<https://helda.helsinki.fi>

Subtropical streams harbour higher genus richness and lower abundance of insects compared to boreal streams, but scale matters

Heino, Jani

2018-09

Heino , J , Melo , A S , Jyrkänkallio-Mikkola , J , Petsch , D K , Saito , V S , Tolonen , K T , Bini , L M , Landeiro , V L , Freire Silva , T S , Pajunen , V , Soininen , J & Siqueira , T 2018 , ' Subtropical streams harbour higher genus richness and lower abundance of insects compared to boreal streams, but scale matters ' , Journal of Biogeography , vol. 45 , no. 9 , pp. 1983-1993 . <https://doi.org/10.1111/jbi.13400>

<http://hdl.handle.net/10138/327281>

<https://doi.org/10.1111/jbi.13400>

acceptedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

Running head: Stream insect diversity and abundance in different climatic regions

**Subtropical streams harbour higher genus richness and lower abundance of insects
compared to boreal streams, but scale matters**

Jani Heino¹, Adriano S. Melo², Jenny Jyrkänkallio-Mikkola³, Danielle Katharine Petsch⁴,
Victor Satoru Saito⁵, Kimmo T. Tolonen^{1,6}, Luis Mauricio Bini², Victor Lemes Landeiro⁷,
Thiago Sanna Freire Silva⁸, Virpi Pajunen³, Janne Soininen³ and Tadeu Siqueira⁹

¹Finnish Environment Institute, Biodiversity Centre, Oulu, Finland.

²Departamento de Ecologia, ICB, Universidade Federal de Goiás, Goiânia, GO, Brazil

³University of Helsinki, Department of Geosciences and Geography, University of Helsinki,
Helsinki, Finland.

⁴Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de Goiás,
Goiânia, GO, Brazil.

⁵Universidade Federal de São Carlos (UFSCar), Departamento de Ciências Ambientais, São
Carlos, Brazil.

⁶University of Jyväskylä, Department of Biological and Environmental Sciences, Jyväskylä,
Finland.

⁷Departamento de Botânica e Ecologia, IB, Universidade Federal de Mato Grosso, Cuiabá,

MT, Brazil.

⁸Universidade Estadual Paulista (Unesp), Instituto de Geociências e Ciências Exatas,
Ecosystem Dynamics Observatory, Rio Claro, Brazil.

⁹Universidade Estadual Paulista (Unesp), Instituto de Biociências, Departamento de Ecologia,
Rio Claro, Brazil.

Correspondence: jani.heino@environment.fi

JH: orcid.org/0000-0003-1235-6613

Acknowledgements

This work was funded by the FAPESP-AKA Joint Call on Biodiversity and Sustainable Use of Natural Resources: grant 2013/50424-1 from São Paulo Research Foundation (FAPESP) to TS, and grants no. 273557 and no. 273560 from the Academy of Finland (AKA) to JH and JS, respectively. TSFS, ASM and LMB acknowledge a research productivity grant from the National Council for Scientific and Technological Development (CNPQ, procs 310144/2015-9, 309412/2014-5 and 304314/2014-5, respectively). We thank Mikko Tolkkinen and Sandra Meier for help with the field work. Peter Linder, Walter Jetz, Richard Pearson and an anonymous reviewer provided excellent comments that improved this paper.

Conflict of Interest Statement. The authors declare no conflict of interest

Abstract

Aim: Biological diversity typically varies between climatically different regions, and regions closer to the equator often support higher numbers of taxa than those closer to the poles. However, these trends have been assessed for a few organism groups, and the existing studies have rarely been based on extensive identical surveys in different climatic regions.

Location: We conducted standardised surveys of wadeable streams in a boreal (western Finland) and a subtropical (south-eastern Brazil) region, sampling insects identically from 100 streams in each region and measuring the same environmental variables in both regions.

Taxon: Aquatic insects

Methods: Comparisons were made at the scales of local stream sites, drainage basins and entire regions. We standardised the spatial extent of the study areas by resampling regional richness based on subsets of sites with similar extents. We examined differences in genus richness and assemblage abundance patterns between the regions using graphical and statistical modelling approaches.

Results: We found that while genus accumulation and rank-abundance curves were relatively similar at the regional scale between Finland and Brazil, regional genus richness was higher in the latter but regional abundance much higher in the former region. These regional patterns for richness and abundance were reproduced by basin and local genus richness that were higher in Brazil than in Finland, and assemblage abundance that was much higher in Finland than in Brazil. The magnitude of the difference in genus richness between Brazil and Finland

63 tended to increase from local through basin to regional scales.

64 **Main conclusions:** Our findings suggest that factors related to evolutionary diversification
65 might explain differences in genus richness between these two climatically different regions,
66 whereas higher nutrient concentrations of stream waters might explain the higher abundance
67 of insects in Finland than in Brazil.

68

69 **Keywords**

70 alpha diversity, latitudinal diversity gradient, nutrients, rank abundance, regional diversity,
71 stream insects, low-high latitude comparison

INTRODUCTION

Biological diversity typically varies among climatically different regions, with regions closer to the equator often harbouring higher numbers of species than those at higher latitudes (Rosenzweig, 1995; Gaston, 2000). This latitudinal gradient in species richness is evident for terrestrial organisms such as vascular plants, butterflies, birds and mammals (Hillebrand, 2004a). It has also been found for marine (Hillebrand, 2004b) and freshwater organisms (Pearson & Boyero, 2009). However, there are also notable exceptions to the latitudinal richness gradient among microbes and invertebrates, to name two highly diverse organism groups (Kouki *et al.*, 1994; Willig *et al.*, 2003; Boulton *et al.*, 2008; Soininen, 2012). Studies on many infrequently studied groups of organisms have rarely used extensive standardised surveys (Vinson & Hawkins, 2003; Pearson & Boyero, 2009). These methodological issues may complicate the examination of the drivers of regional and local richness, although there are successful classical (Stout & Vandermeer, 1975; Lake *et al.*, 1994) and more recent examples (Dias *et al.*, 2014; McCreadie *et al.*, 2017). In general, regional differences in richness may stem from differences in spatial extent, evolutionary diversification, current and past climates, productivity or history (Willig *et al.*, 2003; Mittelbach *et al.*, 2007), whereas local richness gradients may result from differences in biological interactions and abiotic ecosystem features between geographical regions (Vinson & Hawkins, 2003; Heino, 2011).

Stream-dwelling insects are a suitable model group for examining biodiversity patterns between climatically different regions. They comprise many taxonomic orders, of

which mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), beetles (Coleoptera) and true flies (Diptera) dominate stream insect assemblages in terms of abundance and richness over the world (Vinson & Hawkins, 1998; Lancaster & Downes, 2013). Stream insect richness exhibits various patterns along latitudinal gradients, both at regional (Boyero, 2002; Pearson & Boyero, 2009) and local scales (Stout & Vandermeer, 1975; Jacobsen *et al.*, 1997; Vinson & Hawkins, 2003; Boyero *et al.*, 2011b). While some insect groups (e.g. dragonflies and beetles) are more diverse in tropical than in northern regions (Brown, 1981; Pearson & Boyero, 2009), other groups (e.g. mayflies, stoneflies and caddisflies) have also diversified extensively in mid-latitude regions (Illies, 1965; Ward, 1992). The reasons for such anomalous latitudinal patterns may relate to the possibility that many taxa of mayflies, stoneflies and caddisflies originated and thus diversified in cold-water streams (Ward, 1992), following the niche conservatism hypothesis (Wiens & Donoghue, 2004). Alternatively, their high diversity in temperate regions may stem from high environmental heterogeneity along seasonal and altitudinal gradients (Vinson & Hawkins, 2003). The latitudinal gradient in the local diversity of stream insects (i.e. species richness within one stream) may be even more complex than that for regional diversity (i.e. total number of species from several streams in a region), as local abiotic conditions may vary strongly even between neighbouring streams (Hynes, 1970; Allan & Castillo, 2007; Boulton *et al.*, 2008). Such high variation in local conditions dictates that streams close to each other may harbour insect assemblages differing highly in richness, abundance and composition (Grönroos & Heino, 2012; Landeiro *et al.*, 2012). Therefore, although regional-scale stream insect diversity may differ (Brown, 1981; Pearson & Boyero, 2009), among-region differences in local diversity may be less clear (Heino *et al.*, 2003; Vinson & Hawkins, 2003;

McCreadie *et al.*, 2017).

Biological diversity at regional and local scales can be studied by using both graphical pattern-based (Magurran, 2004) and modelling approaches (Legendre & Legendre, 2012). Pattern-based approaches include taxon accumulation curves (Ugland *et al.*, 2003) and rank-abundance distributions (Whittaker, 1965), both applicable at regional and local scales. For example, there were only slight differences in the taxon accumulation curves among three high-latitude regions (Heino *et al.*, 2015b). Taxon accumulation curves have also been used at local scales, where the accumulation curves of temperate stream insects reached an asymptote much earlier than those of tropical streams (Stout & Vandermeer, 1975). Rank-abundance distributions have rarely been applied in stream insect studies at both regional and local scales, but they show a great potential for between-systems comparisons in other contexts (McGill *et al.*, 2007). For example, rank-abundance distributions may reveal whether tropical and boreal regions harbour regional assemblages with different degrees of rarity and commonness. Such differences in rarity and commonness may be due to different degrees of ecological specialization, with tropical taxa being more specialized than those at high latitudes (Mittelbach *et al.*, 2007; Coley & Kursar, 2014).

Modelling approaches have been used extensively to examine how different predictor variables affect variation in biological diversity among regions and among sites (Legendre & Legendre, 2012). For example, based on a comparative analysis of 61 datasets from around the world, Heino *et al.* (2015a) found that stream insect assemblages were more strongly related to the environment than to space, and that the explanatory power of these predictors was low with no obvious latitudinal trend. In a global analysis of local stream insect genus

richness, Vinson and Hawkins (2003) found that linear models based on large-scale climatic and energy variables could explain some variation in local richness. They also found no clear latitudinal gradients in the local genus richness of mayflies, stoneflies and caddisflies, but instead that richness showed multiple peaks and often peaked at mid-latitudes. These two studies, although based on large compilations of datasets, are likely to be limited by different sampling methods as well as distinct environmental and spatial extents in different regions. This might hinder firm conclusions on whether stream insect assemblages in tropical, temperate and boreal regions show differences in richness and abundance patterns. For instance, differences in spatial extent may complicate among-region comparisons because larger study areas exhibit larger environmental heterogeneity, thereby affecting diversity estimates (Chase & Knight, 2013). This issue has been considered in previous local-scale studies by using a long-term sampling approach (Vinson & Hawkins, 2003) and in some regional-scale studies by factoring out the effects of spatial extent (Pearson & Boyero, 2009).

To overcome some of the problems that have affected comparative studies based on datasets produced by different methods (e.g. Nakagawa & Parker, 2015) and complement previous findings on global gradients (e.g. Pearson & Boyero, 2009), we conducted identical surveys of wadeable streams in a boreal (western Finland) and a subtropical (south-eastern Brazil) region. We believe that broad-scale studies (e.g. based on gridded data) and comparative studies (i.e. based on standardised sampling protocols) are complementary and offer the possibility to test for patterns using different lines of evidence. Thus, by focusing on two regions, as opposed to previous studies that addressed global gradients, we could take detailed and standardised insect samples from 100 streams in each region and measured the same environmental variables in both regions. We also standardised the extent of the study

area by resampling sites from similar-sized areas in both regions. Our specific aims were threefold. We first (i) examined whether genus accumulation curves differed between the boreal and subtropical regions. We expected that there would be faster accumulation of genera in Brazil than in Finland because alpha and beta diversities are typically higher in the tropics (Soininen *et al.*, 2007). We also (ii) studied whether rank-abundance distributions differed between Brazil and Finland, with the expectation that there would be many more relatively rare genera in the subtropical than in the boreal region, which is more dominated by a few abundant genera (Brown, 2014). Finally, in addition to these aims, we (iii) modelled variation in local genus richness and local assemblage abundance of stream insects in relation to region identity, while controlling for the effects of key local environmental variables. If evolutionary diversification (Willig *et al.*, 2003; Brown, 2014) is contributing to the latitudinal richness gradient, insect genus richness and assemblage abundance should be higher in subtropical than in boreal streams after controlling for the influence of local environmental variables and spatial extent.

MATERIALS AND METHODS

Study areas

Western Finland. Study sites were located between latitudes 60°41'N and 65°12'N, with spatial extents of ca. 500 km and 300 km in north-south and in east-west directions,

respectively (Supporting Information, Fig. S1). The catchments were covered by different land uses, from ones dominated by agriculture to those covered almost entirely by boreal forests (dominated by *Pinus sylvestris* and *Picea abies*). The 100 perennial streams were selected from 20 major river basins, i.e., five separate streams draining into each of 20 boreal rivers were surveyed. Western Finland has the four seasons characteristic of the boreal region: (1) winters lasting from November to March, (2) spring periods in April and May, (3) summers between June and August, and (4) autumn periods generally in September and October. Given the large latitudinal extent, temperature and rainfall vary substantially in the study area. The stream sites were sampled in September 2014. These streams did not experience heavy floods or droughts just before sampling and ranged from pristine forest streams to agricultural streams with little pollution.

South-eastern Brazil. Study sites were located in the State of São Paulo, between latitudes 24°38'S and 23°82'S, with spatial extents of 70 km in north-south and 120 km in east-west directions, respectively (Supporting Information, Fig. S1). The 100 perennial streams, with five streams distributed within 20 different catchments as described above, are located between three major Atlantic Forest protected areas (Carlos Botelho, Intervales and Alto Ribeira State Parks). Land cover varied among catchments, with some dominated by agriculture (mainly pastures, and *Eucalyptus* and *Pinus* plantations) to some entirely covered by Atlantic Forest. This region is characterised by two seasons: a drier season from April to August (average rainfall from 45 to 80 mm per month; average temperature from 16 to 20°C) and a wetter season from September to March (average rainfall from 105 mm to 180 mm per month; average temperature from 20 to 23°C). The sites were sampled from September to

November in 2015. Streams did not suffer from recent floods or droughts and ranged from pristine forest streams to moderately polluted streams in agricultural areas.

Field surveys

We measured 15 physical and chemical variables that have been found to be important for stream insect distributions in boreal (Malmqvist & Mäki, 1994; Grönroos & Heino, 2012) and tropical (Siqueira *et al.*, 2012; Al-Shami *et al.*, 2013) regions. For physical variables, we measured current velocity (m/s) and depth (cm) at 30 (in Finland) and nine (in Brazil) random spots in a riffle site. Particle size classes (%) were visually estimated in 0.25 m² squares at 10 (in Finland) and three (in Brazil) random locations in a riffle site. We used a modified Wentworth's scale of particle size classes: sand (0.25-2 mm), gravel (2-16 mm), pebble (16-64 mm), cobble (64-256 mm) and boulder (256-1024 mm). Based on the mean estimates for each site, we calculated the Shannon diversity of substratum particle sizes for each stream site. We also measured mean stream width of the sampling site based on 10 (in Finland) and three (in Brazil) cross-channel measurements and visually estimated shading (i.e. canopy cover) by riparian vegetation at each sampling site. We used satellite images to estimate native forest cover within a 400-m buffer along tracts of the sampled streams. For chemical variables, we measured pH and conductivity at each site in the field using YSI device model 556 MPS (YSI Inc., Ohio, USA) in Finland and Horiba device U-50 series in Brazil. Water samples were analysed for total nitrogen (TN) and total phosphorus (TP) following national standards for Finland (Finnish Board of Waters and the Environment

1981) and Brazil (Golterman *et al.*, 1978; Mackereth *et al.*, 1978).

We took a 2-minute kick-net sample (net mesh size: 0.5 mm) at each of the stream sites surveyed in Finland and Brazil. The sample for each site consisted of four 30-seconds sample units that were obtained in the main microhabitats (i.e. considering variations in current velocity, depth, particle size and macrophyte cover) at a riffle site of c. 25 to 50 m². The four sample units were pooled, preserved in alcohol in the field and taken to the laboratory for further processing and identification. All insects were separated from debris, and taxa of our interest (Ephemeroptera, Odonata, Plecoptera, Megaloptera, Trichoptera and Coleoptera) were identified to genus level.

Species-level identification is mostly not feasible for aquatic insects in Brazil as many species remain undescribed, particularly their aquatic immature stages, and new species are still being discovered in the region (Cruz *et al.*, 2013). A previous evaluation on the use of coarse family-level identification in the same Brazilian region as studied here indicated that it produces reliable assessment of stream fauna (Melo, 2005). Species-level identification is more feasible in Finland, but regional, basin and local aquatic insect faunas of wadeable streams are still inadequately known. However, genus richness portrays adequately patterns in species richness in Finnish streams (Heino & Soininen, 2007). Accordingly, we opted to use genus identification to enable direct comparisons between Finland and Brazil.

Standardization of sampling effort and spatial extent

We developed different procedures to control for variation in sampling effort and differences in spatial extent, before comparing the two regions. We redirect the reader to the supplementary material (see Supporting Information and Fig. S2) for a detailed account of these procedures. These procedures were needed to ensure that between-region differences in richness were not caused by anomalous sites with low densities and by differences in the number of streams within drainage basins and spatial extents.

Graphical data analysis at the regional scale

To describe regional-scale patterns in the stream insect faunas of Finland and Brazil, we used two graphical approaches using mean values from reduced/standardised datasets. First, we drew genus accumulation curves for each region to see if genus richness accumulated similarly with increasing number of stream sites (Coleman *et al.*, 1982). This approach followed the method “exact” devised by Ugland *et al.* (2003). Second, we used genus rank-abundance curves at regional level to show which genera were most abundant in Finland and Brazil. In these plots, abundance (as proportions of total regional abundance) is on the y-axis, and genera are ranked from the most abundant to the least abundant on the x-axis (Whittaker, 1965). Genus accumulation curves were drawn using the function ‘specaccum’ in the R package ‘vegan’ (Oksanen *et al.*, 2013).

Modelling genus richness and assemblage abundance across the regions and along

environmental gradients

The standardisation of spatial extent (see Supporting Information) and sample sizes (rarefaction) allowed an improved comparison of genus richness between the regions. However, the streams also differed on several environmental features between the regions. We thus estimated differences in abundance, observed genus richness and rarefied genus richness between the two regions after taking into account the environmental variables described earlier and known to affect stream insect assemblages.

Physical variables were similar between regions (Table 1). In contrast, chemical variables differed between the regions, with conductivity, total phosphorous and total nitrogen being much higher in Finland than in Brazil (Table 1). Accordingly, we standardised chemical variables by their maximum within each region before analyses using the function ‘decostand’ in the R package ‘vegan’ (Oksanen *et al.*, 2013). The standardisation reduced the correlation with the ‘region identity’ variable and allowed the evaluation of effects of those variables within the range of variation within each region.

We removed the variable boulder, as the five substrate classes sum to 1, and they would thus be correlated to each other. We then removed collinear environmental variables (i.e. cobble and TN) by sequentially removing those with variance inflation factor (VIF) higher than 2 (Zuur *et al.*, 2010). We fitted linear models with 14 explanatory variables: the 13 environmental variables described earlier and ‘region identity’, our categorical variable of interest. We performed model selection using AIC criterion, although we were most interested in the effect of ‘region identity’ after partialling out the effect of environmental

variables. The model selection employed aimed to provide a simpler model. We ran separate multiple regressions on rarefied richness, observed richness and assemblage abundance using 14 predictor variables. Finally, we ran a commonality analysis in the context of multiple regression (Seibold & McPhee, 1979; Ray-Mukherjee *et al.*, 2014) to infer the unique, common and total contributions of each predictor variable to response variables. VIF analyses were done using the function ‘vif’ in the ‘car’ R package (Fox & Weisberg, 2011). Modelling analyses were run using the functions ‘lm’ and ‘step’ in the R package ‘stats’ (R Core Team, 2017) and ‘commonalityCoefficients’ in the R package ‘yhat’ (Nimon *et al.*, 2015).

RESULTS

Patterns of regional-scale richness and abundance

Stream insect abundance and richness showed interesting differences between Finland and Brazil. First, only four genera were shared between Finland and Brazil, these being the mayfly genus *Caenis* and the caddisfly genera *Hydroptila*, *Oecetis* and *Oxyethira*. Second, total regional abundance was much higher in Finland (total number of insect individuals in 100 streams: 86,048) than in Brazil (16,113), yet regional genus richness ($n = 100$ streams) was slightly higher in Brazil (83) than in Finland (77).

The 97 paired standardised sets of streams included (see Supporting Information and

Fig. S2), on average, 24.5 (min = 17, max = 29) streams in each region, and the average spatial distance among them was 56.0 km (min = 44.1, max = 65.7) in Brazil and 57.6 km (min = 45.3, max = 68.8) in Finland. These results indicate the effectiveness of our standardization protocol. For all standardised pairs, total abundance in the set of streams in Finland was higher than in Brazil (average paired difference = 16,752 individuals). In contrast, observed genus richness was always higher in Brazil and included 40% more genera than in their paired counterparts in Finland (average paired difference = 18.66 genera; Fig. 1A). This difference increased to 76% after taking differences in the number of sampled individuals into account (within-pair rarefaction; average paired difference = 28.54 genera; Fig. 1B).

Sample-based accumulation curves were similar between Finland and Brazil, although genus richness was much higher in Brazil (Fig. S3A, B). In contrast, individual-based accumulation curves indicated that many more genera would be detected in Brazil with additional sampling (Fig. S3C, D).

Rank-abundance curves for Finland and Brazil differed mostly in two aspects (Fig. S4). The two most abundant genera in Finland tended to include much more of the total number of individuals (on average, 32.03 and 19.78%) than the two most abundant in Brazil (14.45 and 12.16%). In contrast, the proportions of rare genera were similar between Brazil (74.5 and 81.6% of the genera with less than 1 and 2% of the total abundance) and Finland (74.5 and 81.8%).

Patterns of basin-scale richness and abundance

335

336 Samples from the 17 basins in Brazil, each including four or five streams, included a total of
337 15,471 individuals. The 19 basins in Finland included 85,050 individuals. Observed genus
338 richness was 31% higher in Brazil than in Finland (37.23 and 28.42, respectively; Fig. 2A).
339 The basin with the lowest abundance was found in Brazil, with 295 individuals. Rarefied
340 genus richness for 295 individuals was 61.3% higher in Brazil than in Finland (30.17 and
341 18.51, respectively; Fig. 2B).

342

343 **Patterns of local-scale richness and abundance**

344

345 The reduced set of streams in Brazil, after removing 12 streams with low insect abundance,
346 included on average 181.5 individuals and 17.84 genera per stream riffle site. The reduced set
347 of streams in Finland included many more individuals (mean = 886.57) and fewer genera
348 (14.01) per stream. Observed mean genus richness per stream was 27% higher in Brazil than
349 in Finland (Fig. 3A). Rarefied genus richness per stream was 64.3% higher in Brazil than in
350 Finland (11.52 and 7.41, respectively; Fig. 3B).

351

352 **Differences in genus richness and assemblage abundance between the regions**

353

354 The reduced model including 'region' and five local environmental variables explained

49.6% of the variation in rarefied genus richness (Table 2). Region had the strongest effect on rarefied genus richness, with Brazil possessing more genera per stream after controlling for the effects of local environmental variables. Rarefied genus richness was also higher in wider streams and those with a high proportion of native forest vegetation cover. Proportion of sand in the stream bottom was negatively related to rarefied richness. A similar reduced model for observed richness explained 37.6% of variation, and the most important predictor variables were region and five local variables. Finally, assemblage abundance was best explained by region and seven local variables, and the model accounted for 61% of variation in assemblage abundance (Table 2). Full models can be found in Supporting Information (Table S1).

Commonality analysis strengthened the findings of basic linear models by showing that ‘region’ typically had the highest unique (14.1% to 18.8%) and total (8.5% to 44.2%) effects on rarefied richness, observed richness and assemblage abundance (Table 2). The only exception was for observed richness as stream width had the highest total effect (11.4%). For rarefied richness, shading and forest cover were also relatively important. For observed richness, stream width and forest cover were important in addition to the region effect. Finally, for assemblage abundance, the second and third most important predictors were shading and velocity, respectively.

DISCUSSION

We found that, for the entire datasets, the regional difference in genus richness was

surprisingly small between Brazil (83 genera) and Finland (77 genera) considering that regions closer to the equator usually harbour more diversity than those closer to the poles (Rosenzweig, 1995; Willig *et al.*, 2003). While differences between tropical and boreal regions are expected for various groups of organisms, many freshwater organisms do not obey such general ‘laws’ (Vinson & Hawkins, 2003; Pearson & Boyero, 2009; Heino, 2011; Soininen, 2012). Rather, aquatic insects, such as mayflies, stoneflies and caddisflies, do not often follow typical latitudinal trends in regional diversity, whereas some other aquatic insects, such as dragonflies and beetles, do so (Brown, 1981; Pearson & Boyero, 2009). In our study, mayflies, dragonflies and beetles were regionally more diverse in Brazil than in Finland, whereas the opposite was true for stoneflies and caddisflies (Supporting Information, Fig. S5). This finding suggests that some insect orders may be more diverse closer to the poles than to the equator. We emphasise, however, that the difference in genus richness between Brazil and Finland was much larger after accounting for spatial extent. Indeed, in the reduced standardised datasets, regional genus richness was clearly higher in Brazil than in Finland. This finding underscores the importance of standardising spatial extent when comparing regional richness estimates. Such standardisation is important because larger spatial extent typically incorporates more environmental heterogeneity, resulting in higher richness (Chase & Knight, 2013) and leading to biased between-region comparisons in the case of different spatial extents.

In general, richness tends to be correlated with abundance especially if sampling effort varies between regions (Gotelli & Collwell, 2001; Evans *et al.*, 2005). However, this was not the case in our study with identical field sampling designs. Hence, it seems that the very high regional abundance does not lead to high genus richness in Finland, and tropical

faunas remain more diverse even when having much lower regional abundances than boreal faunas. Previous studies have detected increasing abundance of stream detritivorous invertebrates with increasing altitude (Yule *et al.*, 2009) and latitude (Boyero *et al.*, 2011), suggesting that stream insect abundance may be lower in higher temperatures. Also, other differences between regions, such as local stream productivity and other environmental features, affect stream insect abundance (Jacobsen *et al.*, 1997; Vinson & Hawkins, 2003). In our study, nutrient concentrations were much higher in Finnish than Brazilian streams (Table 1), which might have contributed to higher insect abundance in Finland. This difference might stem from the generally nutrient-poor soils of tropical landscapes (Reich & Oleksyn, 2004), as catchment features typically determine stream water chemistry (Soininen *et al.*, 2015). However, in the linear models, the effect of nutrients was masked by collinearity with the ‘region’ variable, the latter of which was the variable of our main interest and forced into all models.

Genus accumulation curves differed slightly between the two regions. While the curves in both regions nearly reached an asymptote, the increase of genera was faster in Brazil than in Finland (Fig. S3). Such steeper accumulation curves in the subtropical than in the boreal region might be related to the slightly higher local genus richness in Brazil than in Finland. Working with data from three high-latitude regions (66°N to 70°N), Heino *et al.* (2015b) found only minor differences in species accumulation curves among the regions, suggesting that environmental differences or species pool characteristics did not contribute to differences in species accumulation. The situation should be different between geographically distant regions, harbouring almost completely different stream biotas, such as those in Brazil and Finland.

Despite differences in regional genus richness and total abundance between Brazil and Finland, the rank-abundance curves were rather similar between the two regions (Fig. S4). The curves were characterised by few common genera and several uncommon to very uncommon genera, a pattern that has previously been found for tropical streams (Siqueira *et al.*, 2012). However, the two most common genera in Finland were much more abundant than their counterparts in Brazil. In both study regions, the most common genus belonged to the beetle family Elmidae (*Elmis* in Finland and *Heterelmis* in Brazil). These riffle beetles are typical inhabitants of streams over most of the world, being often common in fast-flowing sites (Elliott, 2008). The second and third most common genera in Finland belonged to mayflies (*Baetis*) and stoneflies (*Nemoura*), whereas those in Brazil belonged to caddisflies (*Smicridea*) and mayflies (*Farrodes*). These insect orders typically dominate stream insect faunas in many parts of the world (Lancaster & Downes, 2013). In general, these results suggest an interesting avenue for further investigations: the existence of a “latitudinal gradient” in niche packing (see also Willig *et al.*, 2003).

We also found differences in local genus richness and local assemblage abundance between Finland and Brazil. However, the richness difference between Finland and Brazil was not as strong at the local scale as at the regional scale (compare Fig. 1 and 2 with Fig. 3), which was evidenced by both the entire dataset and the reduced standardised datasets. While local genus richness was higher in subtropical than in boreal streams, local assemblage abundance showed the opposite pattern. However, both richness and abundance also showed considerable variation within each region (Table 1, Fig. 3). These findings suggest that local richness and local abundance in streams are determined by both regional and local factors, and it seems that genus richness benefits from tropical conditions, whereas assemblage

abundance benefits from boreal ecological features. Higher genus richness in the tropics might result from ice age history and temperature-related evolutionary rates (Mittelbach *et al.*, 2007), which should be less important and more important, respectively, in the tropical than in boreal regions (Brown & Lomolino, 1998). For example, previous evidence indicates that Neotropical areas can act both as “museums” (i.e. with old persistent lineages) and as “cradles” (i.e. with new species continuously originating) of insect diversity (Moreau & Bell, 2013). In addition, regional factors set the upper limits to local genus richness and assemblage abundance, which are further affected by more localised variation in stream environmental variables (Poff, 1997; Vinson & Hawkins, 2003). These environmental variables may vary within regions (e.g. pH) or differ between regions (e.g. TN), as in our case.

An interesting finding was that the between-region richness difference decreased from regional through basin to local scales (40, 31 and 27% for observed genus richness and 76, 63 and 55% for rarefied genus richness; Figs 1, 2 and 3). This finding suggests that evolutionary history and climatic influences are strong in setting up differences in regional genus richness (standardized spatial extents), while local genus richness differences are slightly diminished due to the possible operation of catchment variables (acting on catchment-scale) and local environmental variables (acting on stream-scale) with decreasing spatial grain of a study. While previous studies that were based on intensive site-based inventories (Vinson & Hawkins, 2003) or more extensive regional inventories (Pearson & Boyero, 2009) did not adopt standardized methods, they were able to provide broad generalizations on global richness gradients. However, our study adds to previous findings by providing more precise evidence from explicit consideration of variation of richness and abundance across spatial

scales. Hence, our findings emphasize the need to consider both spatial extent and grain of the study when making comparisons of between-region differences in biodiversity patterns (Vinson & Hawkins, 1998; Heino, 2011).

Conclusions

We found that stream insect genus richness and assemblage abundance differed between our subtropical and boreal regions. Our main finding was that genus richness was higher in Brazil than in Finland (and more so at regional and basin than local scales), yet assemblage abundance was much higher at all spatial scales in Finland than in Brazil. These patterns hold in both entire datasets and in reduced datasets based on resampling of the stream sites from similar-sized areas. Differences in nutrient concentrations and temperature of stream waters might explain the higher abundance of insects in Finland than in Brazil, whereas possibly factors related to evolutionary diversification might explain differences in genus richness between these two regions. Our further studies should shed more light on these issues by focusing on the functional structure and phylogenetic diversity of stream insect faunas in these geographically distinct regions.

REFERENCES

Allan, J.D. & Castillo, M.M. (2007) *Stream Ecology: Structure and Function of Running*

489 Waters. Springer, New York.

490 Al-Shami, S.A., Heino, J., Che Salmah, M.R., Ahmad, A.H., Hamid, S.A. & Madrus, M.R.

491 (2013) Drivers of beta diversity of macroinvertebrate communities in tropical forest

492 streams. *Freshwater Biology*, **58**, 1126-1137.

493 Boulton, A.J., Boyero, L., Covich, A.P., Dobson, M.K., Lake, P.S. & Pearson, R.G. (2008)

494 Are tropical streams ecologically different from temperate streams? In: Tropical

495 Stream Ecology (Ed. Dudgeon D), Academic Press, San Diego. pp. 257-284.

496 Boyero, L. (2002) Insect biodiversity in freshwater ecosystems: is there any latitudinal

497 gradient? *Marine and Freshwater Research*, **53**, 753-755.

498 Boyero, L., Pearson, R. G., Dudgeon, D., Graça, M. A. S., Gessner, M. O., Albariño, R. J.,

499 Ferreira, V., Yule, C. M., Boulton, A. J., Arunachalam, M., Callisto, M., Chauvet, E.,

500 Ramírez, A., Chará, J., Moretti, M. S., Gonçalves, J. F., Helson, J. E., Chará-Serna, A.

501 M., Encalada, A. C., Davies, J. N., Lamothe, S., Cornejo, A., Li, A. O. Y., Buria, L.

502 M., Villanueva, V. D., Zúñiga, M. C. & Pringle, C. M. (2011) Global distribution of a

503 key trophic guild contrasts with common latitudinal diversity patterns. *Ecology*, **92**,

504 1839–1848.

505 Brown, H.P. (1981) A distributional survey of the world genera of aquatic dryopid beetles

506 (Coleoptera Dryopidae, Elmidae and Psephenidae). *Pan-Pacific Entomologist*, **57**,

507 133-148.

508 Brown, J.H. (2014) Why are there so many species in the tropics? *Journal of Biogeography*,

509 **41**, 8–22.

510 Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*. Sinauer, Sunderland.

511 Chase, J.M. & Knight, T.M. (2013) Scale-dependent effect sizes of *ecological* drivers on
512 biodiversity: why standardised sampling is not enough. *Ecology Letters*, 16, 17-26.

513 Coleman, B. D., Mares, M. A., Willig, M. R. & Hsieh, Y.-H. (1982) Randomness, area, and
514 species richness. *Ecology*, **63**, 1121–1133.

515 Coley, P.D. & Kursar, T.A. (2014) Is the high diversity in tropical forests driven by the
516 interactions between plants and their pests? *Science*, **343**, 35-36.

517 Cruz, P.V., Salles, F.F. & Hamada, N. (2013) A new genus and species of Baetidae (Insecta:
518 Ephemeroptera) from Brazil. *International Journal of Limnology*, **49**, 1-12.

519 Dias, M.S., Oberdorff, T., Hugueny, B., Leprieur, F., Jézéquel, C., Cornu, J.-F., Brosse, S.,
520 Grenouillet, G. & Tedesco, P. (2014) Global imprint of historical connectivity on
521 freshwater fish biodiversity. *Ecology Letters*, **17**, 1130-40.

522 Elliot, J.M. (2008) The ecology of riffle beetles (Coleoptera: Elmidae). *Freshwater Reviews*,
523 **1**, 189-203.

524 Evans, K.L., Warren, P.H. & Gaston, K.J. (2005a) Species–energy relationships at the
525 macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1–25.

526 Fox, J. & Weisberg, S. (2011) An R companion to Applied Regression, Second Edition.
527 Thousand Oaks CA: Sage. URL:
528 <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>

529 Gaston, K. J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227.

530 Golterman, H.L., Climo, R.S. & Ohnstad, M.A.M. (1978) *Methods for Physical and*

531 *Chemical Analysis of Freshwaters*. IBP, Oxford.

532 Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the
533 measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

534 Grönroos, M. & Heino, J. (2012) Species richness at the guild level: effects of species pool
535 and local environmental conditions on stream macroinvertebrate communities.
536 *Journal of Animal Ecology*, **81**, 679–691.

537 Heino, J. (2011) A macroecological perspective of diversity patterns in the freshwater realm.
538 *Freshwater Biology*, **56**, 1703–1722.

539 Heino, J., Melo, A.S., Bini, L.M., Altermatt, F., Al-Shami, S.A, Angeler, D., Bonada, N.,
540 Brand, C., Callisto, M., Cottenie, K., Dangles, O., Dudgeon, D., Encalada, A., Göthe,
541 E., Grönroos, M., Hamada, N., Jacobsen, D., Landeiro, V.L., Ligeiro, R., Martins,
542 R.T., Miserendino, M. L., Md Rawi, C.S. Rodrigues, M., Roque, F.O., Sandin, L.,
543 Schmera, D., Sgarbi, L.F., Simaika, J., Siqueira, T., Thompson, R.M. & Townsend,
544 C.R. (2015a) A comparative analysis reveals weak relationships between ecological
545 factors and beta diversity of stream insect metacommunities at two spatial levels.
546 *Ecology and Evolution*, **5**, 1235–1248.

547 Heino, J., Muotka, T. & Paavola, R. (2003) Determinants of macroinvertebrate diversity in
548 headwater streams: regional and local influences. *Journal of Animal Ecology*, **72**, 425–
549 434.

550 Heino, J., Nokela, T., Soininen, J., Tolkkinen, M., Virtanen, L. & Virtanen, R. (2015b)
551 Elements of metacommunity structure and community-environment relationships in
552 stream organisms. *Freshwater Biology*, **60**, 973–988.

- 553 Heino, J. & Soininen, J. (2007) Are higher taxa adequate surrogates for species-level
 554 assemblage patterns and species richness in stream organisms? *Biological*
 555 *Conservation*, **137**, 78-89.
- 556 Hillebrand, H. (2004a) On the latitudinal diversity gradient. *American Naturalist*, **163**, 192-
 557 211.
- 558 Hillebrand, H. (2004b) Strength, slope and variability of marine latitudinal gradients. *Marine*
 559 *Ecology Progress Series*, **273**, 251-267.
- 560 Hynes, H.B.N. (1970) *The Ecology of Running Waters*. University of Toronto Press, Toronto.
- 561 Illies, J. (1965) Phylogeny and zoogeography of the Plecoptera. *Annual Review of*
 562 *Entomology*, **10**, 117-140.
- 563 Jacobsen, D., Schultz, R. & Encalada, A. (1997) Structure and diversity of stream
 564 invertebrate assemblages: the influence of temperature with altitude and latitude.
 565 *Freshwater Biology*, **38**, 247-262.
- 566 Kouki, J., Niemelä, P. & Viitasaari, M. (1994) Reversed latitudinal gradients in species
 567 richness of sawflies (Hymenoptera, Symphyta). *Annales Zoologici Fennici*, **31**, 83-88.
- 568 Lake P.S., Schrieber, E.S., Milne, B. & Pearson, R.G. (1994) Species richness in streams:
 569 patterns over time, with stream size and with latitude. *Verhandlungen der*
 570 *Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **25**, 1822-
 571 1826.
- 572 Lancaster, J. & Downes, B.J. (2013) *Aquatic Entomology*. Oxford University Press.

- 573 Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.M.O. & Magnusson, W.E. (2012) The roles of
574 dispersal limitation and environmental conditions in controlling caddisfly
575 (Trichoptera) assemblages. *Freshwater Biology*, **57**, 1554-1564.
- 576 Legendre, P. & Legendre, L. (2012) *Numerical Ecology*. Third Edition. Elsevier, Amsterdam.
- 577 Mackereth, F.J., Heron, H.J. & Talling, J.F. (1978) *Water Analysis: Some Revised Methods*
578 *for Limnologists*. Freshwater Biological Association, London.
- 579 Magurran, A.E. (2004) *Measuring Biological Diversity*. Wiley, Oxford.
- 580 Malmqvist, B. & Mäki, M. (1994) Benthic macroinvertebrate assemblages in north Swedish
581 streams: environmental relationships. *Ecography*, **17**, 9-16.
- 582 McCreddie, J.W., Hamada, N., Grillet, M.E. & Adler, P.H. (2017) Alpha richness and niche
583 breadth of a widespread group of aquatic insects in Nearctic and Neotropical streams.
584 *Freshwater Biology*, **62**, 329–339.
- 585 McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K.,
586 Dornelas, M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A. E.,
587 Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I. and White, E.
588 P. (2007) Species abundance distributions: moving beyond single prediction theories
589 to integration within an ecological framework. *Ecology Letters*, **10**, 995–1015.
- 590 Melo, A.S. (2005) Effects of taxonomic and numeric resolution on the ability to detect
591 ecological patterns at a local scale using stream macroinvertebrates. *Archiv für*
592 *Hydrobiologie*, **164**, 309-323.
- 593 Mittelbach, G.G., Schemske, D. W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B.,

- Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M.,
McCune, A.R., McDade, L.A., McPeck, M.A., Near, T.J., Price, T.D., Ricklefs,
R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M. & Turelli, M. (2007) Evolution
and the latitudinal diversity gradient: speciation, extinction and biogeography.
Ecology Letters, **10**, 315-331.
- Moreau, C.S. & Bell, C.D. (2013) Testing the museum versus cradle tropical biological
diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range
evolution of the ants. *Evolution*, **67**, 2240-2257.
- Nakagawa, S. & Parker, T.H. (2015) Replicating research in ecology and evolution:
feasibility, incentives, and the cost-benefit conundrum. *BMC Biology*, **13**, 88.
- National Board of Waters and the Environment (1981) Vesihallinnon analyysimenetelmät.
Tiedotus 213. Vesihallitus, Helsinki.
- Nimon, K., Oswald, F. & Roberts, J. K. (2015) yhat: Interpreting Regression Effects. R
Package version 2.0-0. <https://cran.r-project.org/web/packages/yhat/index.html> .
Accessed December 15, 2017.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson,
G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community
Ecology Package. R package version 2.0-10. [http://CRAN.R-](http://CRAN.R-project.org/package=vegan)
[project.org/package=vegan](http://CRAN.R-project.org/package=vegan). Accessed January 2, 2014.
- Pearson, R.G. & Boyero, L. (2009) Gradients in regional diversity of freshwater taxa. *Journal*
of the North American Benthological Society, **28**, 504-514.
- Poff, N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and
prediction in stream ecology. *Journal of the North American Benthological Society*,

617 **16**, 391-409.

618 Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D. W., Slotow, R. & Hamer, M.

619 (2014) Using commonality analysis in multiple regressions: a tool to decompose

620 regression effects in the face of multicollinearity. *Methods in Ecology and*

621 *Evolution*, **5**, 320–328.

622 R Core Team (2017) R: A language and environment for statistical computing. R Foundation

623 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

624 Reich P.B. & Oleksyn J. (2004) Global patterns of plant leaf N and P in relation to

625 temperature and latitude. *Proceedings of National Academy of Sciences*, **101**, 11001-

626 11006.

627 Rosenzweig, M. L. (1995) *Species Diversity in Space and Time*. Cambridge University Press,

628 Cambridge.

629 Seibold, D. R. & McPhee, R. D. (1979) Commonality analysis: A method for decomposing

630 explained variance in multiple regression analysis. *Human Communication*

631 *Research*, **5**, 355–365.

632 Siqueira, T., Bini, L.M., Roque, F.O., Marques Couceiro, S.R., Trivinho-Strixino, S. &

633 Cottenie, K. (2012) Common and rare species respond to similar niche processes in

634 macroinvertebrate metacommunities. *Ecography*, **35**, 183–192.

635 Soininen, J. (2012) Macroecology of unicellular organisms – patterns and processes.

636 *Environmental Microbiology Reports*, **4**, 10-22.

637 Soininen, J., Bartels, P., Heino, J., Luoto, M. & Hillebrand, H. (2015) Toward more

638 integrated ecosystem research in aquatic and terrestrial environments. *BioScience*, **65**,
639 174-182.

640 Soininen, J., Lennon, J.J. & Hillebrand, H. (2007) A multivariate analysis of beta diversity
641 across organisms and environments. *Ecology*, **88**, 2830-2838.

642 Stout, J. & Vandermeer, J. (1975) Comparison of species richness for stream-inhabiting
643 insects in tropical and mid-latitude streams. *American Naturalist*, **109**, 263-280.

644 Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003) The species-accumulation curve and
645 estimation of species richness. *Journal of Animal Ecology*, **72**, 888–897.

646 Vinson, M.R. & Hawkins, C.P. (1998) Biodiversity of stream insects: variation at local,
647 basin, and regional scales. *Annual Review of Entomology*, **43**, 271-293.

648 Vinson, M.A. & Hawkins, C.P. (2003) Broad-scale geographical patterns in local stream
649 insect genera richness. *Ecography*, **26**, 751-767.

650 Ward, J. V. (1992) *Ecology of Aquatic Insects: Volume I. Biology and Habitat*. Wiley, New
651 York.

652 Whittaker, R. H. (1965). Dominance and diversity in land plant communities: Numerical
653 relations of species express the importance of competition in community function and
654 evolution. *Science*, **147**, 250–260.

655 Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species
656 richness. *Trends in Ecology and Evolution*, **19**, 639-644.

657 Willig, M. R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity:
658 pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and*

Systematics, **34**, 273-309.

Yule, C.M., Leong, M.Y., Liew, K.C., Ratnarajah, L., Schmidt, K., Wong, H.M., Pearson, R.G. & Boyero, L. (2009) Shredders in Malaysia: abundance and richness are higher in cool upland tropical streams. *Journal of the North American Benthological Society*, **28**, 404-415.

Zuur, A.F., Leneo, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3-14.

DATA ACCESSIBILITY

The data used in this work are stored in PANGAEA (<https://www.pangaea.de/>). The datasets can also be found in Supporting Information of this paper.

BIOSKETCH

Our Finnish-Brazilian team is interested in biodiversity patterns in general and those from stream ecosystems in particular. This research originated during a joint research project funded by the Academy of Finland and FAPESP. Author contributions: JH, JS, TS, ASM, VLL and LMB conceived the ideas; JJM, DKP, KTT, VP and TSFS collected the data; DKP, VSS and KTT identified the insects; ASM analysed the data; and JH and TS led the writing. All authors contributed to the ideas and approved the final version of the manuscript.

679 **SUPPORTING INFORMATION**

680 Additional Supporting Information is available in the online version of this paper.

Tables and Figures

Table 1. Descriptive statistics of local genus richness, local rarefied genus richness and local assemblage abundance, of stream insects, as well as of selected physical and chemical variables measured in streams in Finland (N = 97) and Brazil (N = 88). These values are based on the reduced datasets after removal of anomalous sites. SD = standard deviation, IQR = interquartile range, CV = coefficient of variation.

Variable	Finland				Brazil			
	Mean	SD	IQR	CV	Mean	SD	IQR	CV
Observed richness	14.01	5.07	8.00	0.36	17.84	7.46	11.25	0.42
Rarefied richness	7.41	2.39	2.80	0.32	11.53	3.60	4.46	0.31
Abundance	886.57	700.73	852.00	0.79	181.50	111.38	190.00	0.61
pH	7.13	0.57	0.86	0.08	6.60	0.51	0.70	0.08
Conductivity (µS/cm)	88.17	84.19	86.90	0.95	55.79	58.68	29.00	1.05
TN (µg/L)	852.84	507.46	537.50	0.60	119.60	34.59	41.67	0.29
TP (µg/L)	72.14	58.52	65.67	0.81	15.33	12.47	9.30	0.81
Stream width (m)	3.84	2.53	2.95	0.66	2.60	1.75	0.84	0.67
Shading (%)	37.93	23.03	37.75	0.61	72.70	20.39	25.00	0.28
Mean velocity (m/s)	0.25	0.11	0.14	0.43	0.21	0.08	0.12	0.38
Mean depth (m)	0.18	0.07	0.07	0.37	0.13	0.07	0.07	0.54
Substratum diversity	1.06	0.33	0.39	0.31	1.29	0.20	0.25	0.16

Table 2. Reduced multiple regression models showing the effects of ‘region’ and local environmental variables on rarefied richness (a; $F_{13,177} = 24.86$, $p < 0.001$), observed richness (b; $F_{13,178} = 17.88$, $p < 0.001$) and assemblage abundance (c; $F_{13,176} = 34.41$, $p < 0.001$) of stream insects in Finland and Brazil. Also shown are unique, common and total effects of each predictor variable from commonality analysis. See Supporting Information Table S1 for full models.

a) Rarefied richness								
	Estimate	SE	t	p	Unique	Common	Total	
(Intercept)	5.504	0.792	6.946	<0.001				
region	4.506	0.542	8.309	<0.001	0.188	0.130	0.318	
width	0.439	0.095	4.639	<0.001	0.072	-0.050	0.022	
forest cover	1.654	0.679	2.438	0.016	0.020	0.085	0.105	
sand	-0.027	0.013	-2.156	0.032	0.009	0.001	0.010	
total P	-2.388	1.204	-1.983	0.049	0.013	0.016	0.029	
shading	0.016	0.009	1.716	0.088	0.008	0.121	0.129	
								0.496 0.476
b) Observed richness								
	Estimate	SE	t	p	Unique	Common	Total	
(Intercept)	-0.609	5.394	-0.113	0.910				
region	5.428	0.852	6.369	<0.001	0.142	-0.057	0.085	
width	1.046	0.187	5.607	<0.001	0.110	0.004	0.114	
forest cover	4.368	1.382	3.160	0.002	0.035	0.057	0.092	
sand	-0.069	0.025	-2.723	0.007	0.026	0.026	0.052	
pH	11.654	6.060	1.923	0.056	0.013	-0.012	0.001	
total P	-4.493	2.395	-1.876	0.062	0.012	0.042	0.054	
								0.376 0.355
c) Abundance								
	Estimate	SE	t	p	Unique	Common	Total	
(Intercept)	3.328	0.770	4.319	<0.001				
region	-1.186	0.149	-7.971	<0.001	0.141	0.301	0.442	
shading	-0.009	0.002	-3.547	<0.001	0.028	0.265	0.293	
pH	2.820	0.801	3.518	<0.001	0.027	0.018	0.045	
velocity	2.097	0.599	3.498	<0.001	0.027	0.116	0.144	
sand	-0.011	0.003	-3.469	<0.001	0.027	0.103	0.129	
pebble	0.011	0.003	3.100	0.002	0.021	-0.003	0.018	
particle diversity	0.286	0.194	1.472	0.143	0.005	0.045	0.049	
forest cover	0.274	0.189	1.455	0.147	0.005	-0.002	0.002	
								0.610 0.592

698

699 Fig. 1. Differences in regional stream insect genus richness between Brazil and Finland based
 700 on similar-sized areas after random resampling in both regions. Note that a large number of
 701 resampling analyses show the same pattern, i.e., regional genus richness is much higher in
 702 Brazil than in Finland.

Fig. 2. Boxplots denoting differences in basin-scale stream insect genus richness between the two regions, Brazil (N = 17 basins) and Finland (N = 19 basins). Shown are observed (A) and rarefied (B) genus richness values.

708

709 Fig. 3. Boxplots denoting differences in local stream-scale genus richness between the two
 710 regions, Brazil (N = 88 streams) and Finland (N = 97 streams). Shown are observed (A) and
 711 rarefied (B) genus richness values.