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**TROPICAL STREAM DIATOM COMMUNITIES — THE IMPORTANCE OF
HEADWATER STREAMS FOR REGIONAL DIVERSITY**

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10 **Abstract**

11

12 Understanding how species are distributed in space and time is a focal element guiding conservational
13 efforts under the ongoing climate change and Holocene extinction. Freshwater habitats are currently
14 one of the most threatened ecosystem types and studies aiming to unravel factors that govern
15 biodiversity of tropical stream micro-organisms are especially scarce. Diatoms play an important role
16 as primary producers in streams and are widely used as ecological indicators. Yet, relatively little is
17 known about which factors affect diatom communities in the tropics.

18 Here, we studied benthic diatom diversity across 67 tropical streams spanning stream orders 1 – 5 in
19 Kenya. We examined whether the hypothesis of latitudinal diversity gradient applies for benthic
20 diatoms, i.e. do tropical streams encompass more species than boreal streams using comparable boreal
21 dataset. In addition, we studied which environmental, land use and spatial factors control benthic
22 diatom communities using redundancy analysis. We also examined the nestedness and turnover
23 components of beta diversity, factors contributing to diatom species richness and the uniqueness of
24 the communities across stream orders by using boosted regression trees and local contribution to beta
25 diversity. Finally, we studied whether environmental heterogeneity and beta diversity are related
26 across stream orders and tested their relationship using tests of homogeneity of dispersion and
27 regression analysis.

28 Species richness was not higher in tropical streams than in boreal ones. Tropical diatom communities
29 were controlled jointly by local environmental and spatial factors. Although water chemistry was the
30 most important controlling factor, also physical variables contributed significantly to community
31 variation. Land use had also a significant effect on diatom communities as broad leaved forest streams
32 harboured different diatom communities compared to streams with higher human impact and
33 conductivity, stressing the importance of forests to water quality and diatom biodiversity. Headwater
34 streams encompassed highest species turnover, whereas nestedness was higher in higher order

streams. Species richness was significantly higher in higher order streams than in headwaters, whereas the uniqueness of the communities peaked in headwaters. Environmental heterogeneity was the highest in headwater streams and was related with high beta diversity, which highlights the importance of habitat heterogeneity to biodiversity. Our results stress the management and conservational importance of headwater streams and tropical montane forests as these environments harbour unique diatom communities important for regional diversity.

Keywords: beta diversity, community structure, diatoms, environmental heterogeneity, headwaters, tropics

1. Introduction

How species are distributed across Earth in space and time remains a fundamental topic guiding conservation efforts under the ongoing climate change and Holocene extinction (Pimm *et al.*, 1995; Thomas *et al.*, 2004). Extinction threat concerns not only terrestrial ecosystems but also aquatic communities. Freshwater habitats harbour disproportionately large species richness in relation to habitat area in many taxonomic groups and freshwater biodiversity is more threatened than biodiversity in other ecosystems (IUCN, 2009; Strayer and Dudgeon, 2010; Wiens, 2016). Thus, understanding of the drivers that maintain species diversity is urgently needed in order to combat severe biodiversity losses taking place at present.

While studies aiming to unravel the determinants of macro-organismal biodiversity have been extensive (Rosenzweig, 1995), microbial communities (e.g. bacteria, unicellular algae and fungi) have received less attention in this regard (Green *et al.*, 2004; Zeglin, 2015). For example, whereas

latitudinal diversity gradients are well documented for macro-organisms (Gaston, 2000; Hillebrand, 2004; Lawton, 1999), the existence of such pattern for micro-organisms remains a controversial issue (Hillebrand and Azovsky, 2001; Passy, 2010; Salinas *et al.*, 2015). Furthermore, microbial biodiversity studies in boreal and temperate regions have been far more numerous than in the tropics but see for example (Bellinger *et al.*, 2006; Bere, 2014; Bojorge-Garcia *et al.*, 2014; Mangadze *et al.*, 2015).

The diversity and composition of microbial communities are affected by a wide range of determinants and there is still no consensus whether the key drivers are more related to the local environment (Gothe *et al.*, 2013; Maloufi *et al.*, 2016) or spatial factors (Crump *et al.*, 2007; Soininen *et al.*, 2004). Also land use (Bere and Tundisi, 2011; Carpenter and Waite, 2000) or climatic factors (Pajunen *et al.*, 2016) may affect aquatic microbial communities. Finally, spatial scale of the study influences the factors which govern microbial communities (Lindstrom and Langenheder, 2012) and communities may thus often be described by the shared influence of spatial and environmental factors with increasing spatial influence in larger studies (Heino *et al.*, 2014; Soininen *et al.*, 2016; Verleyen *et al.*, 2009).

Freshwater organisms may be especially vulnerable to changes in precipitation and possible droughts can quickly alter the freshwater habitat and thus their biodiversity (Wiens, 2016). Streams encompass disproportionately high biodiversity (Vinson and Hawkins, 1998; Vorosmarty *et al.*, 2010) and stream network provides an excellent environment to study diversity patterns via its hierarchic dendritic organization (Grant *et al.*, 2007). River Continuum Concept (RCC) predicts biological diversity to peak at mid-order streams, whereas headwaters and large rivers should be less diverse (Vannote, 1980). However, while this prediction might hold true for alpha (local) diversity, beta (between-site) and gamma (regional) diversity may show different patterns as especially headwater streams (orders 1–2) may harbour a great proportion of biodiversity compared to higher order stream branches (Meyer *et al.*, 2007). Moreover, human induced disturbances usually increase with increasing stream order

83 (Januchowski-Hartley *et al.*, 2011), which may affect biodiversity. Headwater streams may also be
84 more physically variable promoting environmental heterogeneity and subsequently also beta diversity
85 (Finn *et al.*, 2011). Consequently, possible environmental homogenisation in higher order streams
86 may decrease beta diversity compared to headwaters.

87 High beta diversity in headwaters may also be caused partly by the more isolated position of
88 headwater streams compared to higher order branches (Finn *et al.*, 2011). Thus, highly connected
89 sites at lower reaches harbour lower beta diversity due to higher exchange of individuals between
90 sites leading to homogenisation of communities (Lopes *et al.*, 2014). Furthermore, anthropogenic and
91 natural stressors may cause different patterns to beta diversity given that beta diversity under natural
92 disturbances may be caused more by species turnover (i.e. the shared number of species between sites
93 is small), whereas community dissimilarities under anthropogenic stressors may be more generated
94 by nestedness (i.e. poorer assemblages are subsets of those of richer sites) (Gutierrez-Canovas *et al.*,
95 2013). These patterns are largely unresolved in tropics, however, as stream beta diversity has not been
96 studied extensively in tropical regions (but see (Al-Shami *et al.*, 2013; Tonkin *et al.*, 2016) and
97 microbial communities have received even less attention.

98 Sub-Saharan Africa is going through an intense land cover change due to human population growth
99 and subsequent cuts of forests into arable land (Brink *et al.*, 2014; Pellikka *et al.* 2017a). Land cover
100 changes can have severe effects to the environment and natural resources (Alcantara-Ayala *et al.*,
101 2006; Hohenthal *et al.*, 2015). Furthermore, land use changes in the catchments may have profound
102 effects also on aquatic ecosystems via water scarcity, increased turbidity and nutrient fluxes (Allan
103 and Castillo, 2007; Hohenthal *et al.*, 2015; Soininen *et al.*, 2015). Human impact on stream
104 communities usually grow downstream, agricultural effects causing the most severe threat to
105 biodiversity (US - Environmental Protection Agency, 2000; Vorosmarty *et al.*, 2010). The detrimental
106 anthropogenic effects are increased by the poor waste water treatment in many rural areas (Concoran

107 *et al.*, 2010). Indeed, freshwater biodiversity conservation under the increasing human demands of
 108 water poses a true challenge (UNESCO, 2009; Wiens, 2016; Vorosmarty *et al.*, 2010).

109 Benthic diatoms are a pivotal component of stream biodiversity and are widely used as ecological
 110 indicators (Hill *et al.*, 2000; Wang *et al.*, 2005). We studied the diversity and composition of stream
 111 benthic diatom communities in Taita Hills, Kenya. The area is considered as a biodiversity hotspot
 112 with a high rate of endemism of plants (Beentje and Ndiang'ui, 1988; Gereau *et al.*, 2006; Lovett and
 113 Wasser, 1993) and animals (Gereau *et al.*, 2006). At the same time, however, the area is affected by
 114 intensive land use change along with other anthropogenic pressures threatening ecosystems and their
 115 functioning (Pellikka *et al.*, 2013; Pellikka *et al.*, 2009). First (Q_1), we were interested if there are
 116 major richness differences between tropical and boreal stream diatoms. We thus compared diatom
 117 species richness between tropical and boreal streams using two data sets with identical sampling
 118 methods. We expected that species richness is higher in tropics as found for other taxa (Hillebrand,
 119 2004). Second (Q_2), we studied the effects of local environmental, land use and spatial factors on
 120 tropical stream diatom community composition. We expected water chemistry and stream physical
 121 variables to have a significant effect on diatom composition (Soininen, 2007) but also that
 122 communities are spatially structured (Piano *et al.*, 2017). In addition, we expected land use to affect
 123 diatom communities indirectly via affecting water quality (Bere and Tundisi, 2011; Carpenter and
 124 Waite, 2000; Potapova and Charles, 2002). We considered the use of the diatoms and their diversity
 125 as ecological indicators of land cover change by sampling diatoms in four massifs of the Taita Hills
 126 of Kenya, which differ in their land use history, but are similar in their bedrock, soil types, forest
 127 species composition, agricultural crop composition and climate. Thirdly (Q_3), we studied the
 128 distribution of diatom biodiversity across stream orders. We expected headwater sites (orders 1–2) to
 129 harbour more unique diatom communities, and simultaneously, to have lower species richness than
 130 higher stream order sites (Meyer *et al.*, 2007; Sherwood *et al.*, 2000). We also examined beta diversity
 131 components, i.e., species turnover and nestedness across stream orders and expected species turnover

132 to be largest in headwaters while nestedness to be largest in downstream sites. Fourthly (Q₄), we
 133 examined factors contributing to diatom species richness and the uniqueness of the communities. We
 134 expected that species richness is mostly related to conductivity (Heino *et al.*, 2010) and pH
 135 (Jyrkänkallio-Mikkola *et al.*, 2017) whereas uniqueness would be most related to conductivity and
 136 nutrient levels (Pajunen *et al.*, 2017). Finally (Q₅), we studied whether environmental heterogeneity
 137 and diatom beta diversity are related across stream orders and tested their relationship. We expected
 138 headwater streams to harbour higher beta diversity and environmental heterogeneity (Finn *et al.*,
 139 2011; Meyer *et al.*, 2007) than sites at higher order streams.

140 In this study, we characterized diatom communities using species richness, community composition
 141 and the uniqueness of species composition at sites, measured as local contribution to beta diversity
 142 (LCBD; (Legendre and De Caceres, 2013). Since beta diversity provides the most useful measure to
 143 understand the processes that generate and maintain biodiversity (Legendre *et al.*, 2005; Qiao *et al.*,
 144 2015; Socolar *et al.*, 2016) we placed most emphasis on beta (between site) diversity in terms of
 145 dissimilarities and local contribution to beta diversity.

146

147 **2. Material and methods**

148 **2.1. Study area**

149 Taita Hills is the northernmost part of the biodiversity hotspot Eastern Arc located in southeastern
 150 Kenya rising in the middle of plains to hilltops over 2000 m of an altitude (Platts *et al.*, 2011). Taita
 151 Hills can be separated to Dabida massif, Mbololo massif, Sagala Hill and Mt. Kasigau, which are
 152 within 40 km from each other. The mean elevation of Dabida is between 1300 to 1600 m a.s.l., the
 153 highest peaks reaching over 2000 m a.s.l. Mbololo massif reaching 1800 m is located east from
 154 Dabida separated by Paranga valley at 900 m a.s.l. Sagala Hill reaching 1500 m a.s.l. is located 15
 155 km southeast from Dabida and Mbololo, and Mt. Kasigau reaching 1600 m a.s.l. at 40 km southeast

156 from Dabida (Fig. 1). Located in the intertropical convergence zone Taita Hills face bimodal rain
157 pattern having rainy season in November-December and in March-May. Annual rainfall in the hills
158 is normally 1200 mm, while the lowlands receive less than 600 mm per year resulting to rule of the
159 thumb that higher elevations have higher rainfall and are covered more by forests than lower
160 elevations (Erdogan *et al.*, 2011). However, as the rains are orographic in nature, the eastern slopes
161 and hills of Mbololo and Dabida receive more precipitation than the leeward parts and slopes located
162 in the west. A significant addition to the precipitation is occult precipitation, which is estimated to
163 result in 20% addition to precipitation, but only in the forests as forest volume is required to capture
164 the atmospheric moisture, the mist (Pellikka *et al*, 2017b).

165

166 Figure 1 Map of the sampling area

167 It is estimated that the hills over approximately 1220 m a.s.l. prior human disturbance were covered
 168 by forests characterized as evergreen moist lower or upper montane forests. Now only a few percent
 169 of the montane forests are left mainly as protected forests managed by Kenya Forest Service. Below
 170 1220 m a.s.l. the forests can be characterized as Acacia-Commiphora woodland, which is partly
 171 deciduous depending on the species. The hills are cleared for intensive small-scale agriculture the

172 main crop being maize producing to harvest per year (Jaetzold and Schmidt, 1987). The lowlands are
 173 used for dryland farming, grazing by goats and camels, sisal plantations and conservation areas.

174 The four massifs studied differ in their land use. Based on Pellikka *et al.* 2017a, only the hilltops of
 175 Dabida and Mbololo massifs are covered by montane forests. Due to cloudy conditions, the peak of
 176 Vuria (2208 m a.s.l.) is characterized as upper montane forest, elfin forest, with trees covered heavily
 177 by epiphytes (Stam *et al.*, 2017), while the other native forests are lower montane forests with less
 178 epiphytes, but trees reaching up to 40 m of a height. Over 1220 m a.s.l. in 241 km² of an area,
 179 croplands cover nowadays 40.4 %, montane forests 3.2 % and plantation forests of mainly pine and
 180 eucalyptus 10.1%, and woodland, shrubland and thickets all together 44.8% (Pellikka *et al.* 2017a).
 181 The remaining fragments of montane forests in Dabida and Mbololo massifs are 1–2 km² in size:
 182 Mbololo (185 ha), Ngangao (120 ha), Vuria (ha) and Chawia (86 ha) being the largest ones. These
 183 forests are all degraded due to selective timber harvesting and grazing inside of the forest, especially
 184 in Vuria and Chawia. The least degraded is Mbololo forest and then Ngangao (Omoro *et al.*, 2013).

185 Sagala hill has no native montane forests left, but has some plantation forests and degraded
 186 woodlands. The montane forest of Mt. Kasigau can be characterized as upper montane forest over
 187 1500 m a.s.l. due to misty conditions producing fog deposit, and lower montane forest down to 1000
 188 m a.s.l. (Medley and Maingi, 2014) below which dryland forest like Acacia-Commiphora with
 189 Euphorbia ssp. takes place. The montane forest of Kasigau is least disturbed of all the forests of the
 190 Taita Hills being 2.03 km² in size (Medley and Maingi, 2014). Croplands did exist in Mt. Kasigau
 191 few decades ago, but were abandoned in order to safeguard water resources (Rikkinen *et al.*, 2015).
 192 Evidently due to very steep slopes they were also difficult to manage (Adhikari *et al.* submitted).

193

194 **2.2. Biological data collection**

195 Diatom samples were collected at 67 sites from all four mountain massifs (Fig.1). Sampling was
 196 completed in three weeks in January 2016. Diatoms were sampled by randomly selecting and
 197 brushing 10 cobble-sized stones or bedrock. The samples were collected from different part of the
 198 stream site in order to control small-scale variability in the community composition. To standardize
 199 the sampling area we used a 5×5 cm rubber template. The samples were preserved with 99% ethanol
 200 and stored at $+4$ °C. Wet combustion with hydrogen peroxide (20%, H_2O_2) was used to clean diatom
 201 frustules from organic material. Subsequently, samples were mounted on microscope slides using
 202 high-refractive mounting resin Naphrax. We counted and identified at least 500 frustules from each
 203 sample using phase contrast light microscope with $1000 \times$ magnification. Species identification was
 204 based on Krammer and Lange-Bertalot (1986-1991) and Taylor *et al.* (2007).

205

206 **2.3. Chemical and physical measurements**

207 Water samples for total nitrogen, total phosphorus and water colour were collected a few meters
 208 upstream from each sampling site. Total nitrogen was determined by using alkaline persulfate
 209 digestion where alkaline oxidation is carried out in a thermo digester and the converted total nitrogen
 210 quantified colorimetrically. Total phosphorus was determined by inductively coupled plasma-optical
 211 emission spectrometry (ICP-OES). However, as the method lacked the sensitivity to determine
 212 phosphorus concentrations below $10 \mu\text{g L}^{-1}$ and the phosphorus content of 51 samples were $\leq 10 \mu\text{g}$
 213 L^{-1} we were unable to use total phosphorus in the following analyses. Water colour was analysed
 214 using standardized method (EN ISO7997).

215 To measure conductivity, pH and temperature in the field we used YSI professional plus water quality
 216 meter (YSI Incorporated, Yellow Springs, USA). Current velocity was measured with Schiltknecht
 217 MiniAir 2 flow meter (Schiltknecht, Gossau, Switzerland) from 30 locations covering the sampling

218 site extensively. Water depth was similarly measured from 30 locations and stream width from 10
 219 locations covering the length of the whole sampling site.

220 Substratum particle size was measured from 10 locations using a 50×50 cm quadrat placed in random
 221 sites on the streambed. We used a modified Wentworth scale to visually classify the substratum
 222 particle size: sand (diameter 0.25 mm – 2 mm), gravel (2 mm – 16 mm), pebble (16 mm – 64 mm),
 223 cobble (64 mm – 256 mm) and boulder (>256 mm) (Wentworth, 1922). Canopy shading was
 224 individually estimated from 20 locations covering the whole sampling site. Range and average values
 225 of measured environmental variables are listed in Appendix A in the supplementary material.

226

227 **2.4. Stream order analyses and land cover data**

228 River network and stream ordering were calculated from Digital Elevation Model (DEM) data. DEM
 229 of 1×1 m resolution was derived from airborne laser scanning (ALS) data sets for two parts of the
 230 study area (Taita Hills and Kasigau). Laser scanning data was acquired in 2013 and 2014 (using
 231 Optech ALTM 3100), and data was filtered for buildings, powerlines and outliers using Terrascan
 232 software (Terrasolid Oy), LasTools (Rapidlasso GmbH) and manual editing. For Sagala area, a DEM
 233 was created from scanned Survey of Kenya 1:50 000 scale topographic map from which the contour
 234 lines were digitized and converted to 10 m resolution raster DEM.

235 Watershed delineation was based on the DEM layers and, hydrological modelling tools in ArcGIS
 236 10.3.1. Firstly, elevation grids were filled to create a surface that has no sinks. Then, flow direction
 237 grid was calculated to determine the direction of flow for each cell in the landscape. Flow
 238 accumulation function was used to generate a drainage network for the selected pour points. The Snap
 239 Pour Point tool was used to ensure selection of points of high accumulated flow and finally,
 240 watersheds were automatically delineated. ArcGIS 10.3.1 hydrological tools and Stream Order
 241 function with Strahler method (Strahler, 1957) were used to determine stream ordering from the river

242 networks. Elevation models were harmonized by resampling the DEM layers into 10 m pixel size.
 243 River networks were then determined again and stream ordering calculated.

244 Land cover was assessed from classifies satellite imagery separately for Taita Hills, Kasigau and
 245 Sagala. For Taita Hills, the land cover classification was based on a 20×20 m resolution SPOT 4
 246 satellite image from 23 October 2011 (CNES, 2013). The satellite image was classified into 9 land
 247 cover classes (Pellikka *et al.*, 2017; Appendix A in the supplementary material) using an object-based
 248 approach (Benz *et al.*, 2004) following the methodology presented in Clark and Pellikka (2009).
 249 Segmentation and classification was implemented in the eCognition software (Trimble). After manual
 250 corrections, the overall accuracy of the land cover map was 71.1% when comparing the map with 305
 251 random ground-truth points.

252 For Sagala area, Sentinel-2A MSI Level-1C satellite image from 8 October 2016, downloaded from
 253 the Sentinel's Scientific DataHub (ESA, 2015) and RandomForest (Breiman, 2001) classifier in R
 254 software were used to create the land cover classification. Firstly, Sentinel-2A was DOS1 atmospheric
 255 corrected using Semi-Automatic Classification Plugin in QGIS. Then, classifier training areas were
 256 on-screen digitized from very high-resolution (1 m pixel size) image mosaic from 2004 and from
 257 more up to date satellite imagery (Google Earth, 2016). Then, reflectance values from the four bands
 258 blue, green, red and infra-red from the Sentinel 2A satellite image were used as the predictors for
 259 RandomForest classifier. The image was classified to the following relevant classes: bush, fields,
 260 forest and impervious.

261 For the Kasigau area, information from the same Sentinel 2A satellite image was combined with
 262 canopy height model (CHM) and DEM derived from the ALS data for creating the land cover
 263 classification map. First, the CHM was reclassified to 5 elevation classes in ArcGIS 10.3.1. NDVI
 264 (normalized difference vegetation index) values derived from the Sentinel-2A satellite image were
 265 used to separate non-vegetated areas from different type of green areas. Then, Kasigau study area was
 266 classified into highland and lowland zones based on the 1 m pixel size DEM to separate montane

267 vegetation from lowland vegetation after which ArcGIS Map Algebra tool was used to derive land
 268 cover classes listed in Appendix A in the supplementary material. The resulting land cover map was
 269 evaluated using GPS field measurements, very high resolution airborne imagery (1 m pixel size) and
 270 also the previous knowledge of the area. Prior to statistical analyses, the land cover classes of the 6
 271 sampling sites from Sagala and Kasigau were equated with those classified from Taita Hills. Finally,
 272 zonal statistics of the percentages of land use and land cover classes were calculated for different
 273 watershed areas based on the land cover layers and delineated watersheds for the whole study region.
 274

275 **2.5. Statistical analyses**

276 Prior to analyses, explanatory variables measured as percentages were arcsine-transformed while
 277 other explanatory variables were log-transformed. In addition, diatom abundance data were Hellinger
 278 transformed to better meet the requirements of linear ordination methods (Legendre and Gallagher,
 279 2001). Correlations between explanatory variables were tested using Pearson correlation. As none of
 280 the correlations exceeded 0.70, we kept all the explanatory variables in the subsequent models
 281 (Dormann *et al.*, 2013).

282 Failure to notice spatial autocorrelation can lead to false interpretations of environmental variables'
 283 effects on community composition. Thus, spatial autocorrelation of the local environmental variables
 284 and species richness was tested using function correlog in the R package 'pgirmess' (Giraudoux,
 285 2015). The significance of the correlogram was tested at level $P \leq 0.05$ with applied Bonferroni
 286 correction (P/k , where k is the number of distance classes used). Here, distance class of 7 km was
 287 used as it was most suitable for the spatial distances in our data.

288 To test whether more species are found from the tropics than boreal areas (Q_1), species accumulation
 289 curves (function specaccum in the R package 'vegan'; (Colwell and Coddington, 1994; Palmer,
 290 1990)) were used. The used boreal stream diatom data are explained in detail in Jyrkänkallio-Mikkola

291 *et al.* (2017). To standardize the number of sampling sites, 67 samples from the boreal data originally
 292 comprising 105 sites were chosen. First order Jackknife method was used to estimate the total species
 293 richness for both biomes.

294 To model spatial structures among tropical study sites, distance-based Moran's eigenvector maps
 295 (dbMEM) derived from spatial coordinates (function dbmem in the R package 'adespatial'; (Dray *et*
 296 *al.*, 2017)) were used. Threshold value was calculated using function give.thresh. Only eigenvectors
 297 with positive autocorrelation were used to model spatial effects in subsequent analyses.

298 Redundancy Analysis (RDA) was applied to study community structure (abundance data)-
 299 environment (excluding land use) relationships (Q_2) for the whole tropical dataset (Legendre and
 300 Legendre, 2012). Another RDA was conducted exclusively for 39 independent sites (i.e., sites that
 301 had independent catchments) to examine the effects of land use and catchment size on the diatom
 302 communities. Stepwise model (forward selection) with 200 permutations was used to create final
 303 RDA models (function ordiR2step in the R package 'vegan'; (Oksanen *et al.*, (2015))).

304 Distribution of biodiversity across stream orders (Q_3) was studied with a set of analyses. To study the
 305 uniqueness of diatom community composition across sites, local contribution to beta diversity
 306 (LCBD) was calculated for each site (function beta.div in the R package 'adespatial'; (Legendre and
 307 De Caceres, 2013)). The analysis was based on abundance data for which Hellinger dissimilarity
 308 coefficient was applied and the analysis was run with 999 permutations. Linear regression was applied
 309 to study the relationship between species richness and LCBD across sites and how richness and LCBD
 310 varied across stream orders. To study whether different dissimilarity components govern diatom beta
 311 diversity across stream orders, species turnover, nestedness and total beta diversity were calculated
 312 for two groups of stream orders, 1-2 and 3-5, respectively (function beta.multi in the R package
 313 'betapart' (Baselga *et al.*, 2017)).

314 To explain variation in species richness and LCBD using environmental variables (Q₄), boosted
 315 regression trees (BRT; function `gbm` in R package ‘`gbm`’, (Elith *et al.*, 2008)) were used. Tree
 316 complexity was set to 3, learning rate to 0.001 and bagging fraction to 0.75. The benefits of this
 317 machine learning technique include, that it can be run with raw values, it takes into account
 318 interactions between predictors and has small prediction errors (Elith *et al.*, 2008).

319 Test of homogeneity of dispersion (PERMDISP, function `betadisper` in the R package ‘`vegan`’
 320 (Anderson, 2006; Anderson *et al.*, 2006)) was applied to relate environmental heterogeneity (habitat
 321 variables) within stream orders with corresponding variation in diatom community composition (Q₅).
 322 Sørensen coefficient was used for presence-absence data and Euclidean distances were applied for
 323 standardized habitat variables. PERMDISP tests among group differences from individual
 324 observation to their group centroid using ANOVA F-statistics (Anderson *et al.*, 2006). Null
 325 hypothesis that there is no difference in diatom beta diversity and environmental heterogeneity among
 326 the different stream orders was tested. All tests were run using 999 permutations. Finally, null
 327 hypothesis that there is no relationship between the degree of beta diversity and the degree of
 328 environmental heterogeneity across the different stream orders was tested using linear regression.

329 Explained variation in RDA and linear regressions were reported using adjusted R²- values. All
 330 analyses were conducted in R version 3.2.2 (R Development Core Team, 2013) using packages
 331 ‘`adespatial`’ (Dray *et al.*, 2017), ‘`betapart`’ (Baselga *et al.*, 2017), ‘`corrplot`’ (Wei and Simko, 2016),
 332 ‘`dismo`’ (Hijmans, 2015), ‘`gbm`’ (Ridgeway, 2013), ‘`pgirmess`’ (Giraudoux, 2015) and ‘`vegan`’
 333 (Oksanen *et al.*, 2015).

334

335 3. Results

336 Altogether 297 taxa were identified from 67 tropical sites, of which 104 were found from only one
 337 site. Local diatom species richness varied from 15 to 71 in the tropical data set. The random selection

338 of 67 sampling sites from comparative boreal dataset resulted in taxa richness of 303. Species
 339 accumulation curves revealed that there was only a minor difference in the proportion of total species
 340 richness for boreal (76.4%) and tropical (74.6%) datasets (Q₁; Appendix B in the supplementary
 341 material).

342 Out of local environmental variables, only water temperature and stream width showed significant
 343 spatial autocorrelation on short distances (Appendix C in the supplementary material). Species
 344 richness showed no spatial autocorrelation. dbMEM returned one spatially autocorrelated eigenvector
 345 (referred henceforth as MEM1), that was used to model spatial structures among sites in the
 346 subsequent RDA and BRT analyses.

347 In the first RDA (67 sites), forward selection method returned seven significant ($P < 0.05$) variables
 348 which together explained 15.6% of the total community variation (Q₂, Fig.2a). Conductivity and pH
 349 were among the most important variables for diatom composition. Also the physical variables
 350 (shading and gravel), spatial (elevation and MEM1) and stream order were among the significant
 351 variables structuring the community. The first RDA-axis divided the sites with high conductivity, pH
 352 and high stream order opposite to those with high elevation. The second RDA-axis was mostly related
 353 to shading. We further tested whether removing singletons would increase the explained variation in
 354 community composition. This resulted only to minor increase (15.9%) of the explained variation with
 355 the same explaining variables. When presence-absence data were used explanatory power decreased
 356 to 10.9%. In the second RDA (39 sites) including land use variables, selection method returned four
 357 ($P < 0.05$) significant variables which explained 14.4% of the total community variation (Q₂, Fig.
 358 2b). The first RDA-axis divided the sites to those with high percent of broad leaved forest and high
 359 elevation opposite to those with high conductivity.

360

361 Figure 2 Ordination plots for redundancy analysis for A) all 67 sampling sites and environmental variables and B) for
 362 39 sites with independent catchment areas and environmental and land use variables. Both ordination plots are based on
 363 Hellinger transformed diatom abundance data. Arrows represent the significant environmental variables. The explained
 364 variation is based on adjusted R^2 . Abbreviations: MEM1 (spatial eigenvector derived from distance-based Moran's
 365 eigenvector maps)

366

367 According to linear regression, species richness increased significantly with increasing stream order
 368 (Q_3 , Fig.3a, $P < 0.001$, $R^2 = 0.142$), whereas LCBD values showed an opposing trend with the highest
 369 values in headwater streams (Q_3 , Fig.3b, $P < 0.05$, $R^2 = 0.053$). LCBD and species richness showed
 370 significant negative relationship (Q_3 , Fig. 3c; $P < 0.001$, $R^2 = 0.425$). Total beta diversity was higher
 371 in headwater streams (Q_3 , orders 1-2, $\beta_{sor} = 0.933$) than in higher order streams (orders 3-5, $\beta_{sor} =$
 372 0.867). Beta diversity components varied across stream orders. As we expected, species turnover was
 373 higher in headwater streams (orders 1-2, $\beta_{sim} = 0.905$) than in higher order streams (orders 3-5, β_{sim}
 374 $= 0.860$), whereas nestedness was lower in headwater streams ($\beta_{nes} = 0.027$) than in higher order
 375 streams ($\beta_{nes} = 0.036$).

376

377 Figure 3 Boxplots representing the relationship between A) species richness and B) LCBD values and stream orders.
 378 Also shown is C) the linear relationship between LCBD and species richness. Abbreviations: LCBD (local contribution
 379 to beta diversity).

380

381 In BRT, the most important factors affecting species richness were pH, temperature, conductivity and
 382 spatial variable (MEM1) all of which showed positive relationship with species richness (Q₄, Fig.4a).
 383 Here, we also used polynomial regression and found that the relationship between species richness
 384 and temperature was unimodal ($P < 0.01$, Adj. $R^2 = 0.148$). According to BRT, the most important
 385 variables affecting LCBD were conductivity, temperature, water color and stream velocity (Q₄,
 386 Fig.4b). Conductivity, temperature and, pH were negatively related with LCBD, whereas water color
 387 scaled positively with LCBD (Fig. 4b).

388

389

390 Figure 4 Boosted regression tree summary showing the relative importance of each variable and related fitted function
 391 curves for the four most important variables on A) species richness and B) LCB values. Abbreviations: LCB (local
 392 contribution to beta diversity), MEM1 (spatial eigenvector derived from distance-based Moran's eigenvector maps)

393

394 PERMDISP revealed that there were significant differences in the degree of beta diversity ($P < 0.01$,
 395 $F = 6.55$) and environmental heterogeneity ($P < 0.05$, $F = 3.30$) among the stream orders (Q_5 , Fig.5a,
 396 b). Beta diversity and environmental heterogeneity were higher in headstreams than in higher order
 397 streams (Q_5 , Fig.5a, b). Albeit based on only five observations, we found a significant positive

relationship ($P < 0.05$, $R^2 = 0.736$) between the degree of beta diversity and environmental heterogeneity.

400

Figure 5 Boxplots representing the relationship of mean distances from group centroids and stream order based on homogeneity of dispersion analysis. Shown are diatom community compositional data using presence/absence and Sørensen dissimilarity (A) and environmental data using Euclidean distance (B).

404

4. Discussion

The tropical studies focusing on diatom community structure, species richness and beta diversity patterns and their underlying processes are still rare compared with the temperate and boreal studies. In addition, diatom diversity patterns along stream networks are also generally relatively poorly understood. Here, our results shed light on the patterns and controlling factors on these important and understudied issues and may be relevant for watershed management and biomonitoring.

411 Even if largely similar sampling methods and efforts were used, we revealed no clear differences in
 412 diatom species richness between tropical and boreal areas. As the sampling area of the boreal dataset
 413 was larger than the tropical, and as species richness usually increases with the size of the sampling
 414 area, we further tested the difference in species richness between boreal and tropical areas by choosing
 415 only the 67 southernmost sites of the boreal dataset in order to have more comparable sampling areas.
 416 This approach resulted in total species richness of 298 in boreal data set and the proportion of total
 417 species richness on species accumulation curve in 77.9%, which indicates that tropical and boreal
 418 streams seem not to differ in diatom species richness. Earlier literature about latitudinal diatom
 419 richness patterns have documented very variable richness gradients. Passy (2010) found the
 420 relationship of benthic diatom richness and latitude to be U-shaped in a study that comprised running
 421 waters of continental U.S.. Highest species richness was found from subtropics and temperate
 422 sampling sites and was related with nutrient resources rather than climate. A positive relationship
 423 between marine diatom species richness and decreasing latitude was found by Salinas *et al.* (2015),
 424 whereas Hillebrand and Azovsky (2001) found no latitudinal effect for diatom species richness and
 425 suggested that latitudinal diversity gradient is determined by body size. Hence, our results add to the
 426 controversy of the subject and call for further investigation in different types of ecosystems.

427 Our results are congruent with previous studies suggesting that diatom communities are shaped by
 428 both environmental and spatial factors (Gothe *et al.*, 2013; Heino *et al.*, 2012; Heino *et al.*, 2014;
 429 Potapova and Charles, 2002; Soininen *et al.*, 2016; Verleyen *et al.*, 2009) indicating both
 430 environmental control and dispersal limitation. However, it cannot be excluded that the observed
 431 spatial structure here was caused by mass effects (i.e. due to high dispersal rates, a species can be
 432 present also in unfavorable sites, (Shmida and Wilson, 1985)) rather than dispersal limitation, due to
 433 the relatively small spatial scale (i.e. < 100 km) of the study and high connectivity among sites
 434 (Astorga *et al.*, 2012). In such conditions, mass effect may be caused by downstream drift of diatom
 435 cells (Gothe *et al.*, 2013).

436 Among local factors, our study highlighted the importance of water pH and conductivity for diatoms.
 437 Conductivity (Astorga *et al.*, 2012; Bere and Tundisi, 2011; Biggs, 1995) and water pH (Bere and
 438 Tundisi, 2011; Soininen *et al.*, 2004; Telford *et al.*, 2006) have been repeatedly found to be important
 439 controlling factors for diatoms also earlier in wide range of study regions, suggesting that these water
 440 chemistry factors are important for diatoms both in tropical and boreal regions. In addition, shading
 441 proved to be another important variable structuring diatom communities, a finding, that is further
 442 supported by Carpenter and Waite (2000), for example. Thus, although water chemistry plays an
 443 indisputable part in structuring diatom communities, it seems that also physical variables may be
 444 important, especially light conditions and the substrate of the stream bed. As similar findings emerged
 445 in boreal region as well (Jyrkänkallio-Mikkola *et al.*, 2016; Jyrkänkallio-Mikkola *et al.*, 2017), the
 446 importance of physical variables in structuring diatom communities applies also to the tropics, which
 447 could be important to take into account in biomonitoring.

448 As expected, land use affected diatom communities indirectly through water chemistry and our results
 449 suggest that forested high elevation sites including montane cloud forests harbored different diatom
 450 communities compared to those found at sites with high conductivity. Similar findings have also been
 451 reported by Carpenter and Waite (2000). Thus, including land use variables when unravelling factors
 452 controlling the diatom communities may be useful, since this approach provides long-term
 453 information of the surrounding habitat in addition to snapshot proximate controlling factors, i.e. water
 454 chemistry (Bere and Tundisi, 2011; Jyrkänkallio-Mikkola *et al.*, 2017). This finding also emphasizes
 455 the importance of montane cloud forests for regional aquatic diversity, and furthermore their
 456 conservational importance in general as they are of great importance to regional tree diversity, for
 457 example in the Taita Hills (Aerts *et al.*, 2011; Schafer *et al.*, 2016) and are currently the most
 458 threatened and one of the least studied tropical ecosystems (Williams-Linera, 2002).

459 The low explanatory power of direct ordination analyses such as RDA used here is common in
 460 microbial studies (Beisner *et al.*, 2006; Heino *et al.*, 2012; Nabout *et al.*, 2009). This might be related

461 to some unmeasured environmental variables although we find this explanation unlikely, since
462 probably the most influential factors structuring diatom communities were included in the analyses.
463 However, we admit that the inclusion of phosphorus might have increased the explanatory power of
464 the model. The surprisingly low phosphorus levels observed might be related to the fact that
465 phosphorus is a major limiting nutrient in old tropical soils (Reich and Oleksyn, 2004) and hence the
466 subsequent leach to the streams may be very low. The low explanatory power might also be due to
467 snap-shot measurements of the local environmental variables, which may not have reflected the
468 prevailing environmental conditions well enough. Indeed, the preceding amount of precipitation may
469 have had an effect on flow conditions, and subsequently, to the diatom community composition.
470 Community assembly mechanisms might also vary for example between generalists and specialists,
471 which may hinder the interpretation of environmental and community relationships (Lindstrom and
472 Langenheder, 2012).

473 As hypothesized, diatom species richness increased with stream order, which is also supported by
474 previous diatom studies (Sherwood *et al.*, 2000; Stenger-Kovacs *et al.*, 2014). Due to the lack of
475 stream sites above order 5, we cannot rule out the possible decrease in species richness in very large
476 streams and thus, the predicted unimodal pattern of species richness along the river network (RCC
477 theory). However, even if headwater streams harbored lower species richness they comprised more
478 unique communities than higher order stream sites. Headwater streams can be regarded as isolated
479 and less connected habitats compared to downstream sites and hence, the connectivity of the sampling
480 sites may have a strong effect on the community composition via the exchange of individuals (Lopes
481 *et al.*, 2014). High uniqueness of headwater assemblages have also been reported for
482 macroinvertebrates (Finn *et al.*, 2011), fish (Paller, 1994) and biofilm assemblages (Besemer *et al.*,
483 2013), stressing the conservational importance of headwater streams, contributing strongly to
484 regional gamma and beta diversity. Our results provide evidence that the high uniqueness of
485 headwater communities prevails also in the tropics, perhaps indicating that there are certain general

486 rules for predicting biodiversity (Finn *et al.*, 2011). This result is especially important in areas, where
 487 major changes in land use occur together with climate change and consequent draughts may
 488 deteriorate or even destroy fragile and important ecosystems such as montane forests. We note that
 489 our results are in contrast with the RCC view of headwaters harboring communities less important
 490 for stream biodiversity and hence, we think that our results are also important for stream ecology in
 491 general.

492 Agreeing with our findings, similar negative pattern between community uniqueness and species
 493 richness across sites has also been found in several biomes and for different organisms; tropical Brazil
 494 for dung beetles (da Silva and Hernandez, 2014), subtropical China for plants (Qiao *et al.*, 2015),
 495 temperate France for phytoplankton (Maloufi *et al.*, 2016) and boreal Sweden for macroinvertebrates
 496 (Heino *et al.*, 2017). Although Legendre and De Caceres (2013) point out that this negative
 497 relationship is not general or obligatory (see paper supporting this view for bacteria in the Canadian
 498 subarctic by (Comte *et al.*, 2016)), it seems to be a relatively common phenomenon at least.
 499 Furthermore, this finding suggests that species richness may not be the only or even the best diversity
 500 measure for conservational efforts (Dormann *et al.*, 2007), whereas community uniqueness might be
 501 in some circumstances more effective in this regard. We thus think that the combination of different
 502 metrics would probably be most informative approach in many ecosystems.

503 Of beta diversity components, species turnover was dominating, whereas nestedness was notably
 504 smaller. Similar results have been reported also by Wetzel *et al.* (2012) and Piano *et al.* (2017). In
 505 our study, it is probable that the high number of singletons contributed to the high turnover rate among
 506 sites while richness differences had smaller influence. Total beta diversity and species turnover were
 507 higher in headwater streams, whereas nestedness component increased downstream, as we expected.
 508 This finding may suggest that the increase of anthropogenic influence downstream changes also the
 509 relative effects of mechanisms contributing to beta diversity, thus supporting the results of Gutierrez-
 510 Canovas *et al.* (2013). Whereas conductivity, temperature and pH were included into the top five

most significant variables affecting species richness and LCBD, stream order played a minor role. As BRT takes into account interaction effects between variables, this finding suggests that conductivity, pH and water temperature were among the proximate factors causing the differences in diatom community composition between stream orders, as all these variables showed significant positive relationship with the stream order (Appendix D in the supplementary material). Thus, this finding is congruent with Stenger-Kovacs *et al.* (2014) who suggested that the stream order may act as a useful parameter summarizing the physical habitat in streams.

As hypothesized, diatom beta diversity and environmental heterogeneity were higher in headwater streams than in larger stream sites. Thus, our results provided evidence that along with a stronger dispersal limitation in headwaters, environmental heterogeneity may have promoted variation in diatom community composition in headwaters, suggesting that decreasing environmental heterogeneity downstream may at least partly cause subsequent decrease in diatom beta diversity towards larger streams. The higher environmental heterogeneity in headwater streams stresses their conservational importance for regional diversity, which gets support from other studies that have found higher habitat heterogeneity to increase beta diversity for planktonic diatoms (Zorzal-Almeida *et al.*, 2017) and phytoplankton in general (Maloufi *et al.*, 2016). Although we admit that the conservation of microbial organisms may not have as strong research need as conservation of larger taxa, similar results have also been reported for stream macroinvertebrates (Astorga *et al.*, 2014) emphasizing the effect of environmental heterogeneity to regional diversity. Consequently strong emphasis should be placed on headwater stream conservation and management in general.

531

5. Conclusions

Our results indicate that tropical streams do not seem to harbor more diatom species compared to boreal streams. Studies aiming to unravel the determinants of diatom communities are encouraged to

535 consider spatial, land use and physical variables in addition to water chemistry variables. Land use
 536 variables may affect diatom communities indirectly through water chemistry and can provide long
 537 term information of the surrounding habitat. Diatom species richness and the uniqueness of the
 538 communities may vary across stream orders with headwater sites encompassing more unique
 539 communities and higher order streams higher species richness. This results is important to take into
 540 consideration in biomonitoring and studies focusing on stream diatom species richness and
 541 community composition. Environmental heterogeneity seems to be higher in headwater streams and
 542 also relate with the degree of diatom beta diversity and, thus, our results emphasize the management
 543 and conservational importance of headwater streams.

544

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841 Appendix A List of measured environmental and land use variables (average values and ranges). * removed from
 842 multivariate analysis due to low concentrations, **removed from further analysis to avoid 100 % coverage of the
 843 variable group.

	Variable	Mean values	Range
Environmental variables (n=67)	Elevation (m)	1293.00	(713.00 – 1929.00)
	pH	7.90	(6.90 – 8.89)
	Conductivity (mSm ⁻¹)	120.28	(15.10- 408.70)
	Colour (Pt mg l ⁻¹)	9.02	(0 - 50)
	Total P(μg l ⁻¹) *	14.46	(<10.00 – 69.00)
	Total N (μg l ⁻¹)	698.06	(150.00 – 2380.00)
	Shading (%)	40.11	(0.00 – 96.30)
	Depth (m)	0.07	(0.01 - 0.23)
	Width (cm)	148.01	(17.00 – 1310.00)
	Velocity (ms ⁻¹)	0.17	(0.02 - 0.73)
	Sand (%)	46.17	(0.00 - 100.00)
	Gravel (%)	5.29	(0.00 – 46.50)
	Pebble (%)	4.66	(0.00 – 35.00)
	Cobble (%)	7.34	(0.00 – 49.50)
	Boulders (%)	9.11	(0.00 – 64.00)
	Moss (%)**	5.73	(0.00 – 90.00)
Land use variables (n=39)	Catchment area (km ²)	2.32	(0.14 – 25.58)
	Cropland (%)	38.00	(0.00 – 77.76)
	Shrubland (%)	1.93	(0.00 – 23.81)
	Thicket (%)	5.75	(0.00 – 39.14)
	Woodland (%)	21.10	(0.00 – 51.42)
	Plantation forest (%)	15.75	(0.00 – 41.56)
	Broadleaved forest (%)	14.70	(0.00 – 93.00)
	Bare soil and built areas (%)	1.10	(0.00 – 14.00)
	Bare rock (%)	1.50	(0.00 – 15.60)
	Water bodies (%)**	0.01	(0.00 – 0.41)

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846 Appendix B Species accumulation curves for A) boreal and B) tropical streams. The proportion of estimated species
 847 richness that 67 sampling sites covered is shown on the lower right corner.

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850 Appendix C Moran's I correlogram representing spatial autocorrelation for 15 environmental variables and diatom
 851 species richness. Black filled circles mark significant values of Moran's I and represent significant positive
 852 autocorrelation.

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Appendix D Boxplots representing the relationship of A) log transformed conductivity, B) pH, C) log transformed temperature and stream order.