Beta diversity of stream insects differs between boreal and subtropical regions, but land use does not generally cause biotic homogenization

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Abstract: Previous studies have found mixed results regarding the relationship between beta diversity and latitude. In addition, by influencing local environmental heterogeneity, land use may modify spatial taxonomic and functional variability among communities causing biotic differentiation or homogenization. We tested 1) whether taxonomic and functional beta diversities among streams within watersheds differ between subtropical and boreal regions and 2) whether land use is related to taxonomic and functional beta diversities in both regions. We sampled aquatic insects in 100 subtropical (Brazil) and 100 boreal (Finland) streams across a wide gradient of land use, including agriculture and exotic planted, secondary, and native forests. We calculated beta diversity at the watershed scale (among 5 streams in each watershed). We found higher taxonomic beta diversity among subtropical than among boreal streams, whereas functional beta diversity was similar between the 2 regions. Total land use was positively correlated with taxonomic and functional beta diversity among subtropical streams, while local environmental heterogeneity was positively correlated with beta diversity among boreal streams. We suggest that different types and intensities of land use may increase among-stream heterogeneity, promoting distinct insect assemblage compositions among streams. Our findings also suggest that beta diversity patterns and their underlying determinants are highly context dependent.

Key words: aquatic insects, functional homogenization, latitudinal diversity gradient, biological traits, environmental heterogeneity

One of the most widely documented patterns in ecology is the latitudinal gradient of diversity, i.e., species richness decreases from the equator towards the poles (Gaston 2000, Brown 2014). Whereas higher species richness in the tropics is a well-known pattern, it is still controversial as to whether beta diversity (i.e., variation in community

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composition among sites) is also higher at low latitudes (see Qian and Ricklefs 2007, Kraft et al. 2011, Qian and Song 2013). For example, while Qian and Ricklefs (2007) found lower plant beta diversity in higher latitudes compared to lower latitudes, Kraft et al. (2011) found no differences in plant beta diversity across a latitudinal gradient.

Biodiversity has been changing globally because of anthropogenic activities. Land-use change, for example, is a worldwide cause of biodiversity loss across different ecosystems (Newbold et al. 2015, 2016). Land-use intensity may drive taxonomic and functional homogenization of communities (i.e., decrease in spatial beta diversity through time) by promoting the expansion of tolerant species and the elimination of sensitive species (McKinney and Lockwood 1999, Castro et al. 2018, Dornelas et al. 2019). Tolerant and sensitive species may respond differently to land-use change because they typically have different environmental requirements (Verberk et al. 2010, Heino and Grönroos 2014), which may be mediated by different biological traits (Gossner et al. 2016, Jonason et al. 2017). The analysis of both taxonomic and functional diversity can, thus, improve our understanding of how biological communities respond to land use (Castro et al. 2018, Roa-Fuentes et al. 2019). For example, land-use intensification may have more severe effects on taxonomic diversity than on functional diversity, especially if communities are composed of many functionally redundant species (Sfair et al. 2016). Alternatively, land-use intensification may decrease functional diversity more severely if disturbed sites gain resistant and widespread species that share the same set of traits (Mori et al. 2015). Functional homogenization is especially worrisome, as it may limit the ecosystem functions and services provided by biological communities (Cardinale et al. 2012, Gámez-Virués et al. 2015).

Land-use intensification is a strong driver of biodiversity loss in stream ecosystems (e.g., Marchetti et al. 2006, Siqueira et al. 2015). Streams surrounded by intensive land use, such as monocultures and pasture, may become harsh habitats for many aquatic species because of flow regime alterations, changes in channel structure, decreased inputs of coarse organic material, and increased loads of sediment and contaminants from terrestrial sources (Allan 2004, Leal et al. 2016, Castro et al. 2018). Additionally, land-use intensification may decrease environmental heterogeneity among streams by homogenizing benthic substrates and flow velocity and, consequently, cause biotic homogenization if community assembly is mainly driven by heterogeneous environmental conditions (e.g., Costa and Melo 2008). Conversely, land-use heterogeneity among streams (e.g., rural, urban, and forestry land uses within the same watershed) may increase biotic differentiation if different species are selected by environmental conditions associated with each land-use type or intensity (e.g., Siqueira et al. 2015). Therefore, land-use intensification may drive beta diversity in different ways according to the specific features of the watersheds under examination, causing beta diversity to decrease (biotic homogenization; e.g., Passy and Blanchet 2007, Maloney et al. 2011), increase (biotic differentiation; e.g., Hawkins et al. 2015, Roa-Fuentes et al. 2019), or remain unchanged (Larsen and Ormerod 2014).

To assess potential latitudinal variation in beta diversity and explore the influence of land use on this diversity, we conducted a large-scale survey of aquatic insects in boreal and subtropical streams covering a wide gradient of land use in each region. First, we investigated whether taxonomic and functional beta diversities within watersheds differ between the 2 regions. Second, we tested whether total land-use intensification decreases (biotic homogenization), increases (biotic differentiation), or does not change taxonomic and functional beta diversities of aquatic insects in both regions. We also explored the influence of local environmental heterogeneity and land-use heterogeneity on aquatic insect beta diversity.

METHODS

Study area and sampling design

To address our research goal, we sampled 20 watersheds in Brazil (a subtropical region) and 20 watersheds in Finland (a boreal region) (Fig. S1). We selected the watersheds primarily based on forest and agricultural field cover to provide a gradient of land-use intensification. In each of the 40 watersheds, we sampled five 2^{nd}- to 3^{rd}-order streams for a total of 200 streams (2 regions × 20 watersheds × 5 streams = 200 streams).

We sampled Finnish streams in September 2014, during the beginning of the Northern Hemisphere autumn, and Brazilian streams between September and November 2015, during the Southern Hemisphere spring. We selected a short sampling period in Finland because of strong seasonal changes in insect composition in that region, and September is the period when most aquatic insect larvae are well developed. In Brazil, we chose a period of low rainfall (i.e., beginning of the wet season) and, consequently, with no intense floods. The longer sampling period in Brazil than in Finland probably did not influence our results given there is low seasonality in our tropical region (Melo and Froehlich 2001).

Streams in Brazil and Finland were surrounded by a wide variation of land-use configurations, from watersheds dominated by monoculture to watersheds covered almost entirely by near-pristine forests. In Brazil, we surveyed streams located in the southeastern region of the country between latitudes 23°49′S and 24°20′S (with a spatial extent of ~120 km in the east–west direction and 70 km in the north–south direction). The main land uses in Brazil were related to exotic tree plantations (*Eucalyptus* and *Pinus* spp.), agriculture, and pasture (Fig. S2). Pristine streams in Brazil were located in watersheds covered by Atlantic Rainforest within 3 important protected areas: Carlos Botelho, Intervales, and

Alto Ribeira state parks. In Finland, we sampled streams located in the western part of the country between latitudes 60°27′N and 65°01′N (study area extending 300 km in the east–west direction and ~500 km in the north–south direction). The main land uses in Finland are agriculture, managed forests, and urbanization (Fig. S2). The pristine streams are within watersheds covered by boreal forests dominated by *Pinus sylvestris* and *Picea abies*. For more details about the study areas, see Heino et al. (2018) and Siqueira et al. (2020). It should be noted that, despite the larger geographical extent of the areas sampled in Finland, we based our analyses on beta diversity among streams within watersheds and not among streams distributed over the study area, minimizing the effects of the differing geographical extents.

Biological data

We used standardized field methods for collecting biological data in Brazil and Finland. In both countries, we sampled 1 riffle site in each stream by using a kick-net (0.5-mm mesh size) for 2 min (four 30-s subsamples). Using a stereo microscope (Finland: model SZX10, Olympus, Tokyo, Japan; Brazil: model M165 C, Leica, Wetzlar, Germany), we identified all sampled aquatic insects from the following orders to genus level: Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Odonata, and Megaloptera. We based our identifications on Pes et al. (2005), Domínguez et al. (2006), Heckman (2006a, b), Domínguez and Fernández (2009), and Ribeiro (2013) for Brazilian aquatic insects and on Lillehammer (1988), Engblom (1996), Meinander (1996), Norling and Sahlen (1997), and Wallace et al. (2003) for Finnish aquatic insects. We selected 6 biological traits of aquatic insects that may be affected by land use: refuge building, body shape, locomotion, functional feeding group, respiration, and body size (see Table S1). For example, reductions in riparian forest cover could decrease the number of shredders (Cummins et al. 1989), while streambed siltation could increase the number of burrowers (Castro et al. 2018). We classified, in a similar way for Brazil and Finland, the collected aquatic insects according to each biological trait. We compiled Brazilian and Finnish insect trait information mainly from the literature (see Table S2) and by consulting a number of regional specialists (see Acknowledgements).

Local environmental data

We collected local environmental data to characterize our study streams. In each stream site, we measured flow velocity (m/s) and depth (cm) at random locations (30/stream in Finland and 9/stream in Brazil). The number of sites/stream was chosen based on the 2 field crews' decisions regarding how much effort was sufficient to characterize their study sites. We estimated mean stream width (m) of each sampled riffle site based on 10 measurements (Finnish streams) or 3 measurements (Brazilian streams). We visually estimated particle size classes in 0.25-m^2 sections at random locations in each riffle site (10/riffle in Finland and 3/riffle in Brazil). We used a modified Wentworth's (1922) 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). We reported each particle size class as a percentage of the section. We also estimated shading as % canopy cover. In Finland, we made these estimates by looking through a tube (~5-cm diameter) at 10 points/stream site. In Brazil, we estimated riparian vegetation in the visual field of the observer at 3 points/stream site. We measured pH and conductivity at each stream in the field with multiparameter probes (Finland: model 556 MPS, Yellow Springs Instruments, Yellow Springs, Ohio; Brazil: model U-50, Horiba, Kyoto, Japan). We took water samples to analyze total nitrogen and total phosphorus following standard protocols for Finland (NBWE 1981) and Brazil (Golterman et al. 1978, Mackereth et al. 1978). A detailed description of the field and laboratory methods can be found in Heino et al. (2018) and Siqueira et al. (2020).

Land-cover data

We characterized the land use and land cover (LULC) for each of the watersheds in our study. We mapped LULC of Brazilian watersheds by manually digitizing LULC at 5-m spatial resolution from orthorectified RapidEye (Berlin, Germany) multispectral imagery (Planet 2016). For Finnish watersheds, we used the pre-existing CORINE LULC dataset (Copernicus 2016). We standardized the land-cover nomenclature among datasets, which resulted in the following LULC categories: native forest, secondary/managed forest, exotic/planted forest, pasture, agriculture, urban, mining, wetland, bare soil, water, and mixed. We established a 500-m radius around each sampling site and manually delineated the stream segments contained within this radius using hydrological and topographic data as well as high-resolution imagery from the Google Earth™ database. We then generated a 200-m-width buffer along each stream segment (100 m downstream and 100 m upstream from a sampling site). We calculated the proportion of land use attributed to each LULC category within the buffer of each stream. Data on insect abundance, local environmental variables, and land cover are archived in Siqueira et al. (2019).

Taxonomic and functional beta diversity

We estimated taxonomic and functional beta diversities of aquatic insects among 5 streams in each watershed. We made these estimates separately for Brazil and Finland ($n = 20$ beta diversity values for each region). Sørensen and Bray–Curtis dissimilarity coefficients are simple and common metrics for beta diversity estimation that are based on incidence and abundance data, respectively (Legendre and Legendre 2012). Both metrics are, however, affected by differences in species richness. To control for such differences, total beta diversity can be partitioned into 1 component related to species replacement across sites (i.e., the turnover component of dissimilarity) and another component related to nestedness (i.e., differences in species richness across sites; Baselga 2010). We focused on the turnover component because we were interested in the replacement of genera among sites. Moreover, the turnover components of beta diversity are often much larger than the nestedness components in ecological datasets (Soininen et al. 2018; in our study: mean contributions of nestedness components for Finland and Brazil, respectively, were 4.25 and 4.44% based on the Sørensen coefficient and 4.16 and 5.16% based on the Bray–Curtis coefficient). We used 2 dissimilarity metrics to calculate taxonomic beta diversity: the turnover component of the Sørensen index (i.e., the Simpson index) and the turnover component of the Bray–Curtis index. We log-transformed abundance data before computing the turnover component of Bray–Curtis. We used the beta.pair function in the *betapart* package (version 1.5.1; Baselga et al. 2018) in R (version 3.6.0; R Project for Statistical Computing, Vienna, Austria) to obtain the turnover and nestedness components of both the Sørensen and Bray–Curtis indices.

To calculate functional beta diversity, we used the modified Gower distance on the genus–traits matrix (separately for Brazil and Finland) to obtain a matrix of genus-by-genus functional distances (Pavoine et al. 2009, Pavoine and Ricotta 2014). We calculated functional beta diversity twice: once with incidence data and once with abundance data. We used the *ade4* package (Dray and Dufour 2007) in R and the code provided by Pavoine and Ricotta (2014) for functional beta diversity estimations.

Finally, we obtained a single beta diversity value for each watershed and for each taxonomic and functional dissimilarity coefficient (i.e., the turnover and nestedness components of the Sørensen coefficient, the turnover and nestedness components of the Bray–Curtis coefficient, and functional beta diversity based on abundance and incidence data) by using the mean distance from streams to their group (watershed) centroid (permutational analysis of multivariate dispersions [PERMDISP]) (Anderson et al. 2006). For this task, we used the betadisper function available in the *vegan* package (version 2.5.6; Oksanen et al. 2017) in R.

Modeling beta diversity along land-use and environmental heterogeneity gradients

To explore how aquatic insect beta diversity may be influenced by heterogeneity in land-use and environmental characteristics, we modeled beta diversity along land-use and environmental heterogeneity gradients. We obtained the mean proportion of each LULC category among the 5 streams in each watershed. Hereafter, total land use refers to the summed proportion of secondary forests, exotic planted forests, pasture, agriculture, and urban land cover in each watershed. We estimated land-use heterogeneity within each watershed (proportions of native forest, secondary/managed forest, exotic/planted forests, pasture, agriculture, urban, mining, wetland, bare soil, water, and mixed) with a procedure similar to that used to estimate beta diversity. This procedure was based on the mean distance from streams to their group centroid in a principal-coordinates ordination space (PERMDISP; Anderson et al. 2006). The ordination was based on the standardized Euclidean distance matrix of land use. We used the same procedure to estimate local environmental heterogeneity (based on stream width, shading, sand, gravel, pebble, cobble, boulders, current velocity, depth, pH, conductivity, nitrogen, and phosphorus).

We built multiple regression models with beta diversity at the watershed level as the response variable (1 model for each beta diversity metric) and region, total land use, land-use heterogeneity, and local environmental heterogeneity at the watershed level as predictor variables. We also included interactions between region and total land use, region and land-use heterogeneity, and region and local environmental heterogeneity. Because our response variables followed a beta distribution (i.e., they ranged between 0 and 1), we used beta regression models (Ferrari and Cribari-Neto 2004). We fitted the models using the betareg function from the *betareg* package (Cribari-Neto and Zeileis 2010) in R. Our R code is provided in Appendix S1.

RESULTS

Our watersheds covered a wide range of total land use, ranging from 0 to ~75%, in Brazil and in Finland. Agriculture (0.13 ± 0.17 in Brazil and 0.41 ± 0.21 in Finland; mean proportion ± standard deviation) and urbanization (0.02 ± 0.03 in Brazil and 0.09 ± 0.06 in Finland) covered larger areas in Finland, whereas native forests (0.55 ± 0.28 in Brazil and 0.37 ± 0.23 in Finland), pasture (0.06 ± 0.10 in Brazil and 0.01 ± 0.02 in Finland), and planted forests (0.16 ± 0.16 in Brazil and 0.0002 ± 0.0007 in Finland) covered larger areas in Brazil (Fig. S2). The proportion of secondary/managed forests was similar between countries (Fig. S2). Total land use (modified area at watershed was 0.37 ± 0.24 in Brazil and 0.50 ± 0.25 in Finland; Fig. S3A), land-use heterogeneity (mean distance to centroid was 0.21 ± 0.13 in Brazil and 0.19 ± 0.06 in Finland; Fig. S3B), and local environmental heterogeneity (mean distance to centroid was 2.53 ± 0.54 in Brazil and 2.53 ± 0.61 in Finland; Fig. S3C) were similar between the regions. Total land use was positively related to higher land-use heterogeneity only in Brazil (adjusted $R^2 = 0.31$; $p < 0.001$; Fig. S4A), but it was not related to local environmental heterogeneity in either country (Fig. S4B). Also, land-use heterogeneity was not related to local environmental heterogeneity in Brazil or Finland (Fig. S4C).

We recorded 16,133 aquatic insects and 83 genera across all subtropical streams. We recorded a much higher number of individuals (86,048), albeit a similar number of genera (77), in the boreal streams compared with the subtropical streams (more details in Heino et al. 2018).

We found higher taxonomic beta diversity among subtropical streams than among boreal streams based on the turnover components of both the Sørensen ($F_{1,38} = 18.47$, $p < 0.001$; Fig. 1A) and the Bray–Curtis dissimilarities ($F_{1,38} = 8.34$, $p = 0.006$; Fig. 1B). However, we did not find differences between subtropical and boreal streams with the nestedness component of either the Sørensen ($F_{1,38} = 0.44$, $p = 0.514$; Fig. S5A) or the Bray–Curtis dissimilarity ($F_{1,38} = 0.17$, $p = 0.686$; Fig. S5B). Functional beta diversity was similar among subtropical and boreal streams based on both incidence ($F_{1,38} = 1.69$, $p = 0.201$; Fig. 1C) and abundance data ($F_{1,38} = 1.29$, $p = 0.263$; Fig. 1D).

We found that total land use had a strong positive correlation with all measures of beta diversity in subtropical streams (turnover component of Sørensen: pseudo $R^2 = 0.44$, $p < 0.001$; turnover component of Bray–Curtis: pseudo $R^2 = 0.45$, $p < 0.001$; functional based on incidence: pseudo $R^2 = 0.29$, $p < 0.001$; functional based on abundance: pseudo $R^2 = 0.27$, $p < 0.001$). However, this relationship was not detected in boreal streams (Fig. 2A, D, G, J). Our different measures of beta diversity were unrelated to land-use heterogeneity in either region (Fig. 2B, E, H, K). We found a positive relationship between environmental heterogeneity and taxonomic beta diversity (for both incidence and abundance data) only in the boreal region (Fig. 2C, F), but this relationship was weak and disappeared when the watershed with the highest environmental heterogeneity was removed from the analyses. We found no relationship between environmental heterogeneity and functional beta diversity in either region (Fig. 2I, L, Table 1). Finally, the nestedness components of the Sørensen and Bray–Curtis dissimilarities were not related to any predictor variable (Table S3).

DISCUSSION

We investigated whether taxonomic and functional beta diversity differ between subtropical and boreal regions, and we examined the relationship between beta diversities and total land use, local environmental heterogeneity, and land-use heterogeneity. Our results indicate that taxonomic and functional beta diversities were not congruent between the regions. We found higher taxonomic beta diversity in Brazil but similar functional beta diversity between the 2 regions. We did not find a substantial negative relationship between beta diversity and land-use intensification, which would be

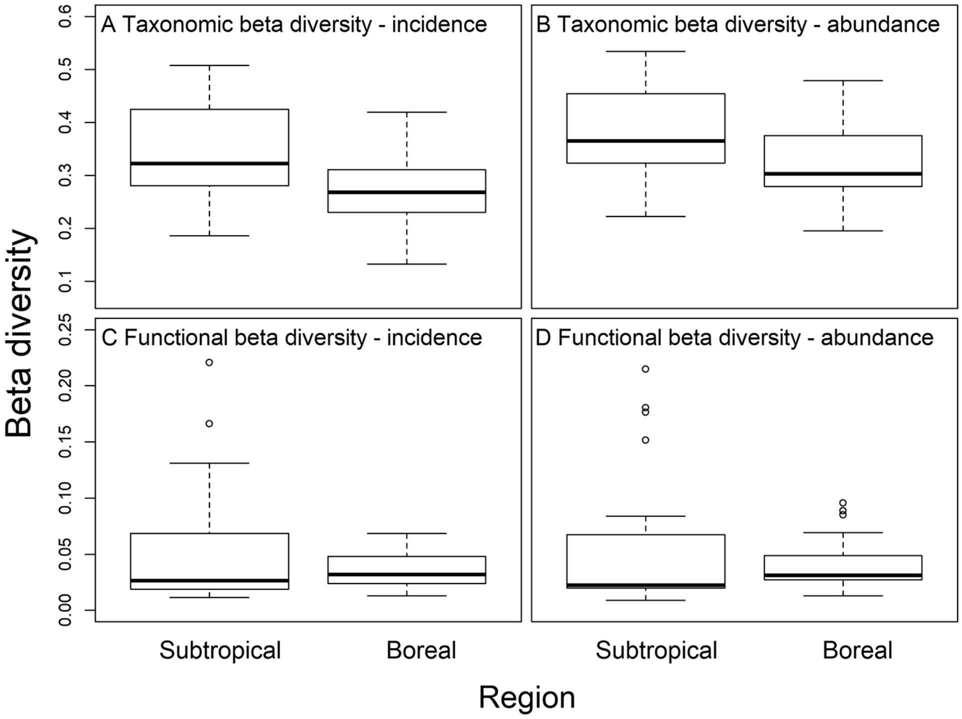

Figure 1. Beta diversity among 100 Brazilian (subtropical) and 100 Finnish (boreal) streams within 20 Brazilian and 20 Finnish watersheds based on the turnover component of the Sørensen dissimilarity (A), the turnover component of the Bray–Curtis dissimilarity (B), functional dissimilarity based on incidence data (C), and functional dissimilarity based on abundance data (D). The bold line in each box indicates the median, the lower boundary of the box indicates the 25th percentile, and the upper boundary of the box indicates the 75th percentile. The whiskers indicate the minimum and maximum values unless discrepant values, defined as those more distant than 1.5× the length of the box away from the box, are present.

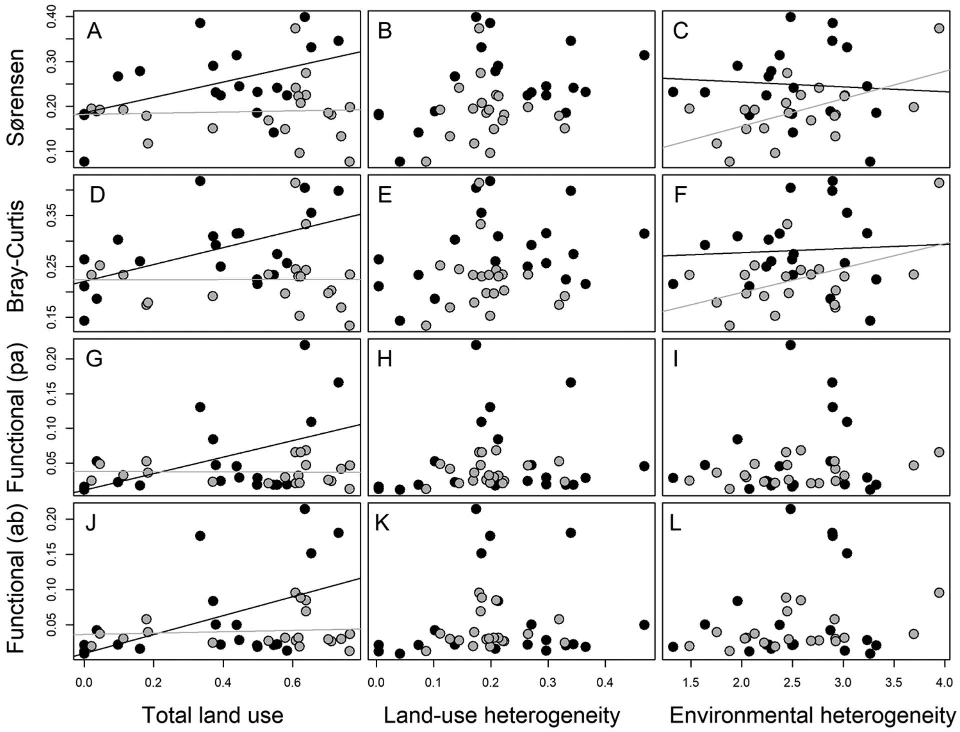

Figure 2. Relationships between beta diversity and total land use (the proportion of modification in each watershed; A, D, G, J), land-use heterogeneity (the mean distance to centroid based on land-use classes; B, E, H, K), and local environmental heterogeneity (the mean distance to centroid on local environmental variables; C, F, I, L) among subtropical (black) and boreal streams (gray) in 20 watersheds in Brazil and 20 watersheds in Finland. We used the turnover component of the Sørensen dissimilarity, the turnover component of the Bray–Curtis dissimilarity, functional dissimilarity based on incidence, and functional dissimilarity based on abundance data as beta diversity metrics. Lines indicate substantial interactions with region (subtropical [black] and boreal [gray]) as shown in Table 1. pa = incidence data, ab = abundance data.

consistent with a process of biotic homogenization. Instead, we found a positive relationship between beta diversity (both taxonomic and functional) and total land use in subtropical streams. We also found a weak positive relationship between beta diversity and local environmental heterogeneity in boreal streams.

Subtropical and boreal taxonomic and functional beta diversity comparison

The existence of latitudinal gradients of taxonomic and functional beta diversity is under discussion in the literature, and the occurrence of latitudinal gradients in functional beta diversity, in particular, is not well established. Most of the evidence for these latitudinal gradients comes from terrestrial and marine systems (Qian and Ricklefs 2007, Kraft et al. 2011, Qian and Song 2013), whereas less is known about freshwater systems (but see García-Girón et al. 2020). Our findings contribute to answering the question of whether there are latitudinal gradients in species turnover (Koleff et al. 2003; see also Qian and Ricklefs 2007 for other studies showing the same pattern). We found that taxonomic beta diversity mimics the well-known latitudinal pattern in alpha diversity: a decrease from low (subtropical) to high (boreal) latitudes. However, our findings did not show differences in insect functional beta diversity between subtropical and boreal streams. This result suggests higher functional redundancy in subtropical streams because subtropical streams, despite being more taxonomically variable than boreal streams, had similar functional variability.

The mechanisms behind the latitudinal pattern of beta diversity are unclear. For instance, we cannot rule out the possibility that the lower taxonomic beta diversity in boreal streams, as compared to subtropical streams, is related to climatic extremes and dispersal. Boreal streams are climatically harsh in terms of high variability in temperature and hydrological conditions (Heino 2011, Hortal et al. 2011). Beta diversity is thought to be lower in harsh habitats because only reduced sets of tolerant species are likely to thrive in such habitats, consequently decreasing among-site variability in species composition. Another possible explanation for the lower taxonomic beta diversity in boreal streams is that boreal aquatic insects may be good dispersers. Because high-latitude areas were totally covered by ice during the last Ice Age (i.e., until ~12,000 y ago; Pielou 2008), most species that have been able to reach these high-latitude areas after glaciation must have relatively

Table 1. Results from beta regression models for taxonomic (using the turnover component of the Bray–Curtis and Sørensen dissimilarities) and functional (using incidence and abundance data) beta diversity in relation to region (boreal and subtropical), total land use (the proportion of area modified in each watershed), land-use heterogeneity (the mean distance to centroid based on land-use classes), and environmental heterogeneity (the mean distance to centroid on local environmental variables) in 40 watersheds (20 in Finland and 20 in Brazil). Bold values indicate $p < 0.05$.

Beta diversity predictors	Estimate	SE	*Z*-value	*p*-value
Turnover Sørensen dissimilarity		Pseudo $R^2 = 0.44$; $p < 0.001$		
Intercept	−1.27	0.39	−3.27	**0.001**
Region	−1.01	0.55	−1.83	0.067
Total land use	0.78	0.43	1.84	0.066
Land-use heterogeneity	0.56	0.77	0.73	0.467
Local environmental heterogeneity	−0.11	0.14	−0.76	0.444
Region × total land use	−1.48	0.58	−2.54	**0.011**
Region × land-use heterogeneity	−1.79	1.66	−1.08	0.281
Region × local environmental heterogeneity	0.66	0.21	3.08	**0.002**
Turnover Bray–Curtis dissimilarity		Pseudo $R^2 = 0.45$; $p < 0.001$		
Intercept	−1.21	0.32	−3.72	<**0.001**
Region	−0.49	0.45	−1.09	0.274
Total land use	0.91	0.35	2.61	**0.009**
Land-use heterogeneity	−0.20	0.64	−0.31	0.757
Local environmental heterogeneity	−0.01	0.12	−0.13	0.899
Region × total land use	−1.51	0.47	−3.19	**0.001**
Region × land-use heterogeneity	−1.52	1.37	−1.11	0.265
Region × local environmental heterogeneity	0.44	0.18	2.52	**0.012**
Incidence-based functional dissimilarity		Pseudo $R^2 = 0.28$; $p < 0.001$		
Intercept	−3.45	0.71	−4.85	<**0.001**
Region	−0.27	0.97	−0.28	0.782
Total land use	2.41	0.73	3.29	**0.001**
Land-use heterogeneity	−1.45	1.33	−1.09	0.276
Local environmental heterogeneity	−0.07	0.26	−0.26	0.793
Region × total land use	−3.10	0.99	−3.12	**0.002**
Region × land-use heterogeneity	0.800	2.82	0.28	0.777
Region × local environmental heterogeneity	0.492	0.37	1.31	0.188
Abundance-based functional dissimilarity		Pseudo $R^2 = 0.27$; $p < 0.001$		
Intercept	−3.53	0.78	−4.54	<**0.001**
Region	−0.25	1.05	−0.24	0.810
Total land use	2.55	0.79	3.25	**0.001**
Land-use heterogeneity	−1.84	1.45	−1.27	0.203
Local environmental heterogeneity	0.01	0.28	0.02	0.986
Region × total land use	−3.09	1.07	−2.88	**0.004**
Region × land-use heterogeneity	1.42	3.04	0.47	0.640
Region × local environmental heterogeneity	0.44	0.40	1.09	0.276

strong dispersal capabilities (Hof et al. 2006, 2008, Dehling et al. 2010, Homburg et al. 2013). High dispersal rates may homogenize among-site variation in local community composition within a metacommunity (Mouquet and Loreau 2003). It is unlikely that a difference in local environmental heterogeneity explains our finding of higher beta diversity in subtropical than in boreal streams because environmental heterogeneity did not differ between the streams located in Finland and Brazil (Fig. S3C).

We believe that fine-grained field data (a strength of our work) are crucial to showing the prevalence (or lack) of latitudinal patterns in beta diversity (Beck et al. 2012; see also De Cáceres et al. 2012 and Myers et al. 2013 for other studies with tropical and temperate forests using fine-grained data).

Most previous studies investigating such patterns were based on data obtained from atlases, which may include comparisons among data obtained in different ways (Rodríguez and Arita 2004, McKnight et al. 2007, Melo et al. 2009; but see Soininen et al. 2007). By using large-scale field studies, our approach allowed us to compare beta diversity among boreal and subtropical streams through a standardized method, avoiding different sampling bias among regions. Indeed, many previous studies have shown that latitudinal differences in beta diversity were simply due to sampling effects (Kraft et al. 2011, De Cáceres et al. 2012, Myers et al. 2013). However, our results were produced using metrics that accounted for at least some of these effects (e.g., the turnover components of total beta diversity indices that minimize the effect of differences in species richness).

Land-use effects on taxonomic and functional beta diversity

While the negative effects of land-use intensification on stream species richness have been frequently observed (Corbi et al. 2013, Martins et al. 2017), its effect on beta diversity in streams is still controversial. Some studies have found a negative effect of total land use on beta diversity (e.g., Passy and Blanchet 2007, Maloney et al. 2011, Siqueira et al. 2015), but others have shown a positive effect (e.g. Hawkins et al. 2015, Fugère et al. 2016, Roa-Fuentes et al. 2019) or have failed to find a relationship (e.g., Larsen and Ormerod 2014) in stream ecosystems. Using 2 contrasting climatic regions with different predominant land use (i.e., agriculture and urban areas in Finland and planted forests, agriculture, and pasture in Brazil), we did not find a negative relationship between beta diversity and total land use in the watersheds, which would have indicated a process of biotic homogenization. Instead, we found a positive relationship between total land use and beta diversity in subtropical streams, but more studies are necessary to understand why beta diversity increased with total land use only in Brazil. Similarly, Johnson and Angeler (2014) observed higher taxonomic beta diversity of macrophytes and benthic diatoms in rural streams because identities of tolerant species differed among modified streams, thereby creating high beta diversity. It is plausible that, in our study, different land uses selected different tolerant species, producing increased beta diversity in Brazil, although we did not specifically investigate this possibility.

Land-use change may increase environmental heterogeneity among streams if it results in differences in disturbance intensity or land-use types in the same watershed (Barboza et al. 2015, Fugère et al. 2016). Different land-use types may be indirectly related to high environmental differentiation among streams and, consequently, result in distinct community composition with taxa adapted to local environmental conditions (Siqueira et al. 2015). For example, Hawkins et al. (2015) and Fugère et al. (2016) found higher taxonomic beta diversity of macroinvertebrate assemblages in disturbed streams as compared to undisturbed ones and suggested among-taxon differences in stress tolerance as the underlying mechanism (see also Mykrä and Heino 2017). We found a positive relationship between total land use and land-use heterogeneity in subtropical streams (Fig. S4A), but we did not find a positive relationship between land-use heterogeneity and environmental heterogeneity. However, the streams in watersheds with heterogeneous land use could differ in other environmental features that were not included in our measure of local environmental heterogeneity, such as amount of organic matter or increased concentrations of contaminants.

Higher species richness in more heterogeneous habitats is a well-established relationship in ecology (Stein et al. 2014, Ortega et al. 2018). For beta diversity in stream ecosystems, however, this relationship is still unclear and likely scale or context dependent. For example, Heino et al. (2013) found that the beta diversity of benthic macroinvertebrates was not correlated with instream habitat heterogeneity, suggesting that individual species–environment responses and mass effects masked this relationship at the stream scale they studied in northern Finland. However, Astorga et al. (2014) found that environmental heterogeneity was the main driver of beta diversity of stream macroinvertebrates in New Zealand. These contrasting findings are likely to be due to different spatial scales (Heino et al. 2015). Similar to Astorga et al. (2014), we studied beta diversity at the watershed scale. However, taxonomic beta diversity in Brazil was unrelated to environmental heterogeneity and in Finland the relationship was very weak, indicating results are context specific or that other unmeasured factors may modulate the relationship.

Caveats

We recognize some potential caveats of our study. First, we did not include midges and flies (Diptera) despite their high abundance and species richness in some freshwater ecosystems (Ferrington 2008, Dijkstra et al. 2014). However, compared to other macroinvertebrate taxa, dipterans, like those belonging to the family Chironomidae, usually show similar or lower sensitivity to changes in environmental conditions (Rabeni and Wang 2001). Thus, we had no strong reasons to expect their inclusion would change the conclusions of our study, and given that the identification of dipteran larvae often demands considerable efforts (including the examination of mouthparts under a microscope), we chose not to include them. Second, we identified aquatic insects only to genus level because many immature stages of aquatic insects in Brazil are undescribed (Mugnai et al. 2010, Hamada et al. 2014). However, genus-level identification is usually enough to represent the main biodiversity patterns (Heino and Soininen 2007, Oliveira et al. 2020). Finally, another possible limitation of our study was the coarse information on traits of aquatic insects in Brazil. This limitation prevented the use of more traits and affinities (e.g., 0 to no affinity and 3 to high affinity) of each genus of aquatic insects to trait categories (i.e., "fuzzy coding"; Chevenet et al. 1994), which could have created more variability among aquatic insect assemblages and, consequently, among streams within watersheds. However, the selected traits should be adequate to show aquatic insects' responses to land use, and similar sets of traits have been extensively used in previous studies (e.g., Colzani et al. 2013, Castro et al. 2018).

Final considerations

Overall, we showed that stream insect assemblages had higher taxonomic beta diversity in a low-latitude region, whereas stream insect functional beta diversity was similar between subtropical and boreal regions. We also found that neither taxonomic nor functional beta diversity was homogenized by increasing total land use in these 2 climatically different regions. We highlight that 1) taxonomic beta diversity is not a proxy for functional beta diversity in comparisons between high-latitude and low-latitude regions and 2) land-use effects on beta diversity are still controversial, requiring additional investigations across distinct regions.

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