models. Mixing models converged with three 50,000 iteration chains and a 25,000 iteration burn in.

Isotopic and functional diversity amongst the fish community was estimated using the Niche Rover package (Swanson et al., 2015) in R. Isotopic diversity was estimated as the area of a convex hull encompassing the $\delta^{15}N$, $\delta^{13}C$ and dietary $\delta^{2}H$ is all fish sampled in that stream. Functional diversity was estimated as the area of a convex hull encompassing the trophic position, estimated allochthonous resource use based on $\delta^{13}C$ and estimated allochthonous resource use based on dietary $\delta^{2}H$ in each stream. Both of these estimates were derived using the two-source stable isotope mixing model defined by Post (2002) incorporating food web endmember and fraction values outlined previously. The maximum trophic position (TPmax), a proxy for food chain length, observed at each site was estimated as the difference between the maximum $\delta^{15}N$ value observed for any consumer and the mean $\delta^{15}N$ value of autochthonous endmembers, divided by 3.4, an estimate of discrimination per trophic level following Post (2002).

The relationship between the trophic ecology of consumers and environmental characteristics of each steam was assessed using Generalised Linear Models. Stream size (a principal component accounting for 85.1% of variation in stream width, depth, canopy cover, and velocity), conductivity, discharge and temperature were included as independent predictor variables in each model. We performed separate models to test the effect of these on allochthonous resource use by invertebrates and fishes, in addition to community wide measurements isotopic and function diversity, and TPmax. Predictor variables were scaled prior to running the models meaning that Coefficients of Variation values may be interpreted as effect sizes in these models. Model selection was performed using the stepAIC function in R.

Results

Spatial variation in isotope ratios

Variance in isotope ratios among sites was not homogenous among sites (N permutations = 9,999, $F_{2,260}$ - 2.46, P = 0.02), however post-hoc tests indicated that this was solely due to differences between the Nong and Lichia samples (Supporting Table 2). In contrast, pairwise PERMANOVA analysis identified variance in isotope ratios among 19 of the 21 site combinations (Supporting Table 3). As such, we considered the PERMANOVA results reliable though direct comparisons of Nong and Lichia data was not included in subsequent analyses. PERMANOVA revealed significant variation between regions, streams within each region and fish species within each stream (Table 1). The largest amount of variation was explained by the difference between species and stream, with comparatively less variation ascribed to region. The interactions between species and stream was also statistically significant indicating that fish species have distinct isotopic niches within each stream (Fig. 2, Supporting Fig. 2).

We observed considerable variation in the $\delta^{13}C$ and $\delta^{15}N$ values of isotopic endmembers between sites. The autochthonous endmember values of both isotopes were positively correlated with stream size, whereas the allochthonous endmember values were similar across all sites (Fig. 3). Consequently, the range between endmembers was greater in larger streams than small streams. No comparable variation was observed in the δ^2H values of either food web endmember. Carbon isotope ratios of BMI and fishes were positively correlated with autochthonous endmembers across the study region (BMI: n = 34, r_s = 0.57, $P < 0.001$; fish: n = 265, r_s = 0.36, $P < 0.001$) as the values were similar to those of autochthonous baseline sources in the smallest streams but did not follow the pattern of depletion in ^{13}C in larger streams which was evident in the autochthonous endmembers. In contrast, dietary δ^2H of BMI and fishes was aligned with autochthonous endmembers across all sites. However, in the largest streams several fish samples had dietary δ^2H which were ^{2}H depleted relative to the autochthonous endmember (Fig. 3). The δ^{15}N values of BMI and invertebrates were positively correlated with autochthonous endmembers across sites (BMI: n = 34, r_s = 0.61, $P < 0.001$; fish: n = 265, r_s = 0.56, $P < 0.001$), indicating that both BMI and fishes receive most of their nitrogen from autochthonous sources in all streams.

Allochthony in benthic macroinvertebrates

Benthic macroinvertebrates (BMI) assimilated more autochthonous (median & 95% Credibility interval: 61%; 37 - 85%) than allochthonous (39%; 14 – 64%) materials across all sites, but resource use differed considerably between steams (Supporting Fig. 2). Pooled BMI obtained approximately 12% of their energy from allochthonous resources in the small Lichia stream, but over 50% in the larger Nong and Sato streams (Fig. 4a). GLM indicated that median allochthonous resource use of BMI was positively related to stream size, but this relationship was not statistically significant as the effect size (11.9) was countered by a substantial standard error (8.4), due to the low estimate of allochthonous resource use by pooled invertebrates in the largest streams, Khayeng and Pakkok (Fig. 4a, Table 2). Allochthonous resource use also displayed a weak, negative relationship with discharge, although again this is not statistically significant due to high degree of variance between sites. No relationship was evident between water temperature and resource use of BMI. Similar patterns were evident among all BMI groups, though shrimp consistently assimilated a smaller proportion of allochthonous resources than other taxa, whereas snails and water striders were more reliant on allochthonous materials (Fig. 4, Supporting Table 4). Taxon specific estimates of resource use were associated with a large degree of error as each group is represented by a single sample of several pooled individuals collected at each site and as such should be interpreted with some caution.

Allochthony in fishes

We observed a very strong positive correlation between estimated allochthony of benthic macro-invertebrates and fishes among sites ($n = 7$, $r_s = 0.95$, $P < 0.001$). Fishes assimilated more autochthonous (median: 60%, 95% CI: 39 - 79%) than allochthonous (median: 40%, 95% CI: 21 - 61%) resources, and variation in resource use was evident between streams and also between fish species within each stream. When assessed across the pooled fish community median estimates of allochthonous resource use ranged between 13% (2 - 28 CI) in the Pakkok and 60% (50 - 69 CI) in Pilok streams. Despite this variation between sites, stream size and temperature were omitted from during model selection, indicating that they are not related to allochthonous resource use (Table 2). At the species level, considerable variation in resource use was evident between fishes (Fig. 4b). *Channa gachua, Systomus binotatus,* and *Rasbora* spp., predominately assimilated allochthonous material, whereas *Macrognathus circumcinctus, Glyptothorax laosensis* and *Homalopteroides smithi* were more reliant on autochthonous material (Fig. 4b, Table S1). Where present, *Neolissochilus blanci* obtained the majority of their resources from autochthonous materials. Fishes sampled in the Pakkok stream, the largest system studied, were all primarily reliant on autochthonous material, with the sole exception of *C. gachua*, which continued to integrate allochthonous derived energy (40 - 50% CI).

Functional diversity

There was little evidence of variation in functional diversity among the fish communities sampled. We observed a positive relationship between isotopic diversity of the fish community and stream size (Fig. 5, Table 2). However, this appears to be driven by the variation in the isotope ratios of food web endmembers between sites as comparable tests of functional diversity revealed no relationship (Fig. 5; Table 2). Similarly, while $\delta^{15}N$ values of consumers were positively related to stream size, this was primarily driven by variation in the δ^{15}N values of the autochthonous end-member (Fig. 5). Maximum trophic position (TPmax) was positively related to stream size however, though Pakkok stream was out an outlier in this relationship (Fig. 5)

Discussion

We examined food web structure in seven tropical headwater streams in Thailand. In keeping with previous research of tropical headwater streams, we found that the stream food webs are predominantly fuelled by autochthonous production, but our results also reveal a range in the resource use of fishes in most streams, supporting our hypothesis that taxonomic diversity in these systems is underpinned by functional diversity. However, in contrast to our expectation, functional diversity in the streams analysed was not related to stream size.

We observed variation in isotope ratios and estimated resource use amongst BMI taxa but it is difficult to adequately quantify this due to small sample sizes and low replication within streams. Variation amongst fishes is easier to interpret as we had had considerably more replicates in each stream. We identified three distinct trophic levels amongst the fish community. *Garra fuliginosa* and *Neolissochilus blanci* had lower δ^{15}N values than all other fishes and a high reliance on autochthonous energy in all steams, indicating that both species are primary consumers, likely foraging on algae within the biofilm (Rainboth, 1996). We observed greater variation in resource use amongst secondary consumer fishes. Most rely on autochthonous production but *Channa gachua*, and where present, *Rasbora caudimaculata*, *Rasbora paviei* & *Systomus binotatus* integrated more allochthonous derived resources. Where present, *Glyptothorax laosensis* is the top predator and is also reliant on autochthonous energy in all streams, further evidence that the food web is predominantly fuelled by autochthony. Interestingly, the majority of fishes were trophic specialists, with 95% creditability intervals on estimates of resource use rarely exceeding 15 - 20%.

Our findings are commensurate with those of other tropical headwater streams. March and Pringle (2003) examined second order, headwater streams in Puerto Rico, their data, based on carbon and nitrogen stable isotopes alone, indicated that invertebrates and fishes primarily assimilated algal derived energy, even in sites with 70% canopy cover. Their findings are similar to substantial body of work focussing on Asian streams which indicates that autochthonous production is the primary pathway supporting tropical stream food webs (Dudgeon et al., 2010; Lau et al., 2009). While in broad agreement with this, our data do show interesting variation between populations and indicate that the community ecology within these headwater systems somewhat is influenced by stream size. We see some evidence of a possible non-linear relationship between stream size and functional diversity. For example, Sato, Stornoi and Nong streams had higher functional diversity than either the smallest or largest streams included in the study. These streams contained several BMI and fish specialising on allochthonous resources in addition to the autochthonous specialists found elsewhere. This was further evident in the community metrics which revealed greater community level variation in $\delta^{13}C$ and $\delta^{2}H$ in mid-size streams, likely reflecting the presence of several distinct functional feeding groups of fishes. Increased functional diversity in larger streams was also evident through a slightly higher maximum trophic position in these streams, additional evidence for larger and more complex food chains. Further study involving a greater number of streams would be necessary to determine whether the trends evident here reflect a truly non-linear pattern or are simply noise within the data.

Contrary to our expectations however, the increased isotopic diversity in large stream communities was driven by an increase in the difference between autochthonous and allochthonous food web endmembers rather than an increase in the functional diversity of the community. This was primarily due to an enrichment in ^{13}C and ^{15}N in larger streams relative to smaller streams and likely reflects increased productivity in these larger streams. An association between $\delta^{13}C$ of autochthonous primary producers and stream size is well established (Finlay, 2001; Rasmussen, 2010) Higher productivity in larger systems results in a depletion of DIC in the water column, which in turn leads to reduced fractionation of ^{13}C by primary producers resulting in autochthonous $\delta^{13}C$ values which are closer to atmospheric CO_2

(circa -8‰; Finlay, 2001; Kendall et al., 2001). In contrast, terrestrial C3 plants, dominant in the study region, typically have $\delta^{13}C$ values of approximately -28‰,meaning that the allochthonous values will not change across the study region (Boecklen et al., 2011). The observed enrichment in ^{15}N of autochthonous primary producers likely reflects increased rates of assimilation/denitrification in larger, more productive streams and, as seen in $\delta^{13}C$ this is not reciprocated in the allochthonous end member (Finlay and Kendall, 2007).

Our data are amongst the first to detail stable isotopes of hydrogen to tropical headwater streams. As is the case in temperate aquatic ecosystems, this provides greater resolution regarding the relative contribution of allochthonous and autochthonous pathways. In our analysis we grouped distinct primary producers into autochthonous and allochthonous sources, however there is evidence that these different producers also have unequal contributions to food web. Biofilm for example, is a complex matrix of algal material, fungi and bacteria. Biofilm scraped from leaves in the Eastern streams had a similar isotope ratio to leaves, but a very different isotope ratio to biofilm scraped from rocks in the same streams. This finding echoes results by Hladyz et al (2011), indicating that microorganisms within biofilm forming on leaves are assimilating carbon from those leaves, rather than solely through photosynthesis. This may account for why gastropods sampled in our study had $\delta^{13}C$ values more typical of allochthonous sources despite typically being considered as grazers. However, despite this, terrestrial carbon is a comparatively minor component of the analysed stream food webs, especially regarding fishes. In addition, filamentous algae was ^{2}H depleted relative to biofilm, as were many fishes, suggesting that this filamentous algae was a prey source for invertebrates in these systems. Further investigation to quantify the composition of biofilm, and the isotope ratios of each of its components, may be necessary to better understand what specific component of the biofilm is fuelling the autochthonous pathway of the stream food web (Larsen et al., 2009).

The inclusion of hydrogen stable isotope data provides additional strength with which to discriminate between allochthonous and autochthonous sources in these sites, however, metadata results show comparability concerns regarding its inclusion in stable isotope mixing models as some aspects relating to the assimilation of ^{2}H and water contribution to tissue H remain inconsistent between studies (Brett et al., 2018), which makes difficult its comparison. The majority of fishes, especially in the Western streams, are ^{2}H depleted relative to both biofilm and filamentous algae. This indicates that either our estimate of the δ^2H value of autochthonous primary producers is not accurate or that our assumption of the contribution of ambient water, or trophic discrimination factors are incorrect. None of these however adequately account for the observed values. Algal δ^2H is depleted relative to ambient water by approximately 150‰ (Brett et al., 2018). In our systems this equates to algal δ^2H values of -170 to -180 ‰, equivalent to the values observed in biofilm and filamentous algae, indicating that our values are reliable. An overestimate of the contribution of ^{2}H of environmental water to fish tissue would result in consumer values being ^{2}H enriched rather than depleted, the opposite of what we observe. Trophic discrimination values for δ^2H are largely unresolved, though one recent experimental study suggested that consumers are ^{2}H depleted relative to their prey by 40 - 50‰ (Newsome et al., 2017). This would result in fish being ^{2}H depleted by at least 80-120‰ relative to primary producers, causing an unlikely scenario whereby consumers sampled in these streams are depleted in ^{2}H relative to both the autochthonous and allochthonous food web endmembers. Discrimination observed in experimental systems however does not necessarily equate to that observed in the wild (Gorokhova, 2018) and as such, true discrimination values for δ^2H in wild fish could fall somewhere between the values reported by Newsome et al (2017) and the common assumption that there is no trophic discrimination in ^{2}H in aquatic consumers (Vander Zanden et al., 2016).

We estimated that *C. gachua* principally assimilated allochthonous resources in all sites. This estimate is primarily driven by hydrogen isotope ratios of this species, as its carbon isotope ratios are similar to all other species in each site. Also, a previous analysis of these systems, based on carbon and nitrogen isotope data indicated that, contrary to our results here, *C. gachua* assimilate similar amounts of allochthonous and autochthonous resources to other fishes in these streams (Hayden et al., 2017). The hydrogen data are somewhat anomalous in this regard, as *C. gachua* exhibited ^{2}H enriched values, characteristic of an autochthonous feeding consumer. Although *C. gachua* are a piscivorous species these individuals do not have elevated ^{15}N isotope ratios and therefore it is unlikely that the ^{2}H values reflect an error in our estimation of trophic compounding of water isotope ratios in the consumer. As no invertebrates or other fishes collected in these sites have similarly higher δ^{2}H values it is difficult to identify why the *C. gachua* had ^{2}H-enriched isotopic composition. One possible explanation is that this could be related to air breathing by *C. gachua*. Several species within the Channidae, including *C. gachua*, have air breathing capacity provided through a suprabranchial assisted adaptation (Munshi et al., 1994; Olson et al., 1994) and it is estimated that Channidae can obtain up to 40% of their oxygen from air rather than water (Singh et al., 1982). This facultative air breathing may have an effect on the evapotranspiration of body water in *C. gachua* resulting in increased levels of ^{2}H in the body tissue relative to other species. Though further investigation is necessary to test this hypothesis it is commensurate with our other findings. If true, this would have implications for our assessment of the importance of allochthonous resources to the fish community as it would mean that we are overestimating the importance of allochthonous resources to *C. gachua*, which is an outlier in terms of estimated resource use in most streams.

Our results provide further evidence that tropical stream food webs break from the stream continuum concept and that these systems require a separate model to describe their energy dynamics (Neres-Lima et al., 2017). Autochthonous materials are typically more labile and energy rich than terrestrial derived materials, consequently where present they have a greater influence of higher trophic levels (Brett et al., 2017; Hayden et al., 2016). In temperate regions, headwater streams are light limited through the summer months but receive a large allochthonous input from leaf fall in autumn and snow melt in spring. This allochthonous material is decomposed and mineralised by assemblages of specialist microorganisms and invertebrates. Tropical streams are similarly light limited, though in the study region this limitation occurs throughout the year rather than a seasonal effect and the paucity of deciduous trees likely means that the invertebrate communities necessary to mineralise allochthonous resources are absent resulting in an annual reliance on autochthonous derived materials. Our findings that autochthony is the dominant food web pathway in headwater streams echo those of Neres Lima et al (2016) and Lau et al (2009) who previously highlighted a reliance on autochthonous primary production even in small steams. These findings are however in stark contrast to other results from Neres-Lima et al (2017), who combined estimates of primary and secondary production with carbon isotope ratios to determine that invertebrate assemblages in a tropical steam in Brazil were fuelled by allochthonous rather than autochthonous production. As such, it is likely that production processes underlying tropical stream food webs are complex and determined by a suite of environmental and physical drivers. The literature regarding tropical stream food webs is extremely limited in comparison to temperate systems and such contrasting findings highlight that further work is required before a standardised model for tropical stream function can be devised.

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Table 1. Results of PERMANOVA analysis of the variation in carbon, hydrogen and nitrogen stable isotope ratios between tropical stream communities.

	Df	SumOfSqs	R^2	F	P
Region	1	0.00771	0.00315	4.4310	0.029 *
Species	15	1.45421	0.59350	55.7388	0.001 ***
Region:Stream	5	0.36197	0.14773	41.6228	0.001 ***
Region:Species	5	0.08449	0.03448	9.7154	0.001 ***
Region:Species:Stream	23	0.08266	0.03374	2.0664	0.004 **

*** $P<0.001$; ** $P< 0.01$; * $P< 0.05$

Table 2. Results of General Linear Models assessing the relationship between trophic isotopic metrics and stream size (a principal component explaining 85% of variation in mean stream depth, velocity, canopy cover and turbidity), mean conductivity, discharge and temperature. Trophic metrics are abbreviated to median allochthonous resource use of pooled benthic macroinvertebrates (Allo - BMI) and fishes (Allo - Fish), a Bayesian estimate of a convex hull encompassing variation in $\delta^{13}C$, dietary $\delta^{2}H$ and $\delta^{15}N$ ($\text{Range}_{\text{iso}}$), variation in allochthony derived from carbon, hydrogen and estimated trophic position of all fishes ($\text{Range}_{\text{res}}$) samples in seven headwater streams, and c) the maximum trophic position (TPmax) observed at each site. Values represent mean (±SE) effect size.

Metric	Stream size	Conductivity	Discharge	Temperature
Allo - BMI	11.9 (8.4)	-	-16.3 (8.4)	-
Allo - Fish	-	-	-10.5 (5.8)	-
$\text{Range}_{\text{iso}}$	830.5 (95.5)**	145.2 (52.5)	-602.7 (85.7)**	-177.1 (54.1)
$\text{Range}_{\text{res}}$	0.1 (0.1)	-0.2 (0.1)	-0.3 (0.1)*	0.1 (0.1)
TPmax	0.2 (0.1)*	0.1 (0.1)		

*** P<0.001; ** P< 0.01; * P< 0.05; - removed during model selection

Water temperature and number of species sampled were removed during model selection

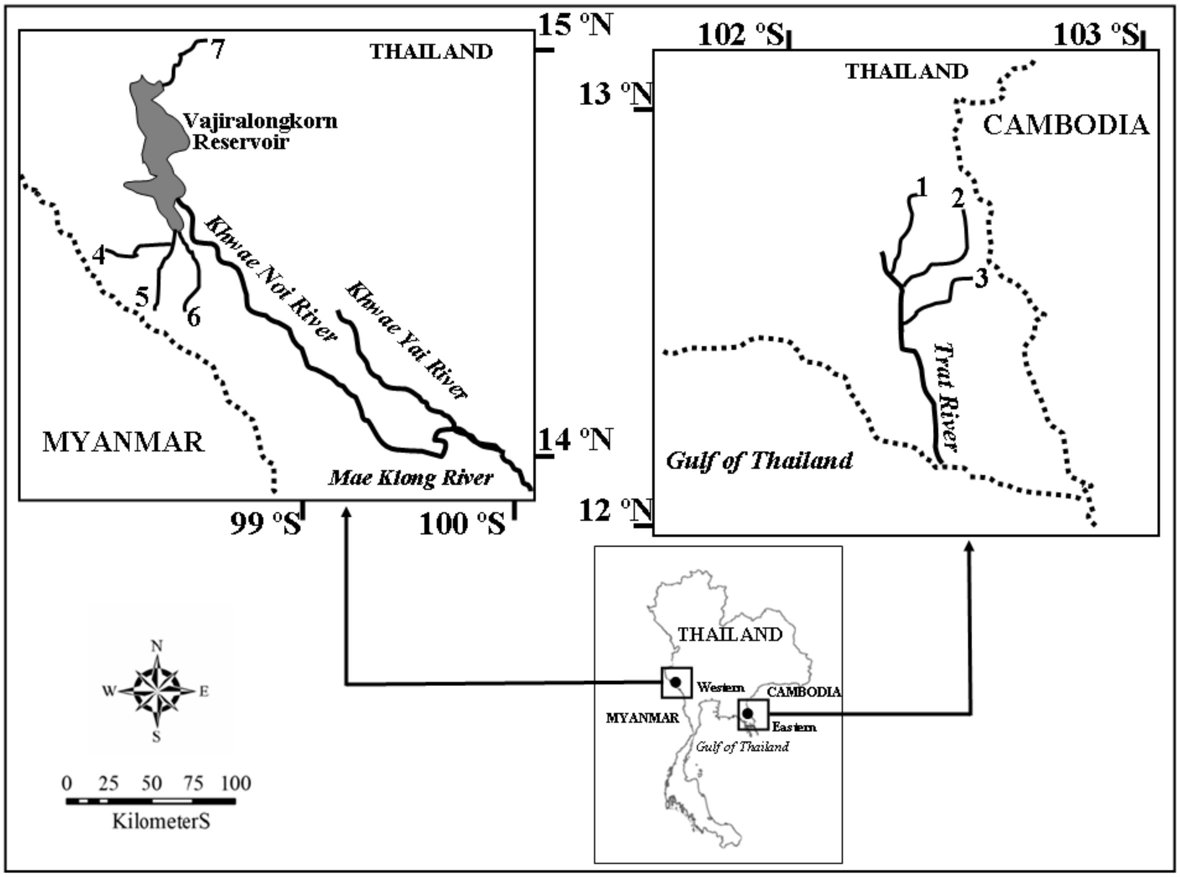


Fig. 1. Map detailing the location of study sites in Eastern (1 - Sato; 2 - Stornoi; 3 - Nong) and Western (4 - Pakkok; 5 - Pilok; 6 - Kayeng; 7 - Lichia) Thailand.

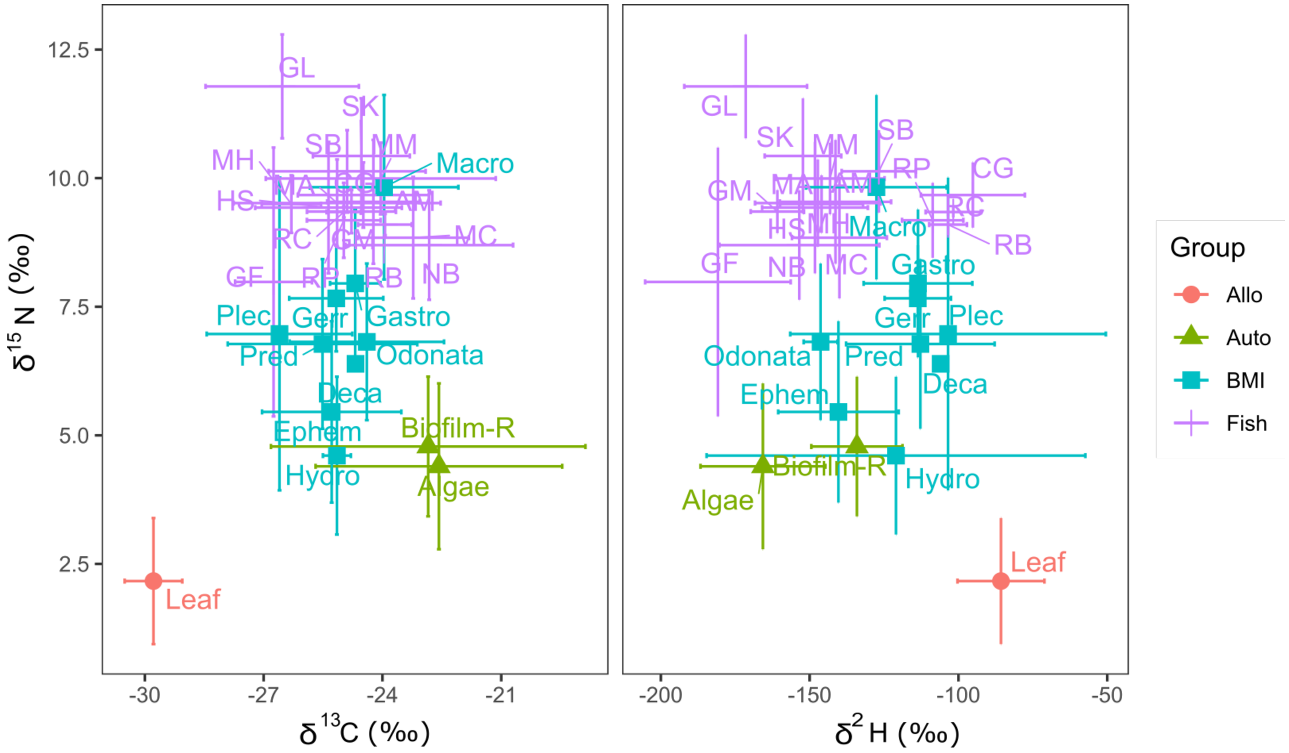


Fig. 2. Scatter plot detailing the mean (±SD) of carbon (δ^{13}C), hydrogen (δ^{2}H) and nitrogen (δ^{15}N) stable isotope ratios of primary producers (algae, biofilm scraped from rock and biofilm scraped from leaves), benthic macro invertebrates (BMI) and fishes collected in seven streams in Western and Eastern Thailand. Biplots detailing the relationships is each stream are presented in Supporting Figure 1. Pred - predatory BMI, Plec - Plecoptera, Ephem - Ephemeroptera, Hydro - Hydropsychidae, Gerr - Gerridae, Macro - Macrobrachium, Deca - Decapoda, Gastro - Gastropoda, AM - *Amblyceps macronatum,* CG - *Channa gachua,* GF - *Garra fuliginosa,* GL - *Glyptothorax laosensis,* GM - *Glyptothorax major,* HS - *Homalopteroides smithi,* MC - *Macrognathus circumcinctus,* MA - *Mastacembelus armatus,* MM - *Mystacoleucus marginatus,* MH - *Mystus havmolleri,* NB - *Neolissochilus blanci,* RC - *Rasbora caudimaculata,* RP - *Rasbora paviei,* SK - *Schistura kohchangensis,* SB - *Systomus binotatus.*

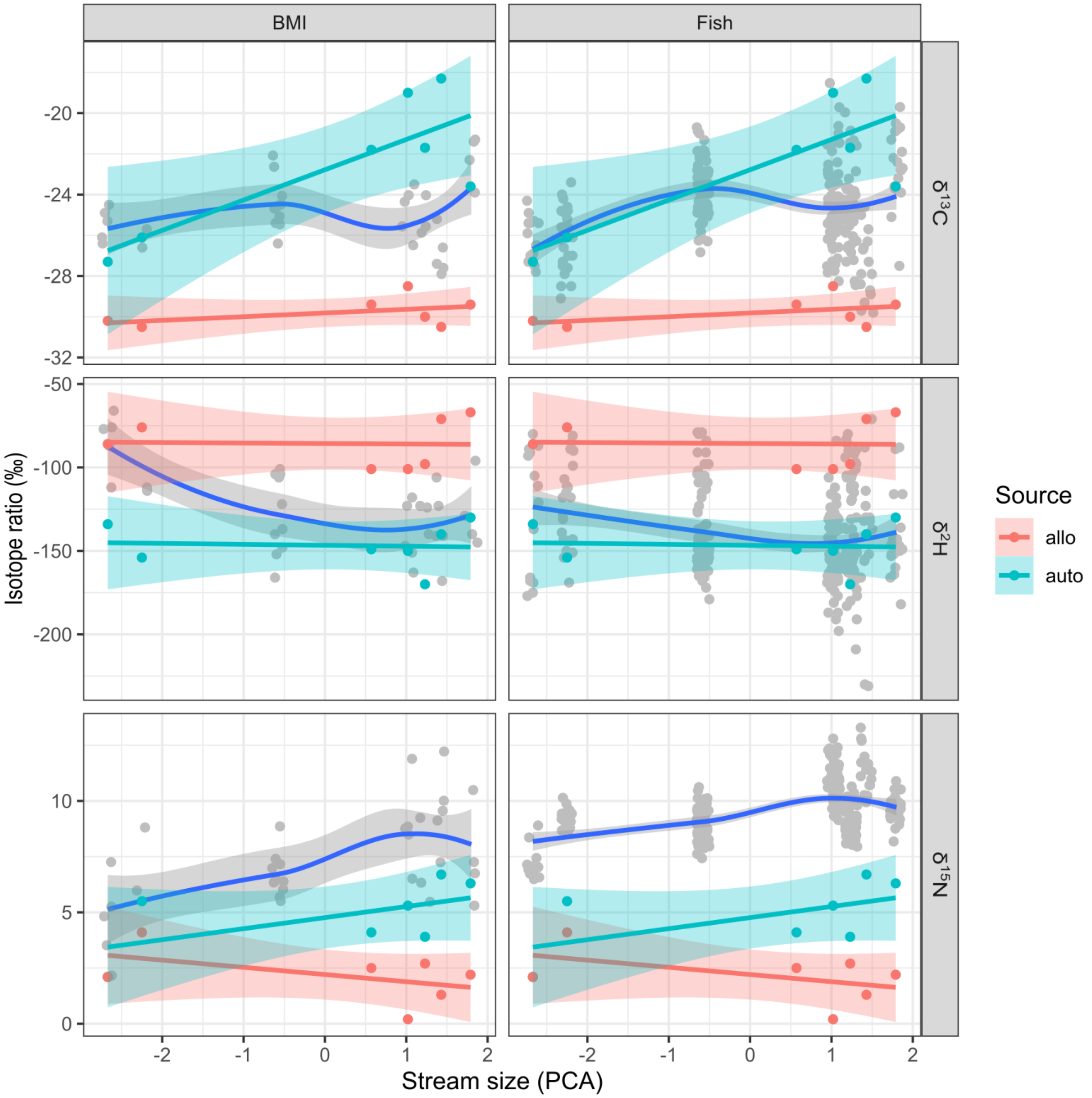


Fig. 3. Variability in carbon ($\delta^{13}C$), dietary hydrogen ($\delta^{2}H$) and nitrogen ($\delta^{15}N$) isotope ratios of a) benthic macroinvertebrates and b) fishes sampled from tropical headwater streams spanning a size gradient (Stream size - a principal component explaining 85% of variation in mean stream depth, velocity, canopy cover and turbidity). Grey circles represent an individual sample, loess smoothers (± 95%CI) are

presented in dark blue along with allochthonous and autochthonous food web endmembers and linear regression lines (± 95%CI) illustrating variation in food web endmembers associated with stream size

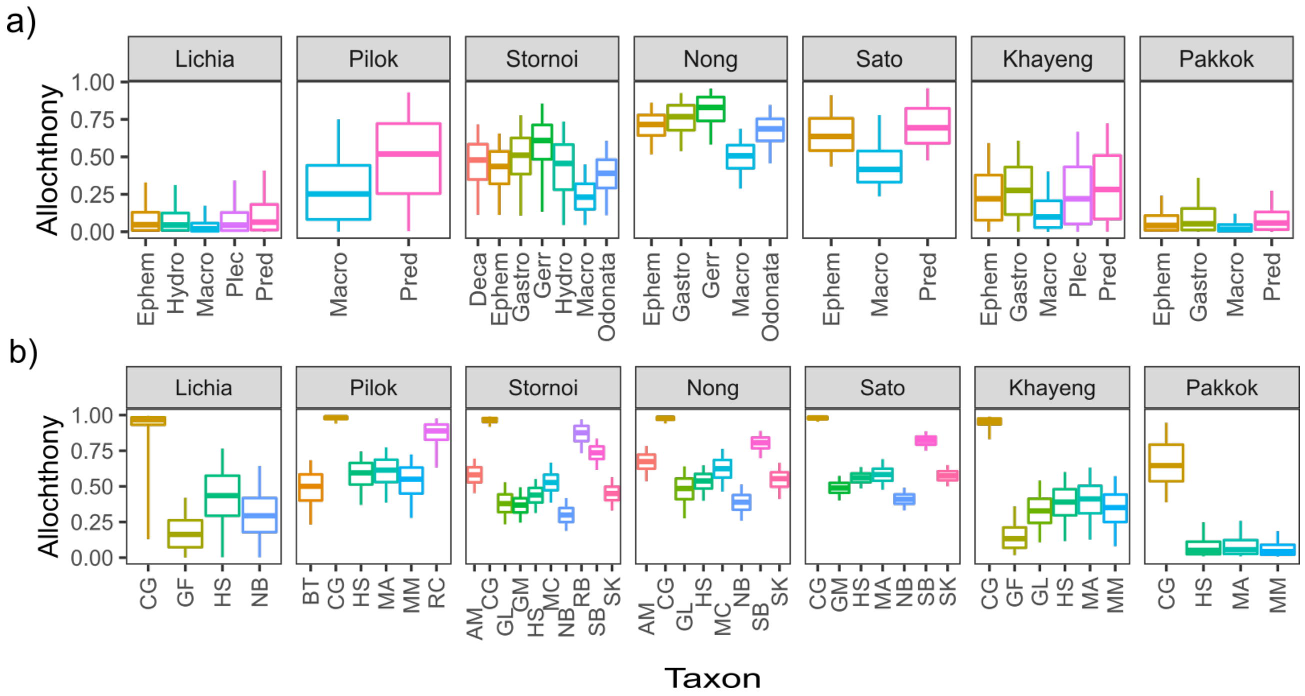


Fig. 4. Estimated resource use of a) invertebrates and b) fishes in head water streams in Western and Eastern Thailand. Panels are presented in order of increasing stream size. Data represent posterior estimates of resource use obtained from MixSIAR model, bold horizontal lines, boxes and whiskers denote, median, 50 and 95% credibility intervals respectively. AM - *Amblyceps macronatum,* BT - *Batasio tigrinus,* CG - *Channa gachua,* GF - *Garra fuliginosa,* GL - *Glyptothorax loasensis,* GM - *Glyptothorax major,* HS - *Homalopteroides smithi,* MC - *Macrognathus circumcinctus,* MA - *Mastacembelus armatus,* MM - *Mystacoleucus marginatus,* NB - *Neolissochilus blanci,* RC - *Rasbora caudimaculata,* RP - *Rasbora paviei,* SK - *Schistura kohchangensis,* SB - *Systomus binotatus.*

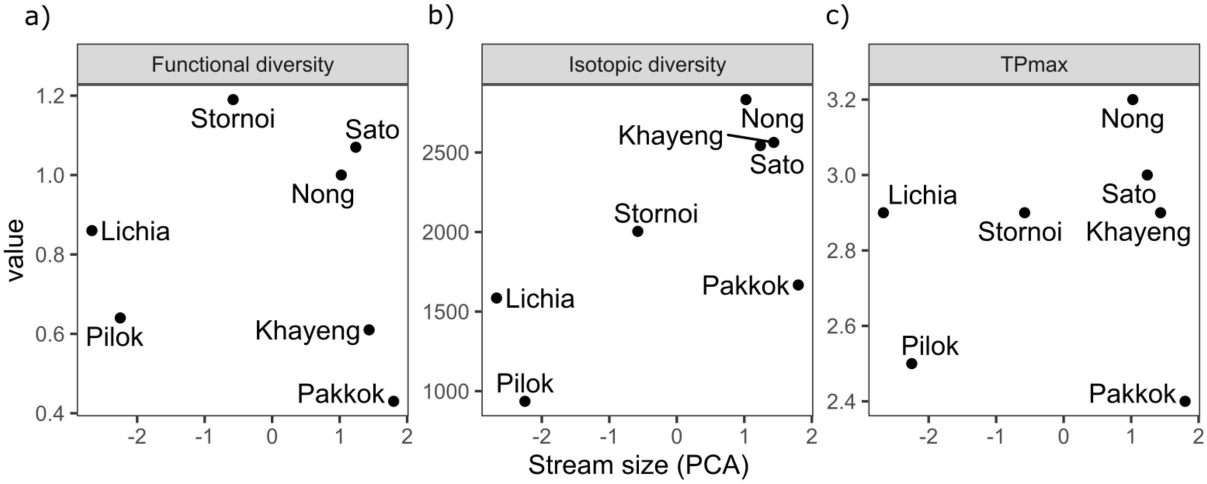
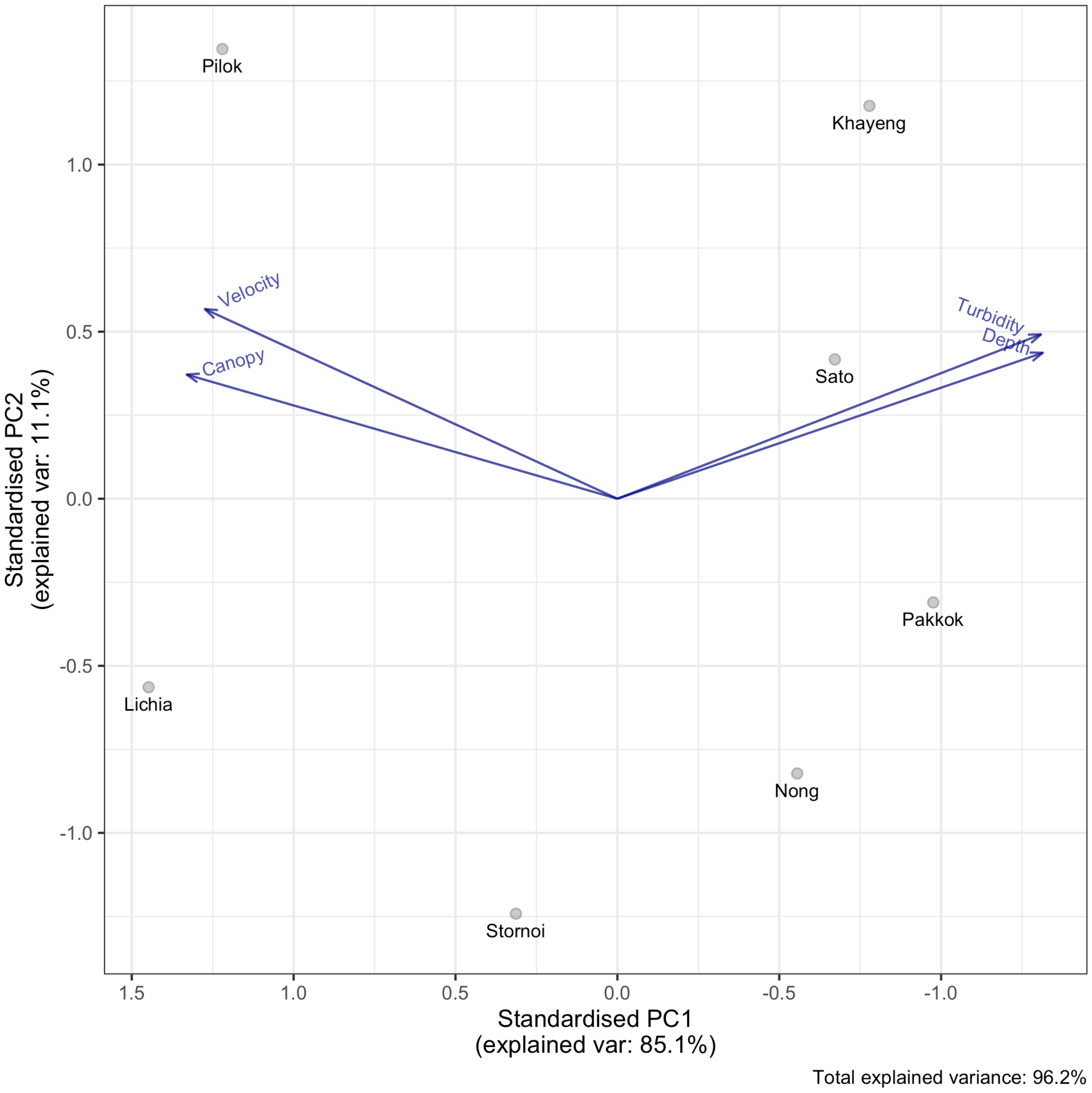
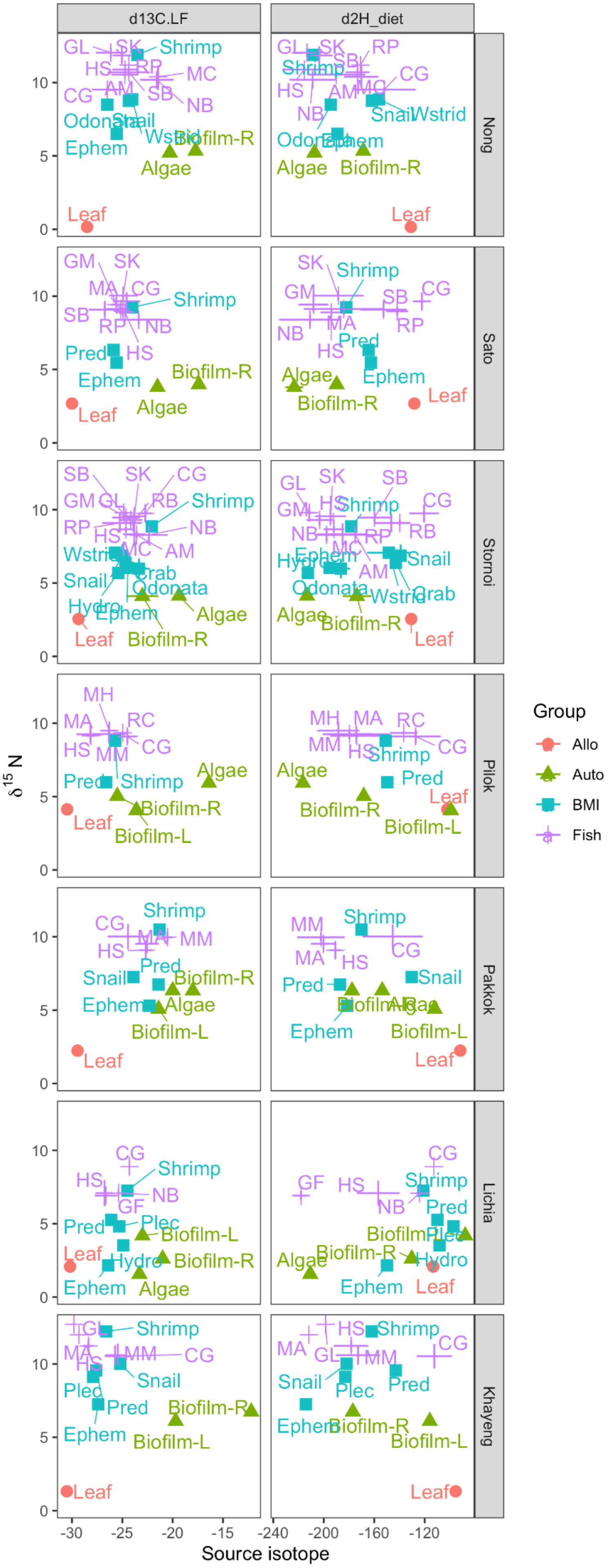


Fig. 5. Scatter plots outlining the relationship between stream size, a principal component explaining 85% of the variation in turbidity, mean depth, channel width, velocity and canopy cover among sites, and a), and Functional diversity (median value of a Bayesian estimate of a convex hull encompassing variation in allochthony derived from carbon, hydrogen and estimated trophic position of all fishes samples), isotopic diversity (median value of a Bayesian estimate of a convex hull encompassing variation in δ^{13}C, dietary δ^{2}H and δ^{15}N) and c) the maximum trophic position (TPmax) observed at each site.

Supporting Figure 1. Scatterplot detailing the collinearity among Turbidity, Depth, Velocity and Canopy cover in the seven sample sites. Axes represent first and second principal components of an PCA assessing these variables.



Supporting Figure 2. Scatter plot detailing the mean (±SD) of carbon, hydrogen and nitrogen stable isotope ratios of primary producers, benthic macro invertebrates (BMI) and fishes collected in seven streams in Western and Eastern Thailand. AM - *Amblyceps macronatum,* CG - *Channa gachua,* GF - *Garra fuliginosa,* GL - *Glyptothorax loasensis,* GM - *Glyptothorax major,* HS - *Homalopteroides smithi,* MC - *Macrognathus circumcinctus,* MA - *Mastacembelus armatus,* MM - *Mystacoleucus marginatus,* MH - *Mystus havmolleri,* NB - *Neolissochilus blanci,* RC - *Rasbora caudimaculata,* RP - *Rasbora paviei,* SK - *Schistura kohchangensis,* SB - *Systomus binotatus.*



Supporting Table 1. Mean (±SE) values of physiochemical measurement recorded at each stream.

Physicochemical factors	Stornoi	Sato	Nong	Kayeng	Pakkok	Pilok	Lichia
Alkalinity (mg/l CaCO3)	33±3.5	35±2.5	40±3.5	123±6.2	70±8.0	72±5.3	80±5.0
Ammonia(mg/l)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Canopy (%)	30±5	20±3	10±2	30±3	5±1.0	70±5	80±2
Conductivity (uS/cm)	18±5	24±4.5	22±3.2	343±6	67±3.5	77±8	104±5.0
Depth (cm)	15.1±3	29.3±5	26.6±3.4	35±7	30±10	15±3	12.5±5
Discharge (L/s)	57.4±3.2	103.7±10.2	71.8±10.2	119±10.2	244±20	119.5±10	66.1±12
Elevation (m)	119±5	98.5±4.5	90±5.2	297±5	168±1.0	206±1.0	169±1.5
Length (m)	50±7	45±2.0	35±0.5	40±3	35±2	45±3	50±5.0
Nitrate (mg No3N/L)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Oxygen (mg/l)	6.7±1	7.6±0.5	7.6±0.7	6.7±0.5	6.8±1.8	6.5±1.2	6.5±1.2
pH	7.7±0.3	7.7±0.2	7.7±1.2	7.8±0.3	7.8±0.3	7.9±0.4	7.9±0.5
Silica (mg SiO2/l)	26.9±2.5	25±2.8	29±3.2	19.8±3.4	22.2±5.4	25±3.0	20±5.0
Temperature (°C)	25±0.2	24±0.3	20.8±0.5	27±1.5	22.7±1.2	23.6±2.0	21.1±3.0
Turbidity (NTU)	3±0.1	4.1±0.3	3.5±0.2	4.2±0.5	4.1±0.2	3±1.5	2±1.2
Velocity (cm/s)	7.6±1.5	5.9±1.3	4.5±1.2	6±1.3	3.2±0.5	17.7±3.0	12.3±3.0
Width (m)	5±0.5	6±0.3	6±2	5.6±2	25±3	4.5±2.5	4.3±2.5

Supporting Table 2. Comparison of homogeneity of variance in stable isotope ratios among sites. Mean difference, upper and lower 95% confidence intervals and P value are presented. Site comparisons with significantly different homogeneity of variance are highlighted in bold.

Site combination	diff	lwr	upr	p adj
Nong-Lichia	**-0.05**	**-0.10**	**0.00**	**0.04**
Sato-Nong	0.03	0.00	0.06	0.13
Pakkok-Lichia	-0.05	-0.11	0.01	0.17
Stornoi-Lichia	-0.04	-0.09	0.01	0.22
Nong-Khayeng	-0.03	-0.08	0.02	0.58
Sato-Pakkok	0.03	-0.02	0.07	0.61
Pilok-Lichia	-0.03	-0.09	0.03	0.66
Stornoi-Sato	-0.02	-0.05	0.01	0.73
Sato-Lichia	-0.03	-0.08	0.03	0.77
Pakkok-Khayeng	-0.03	-0.09	0.03	0.80
Pilok-Nong	0.02	-0.02	0.06	0.81
Stornoi-Nong	0.01	-0.02	0.04	0.92
Lichia-Khayeng	0.02	-0.04	0.09	0.93
Stornoi-Khayeng	-0.02	-0.07	0.03	0.94
Pilok-Pakkok	0.02	-0.04	0.07	0.95
Stornoi-Pakkok	0.01	-0.03	0.06	0.99
Stornoi-Pilok	-0.01	-0.05	0.03	1.00
Sato-Pilok	0.01	-0.04	0.05	1.00
Pilok-Khayeng	-0.01	-0.07	0.05	1.00
Sato-Khayeng	0.00	-0.05	0.05	1.00
Pakkok-Nong	0.00	-0.04	0.05	1.00

Supporting Table 3. Pairwise PERMAONVA assessing differences in stable isotope ratios among sites. Mean sum of squares, F value, R^2 and P value are presented. Statistically different site combinations are highlighted in bold.

Site combination	SumsOfSqs	F	R^2	P value
Lichia <-> Nong	**0.30**	**39.43**	**0.30**	**0.00**
Lichia <-> Pakkok	**0.25**	**20.82**	**0.23**	**0.00**
Lichia <-> Stornoi	**0.15**	**16.23**	**0.13**	**0.00**
Nong <-> Pilok	**0.14**	**22.45**	**0.18**	**0.00**
Nong <-> Stornoi	**0.07**	**12.03**	**0.07**	**0.00**
Khayeng <-> Lichia	**0.18**	**11.86**	**0.16**	**0.00**
Lichia <-> Sato	**0.14**	**12.31**	**0.12**	**0.00**
Nong <-> Sato	**0.06**	**8.94**	**0.06**	**0.00**
Pakkok <-> Pilok	**0.11**	**11.31**	**0.12**	**0.00**
Khayeng <-> Stornoi	**0.07**	**6.82**	**0.05**	**0.01**
Pilok <-> Stornoi	**0.04**	**5.51**	**0.05**	**0.02**
Khayeng <-> Pilok	**0.07**	**5.44**	**0.07**	**0.02**
Pakkok <-> Stornoi	**0.04**	**4.49**	**0.03**	**0.03**
Khayeng <-> Nong	**0.03**	**4.06**	**0.04**	**0.04**
Khayeng <-> Pakkok	**0.05**	**3.79**	**0.04**	**0.04**
Khayeng <-> Sato	**0.04**	**3.85**	**0.03**	**0.04**
Pakkok <-> Sato	**0.04**	**4.03**	**0.03**	**0.05**
Lichia <-> Pilok	**0.04**	**3.75**	**0.06**	**0.05**
Pilok <-> Sato	**0.03**	**3.64**	**0.03**	**0.05**
Nong <-> Pakkok	0.01	1.22	0.01	0.26
Sato <-> Stornoi	0.01	0.63	0.00	0.40

Stream	Taxon	Guild	Species	n	$\delta^{13}C$	$\delta^{2}H$	$\delta^{15}N$	TP	Allo
Nong	Prod	Producer	Algae	1	-20.3 (-)	-207 (-)	5.2 (-)		
Sato	Prod	Producer	Algae	2	-21.5 (0.3)	-223 (0.1)	3.8 (0.1)		
Stornoi	Prod	Producer	Algae	1	-19.4 (-)	-213 (-)	4.1 (-)		
Lichia	Prod	Producer	Algae	1	-23.3 (-)	-211 (-)	1.6 (-)		
Pakkok	Prod	Producer	Algae	1	-20 (-)	-154 (-)	6.3 (-)		
Pilok	Prod	Producer	Algae	1	-16.4 (-)	-217 (-)	5.9 (-)		
Nong	Fish	Insectivore	AM	5	-24.7 (1.3)	-190 (0.1)	10.5 (0.1)	3 (0.1)	0.185 (0.097-0.294)
Stornoi	Fish	Insectivore	AM	4	-23.6 (0.7)	-175 (0.2)	8.3 (0.2)	2.4 (0.1)	0.373 (0.248-0.485)
Pakkok	Fish	Insectivore	AM	2	-22.1 (0.1)	-216 (0)	9.6 (0)	2.6 (0)	
Khayeng	Prod	Producer	Biofilm-L	1	-19.7 (-)	-116 (-)	6.1 (-)		
Lichia	Prod	Producer	Biofilm-L	1	-23 (-)	-88 (-)	4.2 (-)		
Pakkok	Prod	Producer	Biofilm-L	1	-21.4 (-)	-112 (-)	5.1 (-)		
Pilok	Prod	Producer	Biofilm-L	1	-23.6 (-)	-99 (-)	4.1 (-)		
Nong	Prod	Producer	Biofilm-R	1	-17.7 (-)	-169 (-)	5.3 (-)		
Sato	Prod	Producer	Biofilm-R	1	-17.4 (-)	-190 (-)	4 (-)		
Stornoi	Prod	Producer	Biofilm-R	2	-23 (1.5)	-174 (0.2)	4.1 (0.2)		
Khayeng	Prod	Producer	Biofilm-R	1	-12.2 (-)	-177 (-)	6.7 (-)		
Lichia	Prod	Producer	Biofilm-R	1	-21 (-)	-130 (-)	2.6 (-)		
Pakkok	Prod	Producer	Biofilm-R	1	-18 (-)	-178 (-)	6.3 (-)		
Pilok	Prod	Producer	Biofilm-R	1	-25.5 (-)	-168 (-)	5 (-)		
Nong	Fish	Insectivore/piscivore	CG	5	-26.5 (1.5)	-152 (0.1)	9.5 (0.1)	2.7 (0.1)	0.752 (0.65-0.852)
Sato	Fish	Insectivore/piscivore	CG	8	-24.6 (1.3)	-122 (0.6)	9.6 (0.6)	2.8 (0.2)	0.926 (0.883-0.957)
Stornoi	Fish	Insectivore/piscivore	CG	7	-22.7 (0.6)	-120 (0.6)	9.8 (0.6)	2.8 (0.2)	0.889 (0.838-0.933)
Khayeng	Fish	Insectivore/piscivore	CG	4	-25.5 (1)	-115 (0.7)	10.5 (0.7)	2.8 (0.2)	0.32 (0-0.908)
Lichia	Fish	Insectivore/piscivore	CG	1	-24.3 (-)	-113 (-)	8.9 (-)	2.4 (-)	0.184 (0-0.947)
Pakkok	Fish	Insectivore/piscivore	CG	10	-24.4 (1.8)	-151 (0.8)	10 (0.8)	2.7 (0.2)	0.408 (0.271-0.526)

Pilok	Fish	Insectivore/piscivore	CG	5	-24.5 (0.8)	-127 (0.4)	9.2 (0.4)	2.5 (0.1)	0.241 (0-0.684)
Stornoi	BMI		Decapoda	1	-24.7 (-)	-143 (-)	6.4 (-)	1.8 (-)	0.438 (0.208-0.616)
Nong	BMI		Ephemeroptera	1	-25.6 (-)	-189 (-)	6.5 (-)	1.8 (-)	0.114 (0.002-0.32)
Sato	BMI		Ephemeroptera	1	-25.6 (-)	-163 (-)	5.5 (-)	1.5 (-)	0.578 (0.424-0.703)
Stornoi	BMI		Ephemeroptera	1	-24.5 (-)	-195 (-)	6 (-)	1.7 (-)	0.403 (0.208-0.563)
Khayeng	BMI		Ephemeroptera	1	-27.4 (-)	-214 (-)	7.2 (-)	1.9 (-)	0.099 (0.001-0.384)
Lichia	BMI		Ephemeroptera	1	-26.4 (-)	-150 (-)	2.2 (-)	0.4 (-)	0.654 (0.456-0.781)
Pakkok	BMI		Ephemeroptera	1	-22.3 (-)	-181 (-)	5.3 (-)	1.3 (-)	0.143 (0.005-0.33)
Khayeng	Fish	Omnivore	GF	2	-27.3 (0)	-279 (0)	13.3 (0)	3.7 (0)	0.014 (0-0.12)
Lichia	Fish	Omnivore	GF	5	-26.6 (1)	-218 (0.3)	6.9 (0.3)	1.8 (0.1)	0.006 (0-0.15)
Pakkok	Fish	Omnivore	GF	1	-21 (-)	-237 (-)	9.2 (-)	2.4 (-)	
Nong	Fish	Insectivore/piscivore	GL	8	-26.1 (1.4)	-213 (0.3)	12 (0.3)	3.5 (0.1)	0.056 (0.011-0.137)
Stornoi	Fish	Insectivore/piscivore	GL	2	-24.9 (0.1)	-212 (0.4)	9.8 (0.4)	2.8 (0.1)	0.137 (0.033-0.271)
Khayeng	Fish	Insectivore/piscivore	GL	4	-29.8 (0.1)	-266 (0.1)	12.8 (0.1)	3.5 (0)	0.009 (0-0.137)
Sato	Fish	Insectivore/piscivore	GM	6	-25.6 (0.5)	-208 (0.5)	9.4 (0.5)	2.7 (0.1)	0.231 (0.116-0.347)
Stornoi	Fish	Insectivore/piscivore	GM	8	-24.2 (1.1)	-203 (0.4)	9.3 (0.4)	2.6 (0.1)	0.163 (0.077-0.264)
Nong	Fish	Insectivore	HS	10	-24.7 (1.2)	-215 (0.2)	10.9 (0.2)	3.1 (0.1)	0.11 (0.06-0.176)
Sato	Fish	Insectivore	HS	10	-24.7 (0.6)	-194 (0.3)	8.9 (0.3)	2.5 (0.1)	0.329 (0.232-0.428)
Stornoi	Fish	Insectivore	HS	8	-24.6 (0.5)	-192 (0.2)	8.7 (0.2)	2.5 (0.1)	0.242 (0.156-0.341)
Khayeng	Fish	Insectivore	HS	10	-28.4 (0.4)	-196 (0.4)	11.2 (0.4)	3.1 (0.1)	0.018 (0-0.309)
Lichia	Fish	Insectivore	HS	5	-26.8 (0.7)	-160 (0.8)	7 (0.8)	1.8 (0.2)	0.008 (0-0.449)
Pakkok	Fish	Insectivore	HS	10	-22.7 (0.6)	-217 (0.6)	9.1 (0.6)	2.4 (0.1)	0.026 (0.01-0.059)
Pilok	Fish	Insectivore	HS	5	-28.2 (0.4)	-187 (0.1)	9.1 (0.1)	2.4 (0)	0.012 (0-0.095)
Stornoi	BMI		Hydropsychidae	1	-25.4 (-)	-213 (-)	5.7 (-)	1.6 (-)	0.283 (0.101-0.504)
Lichia	BMI		Hydropsychidae	1	-24.9 (-)	-108 (-)	3.5 (-)	0.8 (-)	0.529 (0.314-0.703)
Nong	Prod	Producer	Leaf	1	-28.5 (-)	-131 (-)	0.2 (-)		
Sato	Prod	Producer	Leaf	1	-30 (-)	-128 (-)	2.7 (-)		

Stornoi	Prod	Producer	Leaf	1	-29.4 (-)	-131 (-)	2.5 (-)		
Khayeng	Prod	Producer	Leaf	1	-30.5 (-)	-95 (-)	1.3 (-)		
Lichia	Prod	Producer	Leaf	1	-30.2 (-)	-113 (-)	2.1 (-)		
Pakkok	Prod	Producer	Leaf	1	-29.4 (-)	-92 (-)	2.2 (-)		
Pilok	Prod	Producer	Leaf	1	-30.5 (-)	-102 (-)	4.1 (-)		
Sato	Fish	Insectivore	MA	5	-25.2 (1.3)	-184 (0.4)	9.1 (0.4)	2.6 (0.1)	0.335 (0.167-0.475)
Khayeng	Fish	Insectivore	MA	2	-29.3 (0)	-216 (0)	12 (0)	3.3 (0)	0.017 (0-0.307)
Pakkok	Fish	Insectivore	MA	9	-22.5 (1)	-212 (0.3)	9.5 (0.3)	2.5 (0.1)	0.026 (0.008-0.065)
Pilok	Fish	Insectivore	MA	2	-28.2 (1.3)	-174 (0.2)	9.2 (0.2)	2.5 (0.1)	0.012 (0-0.1)
Nong	Fish	Insectivore/piscivore	MC	2	-21.4 (0)	-170 (0.7)	10.4 (0.7)	3 (0.2)	0.127 (0.051-0.231)
Stornoi	Fish	Insectivore/piscivore	MC	6	-23.8 (1)	-185 (0.7)	8.3 (0.7)	2.4 (0.2)	0.274 (0.145-0.397)
Pilok	Fish	Insectivore	BT	5	-26.3 (0.7)	-188 (0.6)	9.5 (0.6)	2.5 (0.2)	0.012 (0-0.12)
Khayeng	Fish	Insectivore	MM	10	-25.7 (0.9)	-176 (0.6)	10.6 (0.6)	2.9 (0.2)	0.013 (0-0.338)
Pakkok	Fish	Insectivore	MM	10	-20.5 (0.5)	-209 (0.3)	10 (0.3)	2.7 (0.1)	0.022 (0.003-0.085)
Pilok	Fish	Insectivore	MM	7	-26.6 (1.3)	-185 (0.4)	9.1 (0.4)	2.4 (0.1)	0.009 (0-0.108)
Nong	Fish	Omnivore	NB	10	-21.6 (1.6)	-209 (0.5)	10.2 (0.5)	2.9 (0.2)	0.023 (0.005-0.068)
Sato	Fish	Omnivore	NB	13	-23.4 (2.3)	-211 (0.3)	8.4 (0.3)	2.4 (0.1)	0.089 (0.019-0.215)
Stornoi	Fish	Omnivore	NB	11	-22.4 (1.8)	-198 (0.5)	8.3 (0.5)	2.4 (0.1)	0.058 (0.013-0.156)
Lichia	Fish	Omnivore	NB	5	-25.3 (0.1)	-127 (0.2)	7.1 (0.2)	1.8 (0.1)	0.001 (0-0.209)
Nong	BMI		Odonata	1	-26.5 (-)	-194 (-)	8.5 (-)	2.4 (-)	0.058 (0.001-0.221)
Stornoi	BMI		Odonata	2	-23.3 (1)	-186 (0.7)	6 (0.7)	1.7 (0.1)	0.262 (0.065-0.44)
Khayeng	BMI		Plecoptera	1	-27.9 (-)	-183 (-)	9.1 (-)	2.4 (-)	0.066 (0.001-0.354)
Lichia	BMI		Plecoptera	1	-25.3 (-)	-97 (-)	4.8 (-)	1.2 (-)	0.553 (0.313-0.726)
Sato	BMI		Pred	1	-25.9 (-)	-164 (-)	6.3 (-)	1.8 (-)	0.583 (0.418-0.715)
Khayeng	BMI		Pred	1	-27.6 (-)	-143 (-)	9.6 (-)	2.6 (-)	0.102 (0.001-0.42)
Lichia	BMI		Pred	1	-26.1 (-)	-110 (-)	5.3 (-)	1.3 (-)	0.657 (0.476-0.791)
Pakkok	BMI		Pred	1	-21.4 (-)	-187 (-)	6.8 (-)	1.7 (-)	0.146 (0.006-0.333)

Pilok	BMI		Pred	1	-26.6 (-)	-150 (-)	6 (-)	1.5 (-)	0.42 (0.037-0.662)
Stornoi	Fish	Insectivore	RC	4	-23.9 (0.7)	-140 (0.2)	9.1 (0.2)	2.6 (0.1)	0.77 (0.654-0.884)
Pilok	Fish	Insectivore	RC	5	-25.2 (0.6)	-136 (0.3)	9.2 (0.3)	2.5 (0.1)	0.056 (0-0.51)
Nong	Fish	Insectivore	RP	1	-24.4 (-)	-171 (-)	11.2 (-)	3.2 (-)	0.474 (0.338-0.602)
Sato	Fish	Insectivore	RP	8	-25 (0.7)	-142 (0.3)	9 (0.3)	2.6 (0.1)	0.781 (0.704-0.844)
Stornoi	Fish	Insectivore	RP	3	-25.2 (1.7)	-147 (0.6)	9.1 (0.6)	2.6 (0.2)	0.698 (0.603-0.781)
Nong	Fish	Omnivore	SB	12	-24.4 (2)	-173 (0.3)	10.7 (0.3)	3.1 (0.1)	0.376 (0.273-0.471)
Sato	Fish	Omnivore	SB	4	-26.7 (1.5)	-153 (0.5)	9.1 (0.5)	2.6 (0.1)	0.705 (0.615-0.783)
Stornoi	Fish	Omnivore	SB	4	-24.6 (1.3)	-160 (0.3)	9.5 (0.3)	2.7 (0.1)	0.608 (0.506-0.702)
Nong	BMI		Macrobrachium	1	-23.5 (-)	-209 (-)	11.9 (-)	3.4 (-)	0.05 (0.001-0.168)
Sato	BMI		Macrobrachium	1	-24 (-)	-182 (-)	9.2 (-)	2.7 (-)	0.365 (0.206-0.501)
Stornoi	BMI		Macrobrachium	1	-22.1 (-)	-178 (-)	8.9 (-)	2.5 (-)	0.215 (0.089-0.363)
Khayeng	BMI		Macrobrachium	1	-26.6 (-)	-162 (-)	12.2 (-)	3.3 (-)	0.043 (0.001-0.224)
Lichia	BMI		Macrobrachium	1	-24.5 (-)	-121 (-)	7.3 (-)	1.9 (-)	0.444 (0.239-0.594)
Pakkok	BMI		Macrobrachium	1	-21.3 (-)	-170 (-)	10.5 (-)	2.8 (-)	0.064 (0.002-0.182)
Pilok	BMI		Macrobrachium	1	-25.7 (-)	-151 (-)	8.8 (-)	2.3 (-)	0.217 (0.016-0.477)
Nong	Fish	Insectivore	SK	10	-25 (0.8)	-204 (0.6)	11.8 (0.6)	3.4 (0.2)	0.106 (0.055-0.18)
Sato	Fish	Insectivore	SK	9	-24.9 (1.3)	-189 (0.3)	10 (0.3)	2.9 (0.1)	0.32 (0.22-0.43)
Stornoi	Fish	Insectivore	SK	12	-23.8 (1.1)	-195 (0.5)	9.6 (0.5)	2.7 (0.2)	0.234 (0.152-0.329)
Nong	BMI		Gastropoda	1	-24.4 (-)	-162 (-)	8.8 (-)	2.5 (-)	0.175 (0.005-0.414)
Stornoi	BMI		Gastropoda	2	-25 (0.7)	-139 (0.7)	6.9 (0.7)	2 (0.2)	0.518 (0.324-0.677)
Khayeng	BMI		Gastropoda	1	-25.2 (-)	-182 (-)	10 (-)	2.7 (-)	0.159 (0.003-0.452)
Pakkok	BMI		Gastropoda	1	-23.9 (-)	-130 (-)	7.3 (-)	1.9 (-)	0.222 (0.008-0.465)
Nong	BMI		Gerridae	1	-24 (-)	-156 (-)	8.8 (-)	2.5 (-)	0.222 (0.007-0.462)
Stornoi	BMI		Gerridae	2	-25.7 (0.9)	-148 (0.1)	7.1 (0.1)	2 (0)	0.586 (0.404-0.729)