

1 **LRH: Land-use effects on beta diversity** D. K. Petsch et al.

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

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36

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

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

57

58 One of the most widely documented patterns in ecology is the latitudinal gradient of
59 diversity, i.e., species richness decreases from the equator towards the poles (Gaston
60 2000, Brown 2014). Whereas higher species richness in the tropics is a well-known
61 pattern, it is still controversial as to whether beta diversity (i.e., variation in community
62 composition among sites) is also higher at low latitudes (see Qian and Ricklefs 2007,
63 Kraft et al. 2011, Qian and Song 2013). For example, while Qian and Ricklefs (2007)
64 found lower plant beta diversity in higher latitudes compared to lower latitudes, Kraft et
65 al. (2011) found no differences in plant beta diversity across a latitudinal gradient.

66 Biodiversity has been changing globally because of anthropogenic activities.
67 Land use change, for example, is a worldwide cause of biodiversity loss across different
68 ecosystems (Newbold et al. 2015, 2016). Land use intensity may drive taxonomic and
69 functional homogenization of communities (i.e., decrease in spatial beta diversity
70 through time) by promoting the expansion of tolerant species and the elimination of
71 sensitive species (McKinney and Lockwood 1999, Castro et al. 2018, Dornelas et al.
72 2019). Tolerant and sensitive species may respond differently to land use change
73 because they typically have different environmental requirements (Verberk et al. 2010,
74 Heino and Grönroos 2014), which may be mediated by different biological traits
75 (Gossner et al. 2016, Jonason et al. 2017). The analysis of both taxonomic and
76 functional diversity can, thus, improve our understanding of how biological
77 communities respond to land use (Castro et al. 2018, Roa-Fuentes et al. 2019). For
78 example, land use intensification may have more severe effects on taxonomic diversity
79 than on functional diversity, especially if communities are composed of many
80 functionally redundant species (Sfair et al. 2016). Alternatively, land use intensification
81 may decrease functional diversity more severely if disturbed sites gain resistant and
82 widespread species that share the same set of traits (Mori et al. 2015). Functional

83 homogenization is especially worrisome, as it may limit the ecosystem functions and
84 services provided by biological communities (Cardinale et al. 2012, Gámez-Virués et al.
85 2015).

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

104 To assess potential latitudinal variation in beta diversity and explore the
105 influence of land use on this diversity, we conducted a large-scale survey of aquatic
106 insects in boreal and subtropical streams covering a wide gradient of land use in each
107 region. First, we investigated whether taxonomic and functional beta diversities within

108 watersheds differ between the 2 regions. Second, we tested whether total land use
109 intensification decreases (biotic homogenization), increases (biotic differentiation), or
110 does not change taxonomic and functional beta diversities of aquatic insects in both
111 regions. We also explored the influence of local environmental heterogeneity and land-
112 use heterogeneity on aquatic insect beta diversity.

113

114 **METHODS**

115 **Study area and sampling design**

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

122 We sampled Finnish streams in September 2014, during the beginning of the
123 Northern Hemisphere autumn, and Brazilian streams between September and November
124 2015, during the Southern Hemisphere spring. We selected a short sampling period in
125 Finland because of strong seasonal changes in insect composition in that region, and
126 September is the period when most aquatic insect larvae are well developed. In Brazil,
127 we chose a period of low rainfall (i.e., beginning of the wet season) and, consequently,
128 with no intense floods. The longer sampling period in Brazil than in Finland probably
129 did not influence our results given there is low seasonality in our tropical region (Melo
130 and Froehlich 2001).

131 Streams in Brazil and Finland were surrounded by a wide variation of land use
132 configurations, from watersheds dominated by monoculture to watersheds covered

133 almost entirely by near-pristine forests. In Brazil, we surveyed streams located in the
134 southeastern region of the country between latitudes 23°49'S and 24°20'S (with a spatial
135 extent of ~120 km in the east-west direction and 70 km in the north-south direction).
136 The main land uses in Brazil were related to exotic tree plantations (*Eucalyptus* and
137 *Pinus* spp.), agriculture, and pastures (Fig. S2). Pristine streams in Brazil were located
138 in watersheds covered by Atlantic Rainforest within 3 important protected areas: Carlos
139 Botelho, Intervales, and Alto Ribeira State Parks. In Finland, we sampled streams
140 located in the western part of the country between latitudes 60°27'N and 65°01'N (study
141 area extending ~500 km in the north-south direction and 300 km in the east-west
142 direction). The main land uses in Finland were agriculture, managed forests, and
143 urbanization (Fig. S2). The pristine streams were within watersheds covered by boreal
144 forests dominated by *Pinus sylvestris* and *Picea abies*. For more details about the study
145 areas, see Heino et al. (2018) and Siqueira et al. (2020). It should be noted that, despite
146 the larger geographical extent of the areas sampled in Finland, we based our analyses on
147 beta diversity among streams within watersheds and not among streams distributed over
148 the study area, minimizing the effects of the differing geographical extents.

149

150 **Biological data**

151 We used standardized field methods for collecting biological data in Brazil and Finland.
152 In both countries, we sampled 1 riffle site in each stream by using a kick-net (net mesh
153 size = 0.5 mm) for 2 min (four 30-s subsamples). Using a stereo microscope (model
154 Olympus SZX10 in Finland and Leica M165 C in Brazil), we identified all sampled
155 aquatic insects from the following orders to genus level: Ephemeroptera, Plecoptera,
156 Trichoptera, Coleoptera, Odonata, and Megaloptera. We based our identifications on
157 Domínguez & Fernández (1996), Domínguez et al. (2006), Heckman (2006a,b), Pes et

158 al. (2006), and Ribeiro (2013) for Brazilian aquatic insects and on Lillehammer (1988),
159 Engblom (1996), Meinander (1996), Norling & Sahlen (1997), and Wallace et al.
160 (2003) for Finnish aquatic insects. We selected 6 biological traits of aquatic insects that
161 may be affected by land use: refuge building, body shape, locomotion, functional
162 feeding group, respiration, and body size (see Table S1). For example, reductions in
163 riparian forest cover could decrease the number of shredders (Cummins et al. 1989),
164 while streambed siltation could increase the number of burrowers (Castro et al. 2018).
165 We classified, in a similar way for Brazil and Finland, the collected aquatic insects
166 according to each biological trait. We compiled Brazilian and Finnish insect trait
167 information mainly from the literature (see Table S2) and by consulting a number of
168 regional specialists (see Acknowledgments).

169

170 **Local environmental data**

171 We collected local environmental data to characterize our study streams. In each
172 stream site, we measured flow velocity (m/s) and depth (cm) at random locations (30
173 per stream in Finland and 9 per stream in Brazil). The number of sites per stream was
174 chosen based on the 2 field crews' decisions regarding how much effort was sufficient
175 to characterize their study sites. We estimated mean stream width (m) of each sampled
176 riffle site based on 10 measurements (Finnish streams) or 3 measurements (Brazilian
177 streams). We visually estimated particle size classes in 0.25 m² squares at random
178 locations in each riffle site (10 per riffle in Finland and 3 per riffle in Brazil). We used a
179 modified Wentworth's (1922) scale of particle size classes: sand (0.25–2 mm), gravel
180 (2–16 mm), pebble (16–64 mm), cobble (64–256 mm), and boulder (256–1024 mm).
181 We reported each particle size class as a percentage of the square. We also estimated
182 shading (canopy cover %). In Finland, we made these estimates by looking through a

183 tube (~5 cm diameter) at 10 points per stream site. In Brazil, we estimated riparian
184 vegetation in the visual field of the observer at 3 points per stream site. We measured
185 pH and conductivity at each stream in the field with a multiparameter YSI 556 MPS
186 probe (YSI Inc., Ohio) in Finland and Horiba device U-50 series in Brazil. We took
187 water samples to analyze total nitrogen and total phosphorus following standard
188 protocols for Finland (Finnish Board of Waters and the Environment 1981) and Brazil
189 (Golterman et al. 1978, Mackereth et al. 1978). A detailed description of the field and
190 laboratory methods can be found in Heino et al. (2018) and Siqueira et al. (2020).

191

192 **Land cover data**

193 We characterized the land use and land cover for each of the watersheds in our
194 study. We mapped land use and land cover (LULC) of Brazilian watersheds by
195 manually digitizing over 5-m spatial resolution orthorectified RapidEye multispectral
196 imagery (Planet 2016). For Finnish watersheds, we used the pre-existing CORINE
197 LULC dataset (Copernicus 2016). We standardized the land cover nomenclature among
198 datasets, which resulted in the following LULC categories: native forest,
199 secondary/managed forest, exotic/planted forest, pasture, agriculture, urban, mining,
200 wetland, bare soil, water, and mixed. We established a 500-m radius around each
201 sampling site and manually delineated the stream segments contained within this radius
202 using hydrological and topographic data as well as high-resolution imagery from the
203 Google Earth™ database. We then generated a buffer of 200 m width along each stream
204 segment (100 m downstream and 100 m upstream from a sampling site). We calculated
205 the proportion of land use attributed to each LULC category within the buffer of each
206 stream. Data on insect abundance, local environmental variables, and land cover are
207 archived in Zenodo (<https://doi.org/10.5281/zenodo.2620550>).

208

209 Taxonomic and functional beta diversity

210 We estimated taxonomic and functional beta diversities of aquatic insects among
211 5 streams in each watershed. We made these estimates separately for Brazil and Finland
212 ($n = 20$ beta diversity values for each region). Sørensen and Bray–Curtis dissimilarity
213 coefficients are simple and common metrics for beta diversity estimation that are based
214 on incidence and abundance data, respectively (Legendre and Legendre 2012). Both
215 metrics are, however, affected by differences in species richness. To control for such
216 differences, total beta diversity can be partitioned into 1 component related to species
217 replacement across sites (i.e., the turnover component of dissimilarity) and another
218 component related to nestedness (i.e., differences in species richness across sites;
219 Baselga 2010). We focused on the turnover component because we were interested in
220 the replacement of genera among sites. Moreover, the turnover components of beta
221 diversity are often much larger than the nestedness components in ecological datasets
222 (Soininen et al. 2018; in our study: mean contributions of nestedness components for
223 Finland and Brazil, respectively, were 4.25 and 4.44% based on the Sørensen coefficient
224 and 4.16 and 5.16% based on the Bray–Curtis coefficient). We used 2 dissimilarity
225 metrics to calculate taxonomic beta diversity: the turnover component of the Sørensen
226 index (i.e., the Simpson index) and the turnover component of the Bray–Curtis index.
227 We log-transformed abundance data before computing the turnover component of Bray–
228 Curtis. We used the `beta.pair` function in the *betapart* package in R (Baselga et al. 2013,
229 R Core Team 2017) to obtain the turnover and nestedness components of both the
230 Sørensen and Bray–Curtis indices.

231 To calculate functional beta diversity, we first used the modified Gower distance
232 on the genus–traits matrix (separately for Brazil and Finland) to obtain a matrix of

233 genus-by-genus functional distances (Pavoine et al. 2009, Pavoine and Ricotta 2014).
234 We calculated functional beta diversity twice, once with incidence data and once with
235 abundance data. We used the *ade4* package in R (Dray and Dufour 2007) and the code
236 provided by Pavoine and Ricotta (2014) for functional beta diversity estimations.

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

244

245 **Modeling beta diversity along land use and environmental heterogeneity gradients**

246 To explore how aquatic insect beta diversity may be influenced by heterogeneity
247 in land use and environmental characteristics, we modeled beta diversity along land use
248 and environmental heterogeneity gradients. We obtained the mean proportion of each
249 LULC category among the 5 streams in each watershed. Hereafter “total land use”
250 refers to the summed proportion of secondary forests, exotic planted forests, pasture,
251 agriculture, and urban land cover in each watershed. We estimated land use
252 heterogeneity within each watershed (proportions of native forest, secondary/managed
253 forest, exotic planted forests, pasture, agriculture, urban, mining, wetland, bare soil,
254 water, and mixed) with a procedure similar to that used to estimate beta diversity. This
255 procedure was based on the mean distance from streams to their group centroid in a
256 principal coordinates ordination space (PERMDISP; Anderson et al. 2006). The
257 ordination was based on the standardized Euclidean distance matrix of land use. We

258 used the same procedure to estimate local environmental heterogeneity (based on stream
259 width, shading, sand, gravel, pebble, cobble, boulders, current velocity, depth, pH,
260 conductivity, nitrogen, and phosphorus).

261 We built multiple regression models with beta diversity at the watershed level as
262 the response variable (1 model for each beta diversity metric) and region, total land use,
263 land use heterogeneity, and local environmental heterogeneity at the watershed level as
264 predictor variables. We also included interactions between region and total land use,
265 region and land use heterogeneity, and region and local environmental heterogeneity.
266 Because our response variables followed a beta distribution (i.e., they ranged between 0
267 and 1), we used beta regression models (Ferrari and Cribari-Neto 2004). We fitted the
268 models using the *betareg* function from the *betareg* package in R (Cribari-Neto and
269 Zeileis 2010). Our R code can be found as supplementary material.

270

271 **RESULTS**

272 Our watersheds covered a wide range of total land use, ranging from 0 to ~75%,
273 in Brazil and in Finland. Agriculture (0.128 ± 0.172 in Brazil and 0.406 ± 0.209 in
274 Finland; mean proportion \pm standard deviation) and urbanization (0.016 ± 0.03 in Brazil
275 and 0.087 ± 0.057 in Finland) covered larger areas in Finland, whereas native forests
276 (0.546 ± 0.278 in Brazil and 0.371 ± 0.235 in Finland), pasture (0.06 ± 0.102 in Brazil
277 and 0.007 ± 0.02 in Finland), and planted forests (0.156 ± 0.163 in Brazil and $0.0002 \pm$
278 0.0007 in Finland) covered larger areas in Brazil (Fig. S2). The proportion of
279 secondary/managed forests was similar between countries (Fig. S2). Total land use
280 (modified area at watershed in Brazil: 0.367 ± 0.237 and in Finland: 0.502 ± 0.251 ; Fig.
281 S3A), land use heterogeneity (mean distance to centroid in Brazil: 0.215 ± 0.128 and in
282 Finland: 0.196 ± 0.059 ; Fig. S3B), and local environmental heterogeneity (mean

283 distance to centroid in Brazil: 2.534 ± 0.541 and in Finland: 2.532 ± 0.609 ; Fig. S3C)
284 were similar between the regions. Total land use was positively related to higher land
285 use heterogeneity only in Brazil (adj. $R^2 = 0.312$; $p < 0.001$; Fig. S4A), but it was not
286 related to local environmental heterogeneity in either country (Fig. S4B). Also, land use
287 heterogeneity was not related to local environmental heterogeneity in Brazil or Finland
288 (Fig. S4C).

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

293 We found higher taxonomic beta diversity among subtropical streams than
294 among boreal streams based on the turnover components of both the Sørensen ($F_{1,38} =$
295 18.47 ; $p < 0.001$; Fig. 1A) and the Bray–Curtis dissimilarities ($F_{1,38} = 8.34$; $p = 0.006$;
296 Fig. 1B). However, we did not find differences between subtropical and boreal streams
297 with the nestedness component of either the Sørensen ($F_{1,38} = 0.44$; $p = 0.514$; Fig. S5A)
298 or the Bray–Curtis dissimilarity ($F_{1,38} = 0.17$; $p = 0.686$; Fig. S5B). Functional beta
299 diversity was similar among subtropical and boreal streams based on both incidence
300 ($F_{1,38} = 1.695$; $p = 0.201$; Fig. 1C) and abundance data ($F_{1,38} = 1.29$; $p = 0.263$; Fig. 1D).

301 We found that total land use had a strong positive correlation with all measures
302 of beta diversity in subtropical streams (turnover component of Sørensen: Pseudo $R^2 =$
303 0.445 ; $p < 0.001$; turnover component of Bray–Curtis: Pseudo $R^2 = 0.451$; $p < 0.001$;
304 functional based on incidence: Pseudo $R^2 = 0.287$; $p < 0.001$; functional based on
305 abundance: Pseudo $R^2 = 0.274$; $p < 0.001$). However, this relationship was not detected
306 in boreal streams (Figs 2A, D, G, and J). Our different measures of beta diversity were
307 unrelated to land use heterogeneity in either region (Figs 2B, E, H, and K). We found a

308 positive relationship between environmental heterogeneity and taxonomic beta diversity
309 (for both incidence and abundance data) only in the boreal region (Figs. 2C, F), but this
310 relationship was weak and disappeared when the watershed with the highest
311 environmental heterogeneity was removed from the analyses. We found no relationship
312 between environmental heterogeneity and functional beta diversity in either region
313 (Figs. 2I and L; Table 1). Finally, the nestedness components of the Sørensen and Bray–
314 Curtis dissimilarities were not related to any predictor variable (Table S3).

315

316 **DISCUSSION**

317 We investigated whether taxonomic and functional beta diversity differ between
318 subtropical and boreal regions, and we examined the relationship between beta
319 diversities and total land use, local environmental heterogeneity, and land-use
320 heterogeneity. Our results indicate that taxonomic and functional beta diversities were
321 not congruent between the regions. We found higher taxonomic beta diversity in Brazil
322 but similar functional beta diversity between the 2 regions. We did not find a substantial
323 negative relationship between beta diversity and land use intensification, which would
324 be consistent with a process of biotic homogenization. Instead, we found a positive
325 relationship between beta diversity (both taxonomic and functional) and total land use
326 in subtropical streams. We also found a weak positive relationship between beta
327 diversity and local environmental heterogeneity in boreal streams.

328

329 **Subtropical and boreal taxonomic and functional beta diversity comparison**

330 The existence of latitudinal gradients of taxonomic and functional beta diversity
331 is under discussion in the literature, and the occurrence of latitudinal gradients in
332 functional beta diversity, in particular, is not well established. Most of the evidence for

333 these latitudinal gradients comes from terrestrial and marine systems (Qian and Ricklefs
334 2007, Kraft et al. 2011, Qian and Song 2013), whereas less is known about freshwater
335 systems (but see García-Girón et al. 2020). Our findings contribute to answering the
336 question of whether there are latitudinal gradients in species turnover (Koleff et al.
337 2003; see also Qian and Ricklefs 2007 for other studies showing the same pattern). We
338 found that taxonomic beta diversity mimics the well-known latitudinal pattern in alpha
339 diversity: a decrease from low (subtropical) to high (boreal) latitudes. However, our
340 findings did not show differences in insect functional beta diversity between subtropical
341 and boreal streams. This result suggests higher functional redundancy in subtropical
342 streams because subtropical streams, despite being more taxonomically variable than
343 boreal streams, had similar functional variability.

344 The mechanisms behind the latitudinal pattern of beta diversity are unclear.
345 However, we cannot rule out the possibility that the lower taxonomic beta diversity in
346 boreal streams, as compared to subtropical streams, is related to climatic extremes and
347 dispersal. Boreal streams are climatically harsh in terms of high variability in
348 temperature and hydrological conditions (Heino 2011, Hortal et al. 2011). Beta diversity
349 is thought to be lower in harsh habitats because only reduced sets of tolerant species are
350 likely to thrive in such habitats, consequently decreasing among-site variability in
351 species composition. Another possible explanation for the lower taxonomic beta
352 diversity in boreal streams is that boreal aquatic insects may be good dispersers.
353 Because high-latitude areas were totally covered by ice during the last Ice Age (i.e.,
354 until ~12,000 years ago; Pielou 1991), most species that have been able to reach these
355 high-latitude areas after glaciation must have relatively strong dispersal capabilities
356 (Hof et al. 2006, 2008, Dehling et al. 2010, Homburg et al. 2013). High dispersal rates
357 may homogenize among-site variation in local community composition within a

358 metacommunity (Mouquet and Loreau 2003). It is unlikely that a difference in local
359 environmental heterogeneity explains our finding of higher beta diversity in subtropical
360 than in boreal streams because environmental heterogeneity did not differ between the
361 streams located in Finland and Brazil (Fig. S3C).

362 We believe that fine-grained field data (a strength of our work) are crucial to
363 showing the prevalence (or lack) of latitudinal patterns in beta diversity (Beck et al.
364 2012; see also De Cáceres et al. 2012 and Myers et al. 2013 for other studies with
365 tropical and temperate forests using fine-grained data). Most previous studies
366 investigating such patterns were based on data obtained from atlases, which may
367 include comparisons among data obtained in different ways (Rodríguez and Arita 2004,
368 McKnight et al. 2007, Melo et al. 2009; but see Soininen et al. 2007). By using large-
369 scale field studies, our approach allowed us to compare beta diversity among boreal and
370 subtropical streams through a standardized method, avoiding different sampling bias
371 among regions. In addition,, many previous studies have shown that latitudinal
372 differences in beta diversity were simply due to sampling effects (Kraft et al. 2011, De
373 Cáceres et al. 2012, Myers et al. 2013). However, our results were produced using
374 metrics that accounted for at least some of these effects (e.g., the turnover components
375 of total beta diversity indices that minimize the effect of differences in species richness).

376

377 **Land-use effects on taxonomic and functional beta diversity**

378 While the negative effects of land use intensification on stream species richness
379 have been frequently observed (Corbi et al. 2013, Martins et al. 2017), its effect on beta
380 diversity in streams is still controversial. Some studies have found a negative effect of
381 total land use on beta diversity (e.g., Passy and Blanchet 2007, Maloney et al. 2011,
382 Siqueira et al. 2015), but others have shown a positive effect (e.g. Hawkins et al. 2015,

383 Fugère et al. 2016, Roa-Fuentes et al. 2019) or have failed to find a relationship (e.g.,
384 Larsen and Omerod 2014) in stream ecosystems. Using 2 contrasting climatic regions
385 with different predominant land use (i.e., agriculture and urban areas in Finland and
386 planted forests, agriculture, and pasture in Brazil), we did not find a negative
387 relationship between beta diversity and total land use in the watersheds, which would
388 have indicated a process of biotic homogenization. Instead, we found a positive
389 relationship between total land use and beta diversity in subtropical streams (but more
390 studies are necessary to understand why beta diversity increased with total land use only
391 in Brazil). Similarly, Johnson and Angeler (2014) also observed higher taxonomic beta
392 diversity of macrophytes and benthic diatoms in rural streams because identities of
393 tolerant species differed among modified streams, thereby creating high beta diversity.
394 Although we did not specifically investigate this possibility, it is plausible that different
395 land uses selected different tolerant species, producing increased beta diversity in
396 Brazil.

397 Land use change may increase environmental heterogeneity among streams if it
398 results in differences in disturbance intensity or land use types in the same watershed
399 (Barboza et al. 2015, Fugère et al. 2016). Different land use types may be indirectly
400 related to high environmental differentiation among streams and, consequently, result in
401 distinct community composition with taxa adapted to local environmental conditions
402 (Siqueira et al. 2015). For example, Hawkins et al. (2015) and Fugère et al. (2016)
403 found higher taxonomic beta diversity of macroinvertebrate assemblages in disturbed
404 streams, as compared to undisturbed ones, and suggested among-taxon differences in
405 stress tolerance as the underlying mechanism (see also Mykrä and Heino 2017). We
406 found a positive relationship between total land use and land use heterogeneity in
407 subtropical streams (Fig. S4A), but we did not find a positive relationship between land

408 use heterogeneity and environmental heterogeneity. However, the streams in watersheds
409 with heterogeneous land use could differ in other environmental features that were not
410 included in our measure of local environmental heterogeneity, such as amount of
411 organic matter or increased concentrations of contaminants.

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

426

427 **Caveats**

428 We recognize some potential caveats of our study. First, we did not include
429 midges and flies (Diptera) despite their high abundance and species richness in some
430 freshwater ecosystems (Ferrington 2008, Dijkstra et al. 2014). However, compared to
431 other macroinvertebrate taxa, dipterans, like those belonging to the family
432 Chironomidae, usually show similar or lower sensitivity to changes in environmental

433 conditions (Rabeni and Wang 2001). Thus, we had no strong reasons to expect their
434 inclusion would change the conclusions of our study, and given that the identification of
435 dipteran larvae often demands considerable efforts (including the examination of
436 mouthparts under a microscope), we chose not to include them. Second, we identified
437 aquatic insects only to genus level because many immature stages of aquatic insects in
438 Brazil are undescribed (Mugnai et al. 2010, Hamada et al. 2014). However, genus-level
439 identification is usually enough to represent the main biodiversity patterns (Heino and
440 Soininen 2007, Oliveira et al. 2020). Finally, another possible limitation of our study
441 was the coarse information on traits of aquatic insects in Brazil. This limitation
442 prevented the use of more traits and affinities (e.g., 0 to no affinity and 3 to high
443 affinity) of each genus of aquatic insects to trait categories (i.e., “fuzzy coding”;
444 Chevenet et al. 1994), which could have created more variability among aquatic insect
445 assemblages and, consequently, among streams within watersheds. However, the
446 selected traits should be adequate to show aquatic insects’ responses to land use, and
447 similar sets of traits have been extensively used in previous studies (e.g., Colzani et al.
448 2013, Castro et al. 2018).

449

450 **Final considerations**

451 Overall, we showed that stream insect assemblages had higher taxonomic beta
452 diversity in a low-latitude region, whereas stream insect functional beta diversity was
453 similar between subtropical and boreal regions. We also found that neither taxonomic
454 nor functional beta diversity was homogenized by increasing total land use in these 2
455 climatically different regions. We highlight that 1) taxonomic beta diversity is not a
456 proxy for functional beta diversity in comparisons between high-latitude and low-

457 latitude regions and 2) land use effects on beta diversity are still controversial, requiring
458 additional investigations across distinct regions.

459

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464 functional traits of aquatic insects. TSFS produced the land use/land cover datasets and
465 designed the land cover sampling method surrounding sampled streams. DKP ran the
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482

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757 **FIGURE CAPTIONS**

758

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

768

769 Fig. 2. Relationships between beta diversity and total land use (the proportion of
770 modification in each watershed; A, D, G, J), land use heterogeneity (the mean distance
771 to centroid based on land use classes; B, E, H, K), and local environmental
772 heterogeneity (the mean distance to centroid on local environmental variables; C, F, I,
773 L) among subtropical (black) and boreal streams (grey) in 20 watersheds in Brazil and
774 20 watersheds in Finland. We used the turnover component of the Sørensen
775 dissimilarity, the turnover component of the Bray–Curtis dissimilarity, functional
776 dissimilarity based on incidence, and functional dissimilarity based on abundance data
777 as beta diversity metrics. pa = incidence data; ab = abundance data. Lines indicate
778 substantial interactions with region (subtropical [black] and boreal [grey]) as shown in
779 Table 1.

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781

782

783 Table 1. Results from beta regression models for taxonomic (using the turnover
 784 component of the Bray–Curtis and Sørensen dissimilarities) and functional (using
 785 incidence and abundance data) beta diversity in relation to region (boreal and
 786 subtropical), total land use (the proportion of modification in each watershed), land use
 787 heterogeneity (the mean distance to centroid based on land use classes), and
 788 environmental heterogeneity (the mean distance to centroid on local environmental
 789 variables) in 40 watersheds (20 watersheds in Finland and 20 watersheds in Brazil). SE
 790 = standard error. Bold values indicate $p < 0.05$.

	Estimate	SE	Z-value	<i>p</i>
Turnover Sørensen dissimilarity	<i>Pseudo R²=0.445; p < 0.001</i>			
Intercept	-1.268	0.388	-3.266	0.001
Region	-1.008	0.551	-1.829	0.067
Total land use	0.783	0.426	1.839	0.066
Land use heterogeneity	0.563	0.774	0.727	0.467
Local environmental heterogeneity	-0.107	0.140	-0.765	0.444
Region × Total land use	-1.477	0.581	-2.544	0.011
Region × Land use heterogeneity	-1.792	1.664	-1.077	0.281
Region × Local environmental heterogeneity	0.658	0.213	3.088	0.002
Turnover Bray–Curtis dissimilarity	<i>Pseudo R²=0.451; p < 0.001</i>			
Intercept	-1.203	0.324	-3.716	<0.001
Region	-0.496	0.453	-1.094	0.274
Total land use	0.912	0.349	2.612	0.009
Land use heterogeneity	-0.199	0.643	-0.310	0.757
Local environmental heterogeneity	-0.015	0.117	-0.126	0.899

Region × Total land use	-1.509	0.473	-3.191	0.001
Region × Land use heterogeneity	-1.524	1.368	-1.114	0.265
Region × Local environmental heterogeneity	0.445	0.177	2.518	0.012
Incidence-based functional dissimilarity				<i>Pseudo R²=0.287; p < 0.001</i>
Intercept	-3.451	0.711	-4.852	<0.001
Region	-0.269	0.971	-0.277	0.782
Total land use	2.412	0.732	3.295	0.001
Land use heterogeneity	-1.452	1.334	-1.089	0.276
Local environmental heterogeneity	-0.067	0.256	-0.262	0.793
Region × Total land use	-3.102	0.994	-3.119	0.002
Region × Land use heterogeneity	0.800	2.825	0.283	0.777
Region × Local environmental heterogeneity	0.492	0.374	1.315	0.188
Abundance-based functional dissimilarity				<i>Pseudo R²=0.274; p < 0.001</i>
Intercept	-3.534	0.778	-4.543	<0.001
Region	-0.254	1.054	-0.241	0.810
Total land use	2.553	0.786	3.249	0.001
Land use heterogeneity	-1.839	1.446	-1.272	0.203
Local environmental heterogeneity	0.005	0.280	0.018	0.986
Region × Total land use	-3.089	1.070	-2.886	0.004
Region × Land use heterogeneity	1.422	3.038	0.468	0.640
Region × Local environmental heterogeneity	0.440	0.404	1.090	0.276