

1 **Different species trait groups of stream diatoms show divergent responses to spatial and environmental**  
2 **factors in a subarctic drainage basin**

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17

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23 **Abstract**

24 Understanding the drivers of community structure is an important topic in ecology. We examined whether  
25 different species trait groups of stream diatoms (ecological guilds and specialization groups) show divergent  
26 responses to spatial and environmental factors in a subarctic drainage basin. We used local- and catchment-scale  
27 environmental and spatial variables in redundancy analysis and variation partitioning to examine community  
28 structuring. Local and catchment conditions and spatial variables affected diatom community structure with  
29 different relative importance. Local-scale environmental variables explained most of the variation in the low-  
30 profile and motile guilds, whereas local and spatial variables explained the same amount of the variation in the  
31 high-profile guild. The variations in the planktic guild and the specialist species were best explained by spatial  
32 variables, and catchment variables explained most variation only in generalist species. Our study showed that  
33 diatom communities in subarctic streams are a result of both environmental filtering and spatial processes. Our  
34 findings also suggested that dividing whole community into different groups by species traits can increase  
35 understanding of metacommunity organization.

36

37 **Keywords:** ecological guilds, ecological specialization, environmental filtering, spatial processes,  
38 metacommunity

39 **Introduction**

40

41 Understanding the drivers that shape community structure is a central theme in community ecology. These drivers  
42 can be studied in the context of a metacommunity (Leibold et al., 2004). A metacommunity is ‘a set of local  
43 communities that are linked by dispersal of multiple potentially interacting species’ (Wilson, 1992; Leibold et al.,  
44 2004). The concept of metacommunity is based on the notion that the variation in community structure is affected  
45 by both local-scale and large-scale environmental and spatial processes (Leibold et al., 2004; Holyoak et al.,  
46 2005). It has also been recognized that environmental filtering and dispersal are the fundamental processes  
47 structuring metacommunities (Lindström & Langenheder, 2012), as are also biological interactions (Cadotte &  
48 Tucker, 2017). Thus, metacommunity studies should focus on the relative roles of these processes (Heino et al.,  
49 2015).

50 The metacommunity has often been treated as a whole without any systematic division within different  
51 organismal groups (e.g. diatoms, macrophytes and macroinvertebrates). However, there is typically variation in  
52 biological and ecological characteristics between different species even if they belong to the same organismal  
53 group (Pandit et al., 2009). The effects of environmental and dispersal processes on local communities may depend  
54 on the differences in species traits in metacommunities. Thus, dividing data matrices into different groups by  
55 species traits can increase understanding of metacommunity organization (Lindström & Langenheder, 2012). This  
56 deconstructive approach has been increasingly applied in recent years when studying community patterns  
57 (Grönroos et al., 2013; Alahuhta et al., 2014; Algarte et al., 2014; Vilmi et al., 2017). One way to approach this is  
58 to split biological data matrices into smaller parts by dividing species into generalists and specialists based on  
59 species ecological specialization (Devictor et al., 2008; Pandit et al., 2009). For example, some studies have shown  
60 that environmental control is more dominant in specialist species while generalist respond mainly to spatial  
61 processes (e.g. Pandit et al., 2009), whereas other studies have shown different patterns, such as environmental  
62 control being dominant independent of specialization (e.g. Székely & Langenheder, 2014). Furthermore, several  
63 studies have produced divergent results regarding which factors are important in determining variation in  
64 community structure. According to Pandit et al. (2009), these divergent results can be due to different ratios of  
65 ecological specialization in different systems studied.

66 In addition to ecological specialization, biological data matrices can be divided into smaller parts using  
67 other biological traits, for example, growth forms and cell sizes (Heino & Soininen, 2006; Rimet & Bouchez,  
68 2012). In the study of freshwater algae, one approach is the use of different guild divisions (Göthe et al., 2013;

69 Vilmi et al., 2017). Many of these studies have used guild classification based on Passy's (2007) study. Originally,  
70 Passy (2007) proposed a diatom guild classification based on the potential of species to use nutrient resources and  
71 to resist physical perturbation. Rimet & Bouchez (2012) modified the classification and added one new guild  
72 corresponding to planktic species.

73 Different ecological guilds can be expected to respond in different ways to environmental and spatial  
74 processes. Several studies have shown that these guilds respond in different ways to environmental conditions  
75 both in lotic (Passy, 2007; Berthon et al., 2011; Rimet & Bouchez, 2012; Göthe et al., 2013) and lentic (Gottschalk  
76 & Kahlert, 2012; Vilmi et al., 2017) environments. However, the patterns found have not always been similar, as  
77 same guilds have shown dissimilar responses to environment in different studies. Also, these studies have been  
78 conducted mainly in areas with relatively high nutrient concentrations, and there is a lack of studies in nutrient  
79 poor, harsh subarctic stream environments (but see, Berthon et al., 2011).

80 In the freshwater realm, studying the relative roles of the environmental and spatial components in  
81 community composition is a commonly used approach for understanding metacommunity organization (De Bie  
82 et al., 2012; Alahuhta et al., 2014; Vilmi et al., 2016; Vilmi et al., 2017). The environmental components of  
83 community variation can be seen as illustrating environmental filtering and the importance of spatial variables  
84 may suggest dispersal as determinants of metacommunity structuring (Hájek et al., 2011). Since it is challenging  
85 to measure dispersal rates directly (Jacobson & Peres-Neto, 2010), spatial-based dispersal proxies are commonly  
86 used (e.g. Grönroos et al., 2013). Specifically, there is very little information available on the dispersal rates of  
87 diatom species, and it is particularly difficult to determine dispersal rates of these passively dispersing species  
88 directly.

89 Environmental filtering has been shown to be the main mechanism structuring metacommunities of various  
90 organisms in different environments (Van der Gucht et al., 2007; Heino et al., 2017). According to the hierarchical  
91 landscape filters model of Poff (1997), species from a regional pool must pass through a series of nested filters in  
92 hierarchical order to join a local community. Until recent years, there has been a prevailing idea that unicellular  
93 organisms are ubiquitously distributed (Finlay, 2002), environmental filtering is the main mechanism structuring  
94 also diatom communities and spatial factors have only minor effects on their community structure (Finlay &  
95 Fenchel, 2004; Soininen, 2012). This has been due to the consideration that diatoms have enormous population  
96 sizes (Finlay, 2002) and are efficient passive dispersers (Kristiansen, 1996). Nevertheless, spatial factors have  
97 been shown to be important structuring elements for diatoms (Hillebrand et al., 2001; Soininen & Weckström,  
98 2009; Heino et al., 2010), and they have been found to be important in determining diatom community structure

99 at continental (e.g. Potapova & Charles, 2002), regional (e.g. Heino et al., 2010) and watershed-scale (e.g. Göthe  
100 et al., 2013). However, many studies have also found that environmental conditions exceed spatial factors in  
101 importance for variation in community structure (e.g. Verleyen et al., 2009; Göthe et al., 2013). It has been  
102 suggested that the effects of spatial factors will increase with the spatial extent of the study area (Verleyen et al.,  
103 2009), and that the ratio of spatial and environmental components can be related to specific habitats (Soininen &  
104 Weckström, 2009). However, these can also be related to different ratios of ecological specialization (Pandit et  
105 al., 2009).

106 In this study, we examined the relative importance of environmental variables at local and catchment scale  
107 and spatial factors structuring stream diatom communities. Our aim was to study whether different species trait  
108 groups of stream diatoms show divergent responses to spatial and environmental factors and which processes are  
109 dominant in structuring a diatom metacommunity in subarctic streams. We tested whether responses to  
110 environmental and spatial variables varied between ecological guilds (i.e. high-profile, low-profile, motile and  
111 planktic guild) and between groups based on ecological specialization (i.e. generalists and specialists). Based on  
112 previous findings, we hypothesized the variation in the structure of the diatom communities as a whole to be  
113 related to both environmental and spatial variables (H<sub>1</sub>), but the environmental control to be more dominant (H<sub>2</sub>).  
114 We hypothesized weaker responses to the spatial variables due to the small study area (i.e. virtually no dispersal  
115 limitation). We also hypothesized that there would be variation in responses to environmental and spatial variables  
116 between the ecological guilds (H<sub>3</sub>), and that generalists and specialists would differ strongly in their responses to  
117 environmental and spatial variables (H<sub>4</sub>). We hypothesized that the environmental control would play a more  
118 important role in explaining the variation of specialist species (H<sub>5</sub>), and that the variation of generalist species  
119 would depend more on spatial factors (H<sub>6</sub>).

120

## 121 **Materials and methods**

122

### 123 *Study area*

124 This study was conducted in the Tenojoki drainage basin (centred on 70°N, 26°E). The drainage basin is located  
125 in northernmost Finland and Norway, and the main river, the River Tenojoki, flows to the Arctic Ocean (Fig. 1).  
126 The total area of the drainage basin is 16 386 km<sup>2</sup>. The study area had a mean annual temperature of -1.3 °C and  
127 a mean annual precipitation of 433 mm in the climatological normal period 1981–2010 (Pirinen et al., 2012). The  
128 study area is mainly in the subarctic deciduous birch zone and it is characterized by arctic-alpine vegetation

129 (Hustich, 1961). At higher altitude, barren fell tundra is typical and at low altitude there are mountain birch (*Betula*  
130 *pubescens* ssp. *czerepanovii*) woodlands. The study area consists mainly of Precambrian bedrock and the  
131 topography of the area is characterized by variable gently sloping fells (i.e. rounded mountains) (Mansikkaniemi,  
132 1970). Peatlands are located mainly in the valleys between fells and they are relatively rare. The percentage of  
133 lakes is quite low (3.1 %; Korhonen & Haavanlammi, 2012) at the study area, and therefore the streams have  
134 rapid fluctuations in discharge especially in the spring season (Mansikkaniemi, 1970). The area is very sparsely  
135 populated and anthropogenic influence is minimal. Thus, headwater streams in the drainage basin range from  
136 near-pristine to pristine (Schmera et al., 2013). Stream waters are circumneutral, and nutrient levels are indicative  
137 of highly oligotrophic systems (Heino et al., 2003).

138 A total of 55 streams from the Finnish side of the Tenojoki drainage basin were surveyed in early June  
139 2012. We aimed to sample all easily accessible sites that met the following criteria: (1) The length of a sampled  
140 stream must be at least 1 km. (2) The distance from the sampling site to a lake or a pond upstream had to be at  
141 least 0.5 km. (3) Only streams with permanent flow were included. (4) Large rivers (i.e. stream width >25 m,  
142 water depth >50 cm) were not included in order to get reliable and comparable samples. The size of the sampling  
143 site at each stream was approximately 50 m<sup>2</sup>. All 55 sampling sites are located in tributary streams and there are  
144 no sites in the main stem of the River Tenojoki. The distance between sampling sites furthest away from each  
145 other is 142 km.

146

#### 147 *Environmental variables*

148 Three types of explanatory variables were used: environmental variables at local and catchment scale (Table 1)  
149 and spatial variables. We decided to divide the environmental variables into two separate groups, as stream  
150 communities are structured by the hierarchical effects of environmental variables at different scales, e.g. local  
151 environmental and catchment variables (Poff, 1997). Local variables were determined at the same time with the  
152 diatom sampling. Variables included both physical habitat and water chemistry variables. Mean width of the  
153 sampling site (m) was determined based on five cross-channel measurements. Height of the lower stream bank  
154 (area of no terrestrial vegetation; cm) and steepness of the stream bank (area of terrestrial vegetation; cm) were  
155 measured at the same locations. Height of the lower stream bank was measured from the water level to the start  
156 of terrestrial vegetation. Steepness of the upper stream bank (how many centimetres the stream bank rises in two  
157 meters' distance from the stream) was measured perpendicular to the stream. Current velocity (m s<sup>-1</sup>) and depth  
158 (cm) were measured at 30 random locations in a sampling site. Moss cover (%) and particle size classes (%) were

159 visually estimated at 10 1 m<sup>2</sup> plots at random locations in each sampling site. A modified Wentworth's (1922)  
160 scale of particle size classes was used: sand (0.25–2 mm), gravel (2–16 mm), pebble (16–64 mm), cobble (64–  
161 256 mm) and boulder (256–1024 mm). Based on visual estimates (%) for each plot, mean values for each site  
162 were subsequently calculated and used in all statistical analyses. Shading (%) by riparian vegetation at each  
163 sampling site was also visually estimated. Conductivity and pH were measured in the field at each sampling site  
164 using YSI device model 556 MPS (YSI Inc., Yellow Springs, OH, USA). Water samples taken during fieldwork  
165 were analyzed for iron, manganese, colour and total nitrogen following European standards. In the study area,  
166 concentration of total phosphorus is mainly below the accuracy limits of the analysis methods used (< 5 µg/l) (e.g.  
167 Heino et al., 2003). Therefore, it was not analysed in this study.

168 The catchment variables of each stream were calculated using ArcGIS 10.1 software (ESRI, Redlands, CA,  
169 USA), and they were based on maps acquired from the National Land Survey of Finland (Table 1). These variables  
170 consisted of drainage basin area (km<sup>2</sup>), proportion of lakes (%), length of the stream (km) and lake distance index.  
171 Lake distance index was formed using the distance to the upstream lake. This index represents the influence of  
172 the lake. There were some streams that did not have a lake upstream, and for those streams a value two times the  
173 longest distance between sampling site and lake found in the study area was given to reflect zero influence.  
174 Additionally, proportion of peatlands (%), proportion of shrub (%) and proportion of rock and cobble deposit (%)  
175 were used to mirror natural background concentrations that influence water quality, as nutrients and other  
176 chemical components are leached from drainage basin to streams to a variable degree depending on land cover  
177 type.

178 In addition, variables representing productivity in catchment area were used: mean and standard deviation  
179 of the NDVI (*normalized difference vegetation index*; Tucker, 1979 and Tasseled Cap greenness (Crist & Cicone,  
180 1984). The mean and standard deviation of both variables were computed, as it has been proposed that mean  
181 values describe the average degree of productivity and standard deviation describes the variation of productivity  
182 (Parviainen et al., 2013). In addition to productivity, it has been proposed that these variables act as proxies for  
183 nutrients leaching from terrestrial areas to aquatic ecosystems (Soininen & Luoto, 2012). NDVI and greenness  
184 indexes were calculated from the Landsat 7 ETM scene (Hjort & Luoto, 2006).

185 Spearman's correlation test (cut-off level:  $r_s = 0.8$ ) was performed between all the environmental variables  
186 to avoid high correlations between variables. Pebble (16–64 mm), length of stream (km) and NDVI variables were  
187 excluded from further analyses based on strong correlations with other variables. There were also high correlations

188 between other variables, but because those variables belong to different variable groups (i.e. local or catchment),  
189 these correlations were not taken into account.

190

#### 191 *Sampling and processing diatoms*

192 Diatom sampling and processing was carried out in accordance with the European standard (SFS-EN 13946,  
193 2003). At each sampling site, diatoms were sampled from randomly collected cobble-sized stones from water  
194 depths of approximately 10 to 30 cm. The upper surface of the stones was scrubbed with a toothbrush and stream  
195 water, the water being pooled into one composite sample for each sampling site. In the laboratory, the diatom  
196 samples were cleaned from organic material using a strong acid solution (HNO<sub>3</sub>:H<sub>2</sub>SO<sub>4</sub>; 2:1) and mounted in a  
197 synthetic resin, Naphrax®. To determine the relative abundance of the diatom species, approximately 500 diatom  
198 valves were counted and identified to the lowest possible taxonomical level for each sample. This was done with  
199 a light microscope using differential interference contrast (1000× magnification). The identification and counting  
200 followed standard methods (SFS-EN 14407, 2005) using the Diatoms of Europe series (Lange-Bertalot, 2000,  
201 2001, 2002, 2011) and Lange-Bertalot (2011) flora and other specialized bibliographical data when needed.  
202 Taxonomic assignments could not be made for some valves and they were omitted from analyses.

203

#### 204 *Dividing diatom data matrices into different groups*

205 For dividing data matrices by species traits, diatoms were assigned into four ecological guilds reflecting their  
206 growth morphology. This was based on the classification made by Rimet & Bouchez (2011): low-profile, high-  
207 profile, motile and planktic guild. The low-profile guild includes species that grow very close to the substrate.  
208 These species are adapted to high current velocities and to low nutrient concentrations (Rimet & Bouchez, 2011).  
209 The high-profile guild includes species of tall stature. These species are adapted to low current velocities and high  
210 nutrient concentrations (Rimet & Bouchez, 2011). The motile guild includes species that can move actively  
211 relatively fast (Passy, 2007; Rimet & Bouchez, 2011). The planktic guild includes species that are adapted to  
212 lentic environments with morphological adaptations that enable them to resist sedimentation (e.g. *Cyclotella* spp.),  
213 and additionally nearly all filamentous diatom species (e.g. *Aulacoseira*) (Rimet & Bouchez, 2011).

214 Diatom species were also assigned into two groups, generalists and specialists, based on their ecological  
215 specialization. This was based on niche breadth measures determined previously by Heino & Soininen (2006) in  
216 northern Finland. The measure of niche breadth should preferably be based on a dataset different from the focal  
217 dataset in community-environment modelling. Heino & Soininen (2006) determined niche breadth that measures

218 amplitude in species habitat distribution using the Outlying Mean Index (OMI; Dolédec et al., 2000) analysis.  
219 This multivariate method measures the marginality of species habitat distribution, i.e. the distance between the  
220 mean habitat conditions used by a species and the mean habitat conditions across the study area (Dolédec et al.,  
221 2000). It provides two relevant niche measures, including OMI (i.e. niche position) and tolerance (i.e. niche  
222 breadth). The latter was hence used as a measure of environmental niche breadth in this study, following previous  
223 studies (Heino & Soininen, 2006; Heino & Grönroos, 2014).

224 The sites, in which species from all four guilds and generalist and specialist species were not found, were  
225 excluded from data analysis. Thus, there were 52 sites left for further analysis (Fig. 1). Since all the diatom species  
226 found in the study area were not included in Rimet & Bouchez's (2011) classification and Heino & Soininen's  
227 (2006) data, we formed a matrix that included all the species that belonged to any of the four guilds and another  
228 matrix that included all generalists and specialist species. Therefore, there were nine species matrices in total for  
229 further analyses (Table 2).

230

### 231 *Statistical methods*

232 To reveal spatial patterns at multiple spatial scales and address complex patterns of spatial variation, the method  
233 of Principal Coordinates of Neighbour Matrices (PCNM; Borcard & Legendre, 2002; Borcard et al., 2004; Fig. 2)  
234 was used. The PCNM analysis creates a number of spatial variables based on Euclidean (geographical) distances  
235 between sampling sites. The Euclidean distance matrix is analysed through a principal coordinate analysis to  
236 reveal spatial relationships among sites in decreasing order of spatial scale. The result are spatial variables  
237 representing spatial structures ranging from small to large-scale across a study area. The first variables with large  
238 eigenvalues represent broad-scale variation and the last ones with small eigenvalues represent finer-scale variation  
239 (Diniz-Filho & Bini, 2005). The PCNM analysis has been used increasingly to describe spatial patterns in various  
240 organism groups (e.g. Vilmi et al., 2017), as it is effective in modelling spatial structures in biological communities  
241 at multiple scales (Dray et al., 2012). The spatial structures represented by the PCNM variables can be the result  
242 of, for example, dispersal, historical factors, or spatial autocorrelation of environmental variables or biological  
243 interaction (e.g. Dray et al., 2012). However, it is also possible that using PCNM-variables in variation partitioning  
244 overestimates the spatial component (Gilbert & Bennett, 2010; Smith & Lundholm, 2010). Spatial variables were  
245 derived from the geographical coordinates of sampling sites using the function *pcnm* in the R package PCNM  
246 (Legendre et al., 2013). In this study, only spatial variables showing positive spatial autocorrelation were  
247 employed (Borcard et al., 2011). Analyses were additionally done using east and north coordinates of the sampling

248 sites instead of PCNM variables, but since the PCNM variables explained more of the variation in community  
249 structure, the coordinates were excluded from the analyses.

250 The effects of local, catchment and spatial scale variables on diatom community structure were quantified  
251 using redundancy analysis (RDA; Rao, 1964; Fig. 2). This method evaluates how much of the variation in  
252 community structure can be explained by these variable groups. The pure and shared variations were analysed  
253 using variation partitioning through the partial redundancy analysis (pRDA; Borcard et al., 1992; Fig. 2). The aim  
254 in variation partitioning is to reveal how much of the variance in species community structure can be explained  
255 uniquely by each explanatory variable group as well as the shared variance explained by different combinations  
256 of these variable groups. Also, the unexplainable variation is revealed. With three groups of explanatory variables,  
257 the result is eight different components of variation (Fig. 3; Anderson & Gribble, 1998).

258 First, all species matrices were Hellinger-transformed, since the species data contained many zeros and  
259 this transformation enables the use of linear methods (Legendre & Gallagher, 2001; Fig. 2). The explanatory  
260 variables were selected for final analyses using the conservative forward selection method developed by Blanchet  
261 et al. (2008; Fig. 2). This method was used to prevent the occurrence of artificially inflated explanatory powers in  
262 models. The forward selection was carried out using function *ordiR2step* in the R package *vegan* (Oksanen et al.,  
263 2013) and it was done separately for each species matrix (i.e. low-profile guild, high-profile guild etc.). The  
264 variation partitioning was done following the protocol of Borcard et al. (1992) using the function *varpart* in the R  
265 package *vegan* (Oksanen et al., 2013). In this study, only adjusted  $R^2$  values were used, as those take into account  
266 the number of explanatory variables at each variable group and sample size (Peres-Neto et al., 2006). The  
267 significance of each testable fraction was observed using test of fraction which is based on permutation (Fig. 2).  
268 This was done by using function *anova* in the R package *vegan* (Oksanen et al., 2013). All these analyses were  
269 performed separately for each species matrices in precisely the same way.

270

## 271 **Results**

272

273 A total of 190 diatom taxa were identified, species richness per site ranging from 19 to 55 (Table 2; Online  
274 Resource). The most common species were *Achnantidium minutissimum* (Kützing) Czarnecki s.l., *Rossithidium*  
275 *pusillum* (Grunow) F.E.Round & Bukhtiyarova and *Fragilaria gracilis* Øestrup. The species with the highest  
276 average abundance were *A. minutissimum* s.l., *R. pusillum* and *Fragilaria arcus* (Ehrenberg) Cleve var. *arcus*,  
277 which all belong to the low-profile guild and are generalists. From the taxa 117 species (62%) belonged to the

278 ecological guild classification made by Rimet & Bouchez (2011). In the sampling sites, an average of 77% of  
279 species belonged to one of the ecological guilds. In the high-profile guild, there were more species than in the  
280 other guilds. Only 57 species of the taxa (33 generalist and 24 specialist species) were found in Heino &  
281 Soininen's (2006) data. However, in the study sites, an average of 60% of species were either generalists or  
282 specialists.

283 Through the PCNM analysis, 15 spatial variables showing positive spatial autocorrelation were formed.  
284 The most common local variable included in the RDAs, determined by the forward selections, was moss cover  
285 (%) and the most common catchment variable was lake distance index (Table 3). Both variables, as well as the  
286 spatial variable describing broad-scale relations among sites (PCNM3), were selected for all analyses made for  
287 all species matrices. In general, the spatial variables representing the broad- and mid-scale relations among the  
288 sites were more commonly selected than the spatial variables illustrating finer-scale relations among sites.

289

#### 290 *The diatom community structure*

291 The local and catchment environmental conditions and the spatial variables all explained the diatom community  
292 structure, yet their relative importance varied for different species matrices (Table 4). Variables describing the  
293 spatial relations among sites at broad and medium scales (PCNM 2, 3, 1, 6, 8) explained slightly more (15.1%) of  
294 the variation of the whole community structure than the other two variable groups separately. The local variables  
295 that explained the variation of the whole community structure (11.9%) were moss cover (%), proportion of  
296 boulders (%), colour (mg Pt/l) and proportion of gravel (%). The catchment variables, lake distance index,  
297 standard deviation of greenness, shrub (%) and rock and cobble deposit (%), explained almost the same amount  
298 of the variation in community structure (12.2%) than the local variables.

299 The variation partitioning analyses showed that for the whole community the variation in community  
300 structure was better explained by the pure spatial (4.9%) than by the pure local (2.6%) or catchment (2.5%)  
301 environmental components (Fig. 3; Table 4). The variations explained jointly by the different pairs of variable  
302 groups were approximately 4 to 5%. The shared fraction between all variable groups was 1.4%. The amount of  
303 unexplained variation was relatively large in all models, with residuals ranging from approximately 65% to 84%  
304 for different ecological guilds and from 68% to 85% for generalist and specialist species matrices.

305

#### 306 *The diatom data matrices divided by ecological guilds*

307 Almost the same pattern as with the whole community matrix emerged when only the species found in the  
308 ecological guild classification were included (i.e. ecological guilds matrix). Here, the environmental variable  
309 groups separately also contributed less than the spatial variables to the explanation of community variation. The  
310 pure catchment component accounted for only 3.6% of the variation, while the pure spatial component explained  
311 7.6% of the variation. However, when the different ecological guilds were analysed separately, slightly different  
312 patterns emerged. Overall, the variations in different ecological guilds were better explained by the pure effects  
313 of the local variables and the spatial variables than by the pure effects of the catchment variables. The pure local  
314 and pure spatial variables explained the same amount of the variation in the high-profile guild. The pure local  
315 component explained more of the variation in the low-profile guild and motile guild than the spatial component.  
316 In explaining the variation in the low-profile guild, the catchment component was also important. Only the  
317 variation in the planktic guild was best explained by the spatial component. The shared fractions between all  
318 variable groups ranged from approximately 0 to 4% in all guilds, but the shared fractions of the spatial variables  
319 and the catchment variables were smallest (0% or negative values to 2%). The variation in the low-profile guild  
320 was explained best, as the unexplained variation was approximately 65%.

321

#### 322 *The diatom data matrices divided by ecological specialization*

323 Almost the same picture as with the whole community emerged when only the species found in the specialist-  
324 generalist classification were included (i.e. generalist and specialist matrix). But as with the ecological guilds,  
325 when the generalists and the specialists were analysed separately, different patterns emerged. The pure catchment  
326 component explained much more of the variation in the generalist species (10.9%) than in the specialist species  
327 (0.9%). The specialists were better explained by the pure effects of spatial variables than by the pure effects of  
328 local or catchment variables. The amount of variation that could be explained was higher for the generalists  
329 (31.9%) than for the specialists (14.7%).

330

#### 331 **Discussion**

332

333 In stream environments, local community structure typically portrays the effects of both environmental and spatial  
334 processes (Heino et al., 2015). Our results showed that local and catchment conditions and spatial variables all  
335 affected the organization of the subarctic diatom metacommunity with different relative importances. Our findings  
336 suggest that local conditions do not solely determine diatom metacommunity organization, but that there are also

337 spatially-structured patterns. Our findings also suggest that diatom communities are jointly structured by  
338 environmental filtering and spatial processes (Soininen & Weckström, 2009; Vilmi et al., 2017). These processes,  
339 however, play different roles in different species trait groups.

340

#### 341 *The factors structuring entire diatom communities*

342 The organization of the entire diatom metacommunity was determined by spatial factors and environmental  
343 variables at local and catchment scales (supports H<sub>1</sub>). Thus, our results are consistent with earlier findings (Pan et  
344 al., 1999; see also reviews by Soininen, 2011, 2012 and references therein). However, when examining the  
345 environmental variable groups separately, our results showed that spatial variables had a relatively large effect on  
346 diatom metacommunity organization (contradicts with H<sub>2</sub>). In combination, local and catchment variables  
347 explained more variation than spatial variables alone. Previous studies have found that environmental factors  
348 exceed spatial factors in importance, and that stream communities are mostly under abiotic control (Verleyen et  
349 al., 2009; Göthe et al., 2013). Our findings are in contrast with many specific studies that suggest that diatom  
350 community structures primarily reflect variation in local conditions (De Bie et al., 2012; Gottschalk & Kahlert,  
351 2012). Strong spatial patterns have previously been found mainly in large-scale studies, as in Heino et al.'s (2010)  
352 study concerning boreal stream diatom communities, or in highly connected environments, as in Vilmi et al.'s  
353 (2017) study in a boreal lake system. Indeed, these differences in findings may be due to different spatial scales  
354 (Mykrä et al., 2007) and environmental variables examined, but also to different ratios of ecological guilds (Göthe  
355 et al., 2013; Vilmi et al., 2017) and ecological specialization (Pandit et al., 2009).

356

#### 357 *The factors structuring ecological guilds*

358 Our results showed that there was variation in responses to environmental and spatial variables between the  
359 ecological guilds (supports H<sub>3</sub>). Overall, the variations in different ecological guilds were better explained by the  
360 local and spatial variables than by catchment variables. Our findings suggest that the high- and low-profile guilds  
361 are simultaneously structured by environmental filtering and spatial processes in subarctic streams. However,  
362 environmental filtering plays a more important role for the motile guild, and spatial-related processes are  
363 important for planktic species. The planktic guild has shown clear spatial patterns in other studies as well (e.g.  
364 Vilmi et al., 2017). In boreal streams (Göthe et al., 2013) and lakes (Vilmi et al., 2017), diatom guilds have also  
365 been structured by various metacommunity processes. Göthe et al. (2013) suggested that the dissimilar findings  
366 between guilds could be due to diatoms' traits related to dispersal capacity. According to Algarte et al. (2014),

367 firmly attached algae (i.e. low-profile guild species) show clear spatial patterns, as they resist high current  
368 velocities (Passy, 2007). Thus, they have lower dispersal rates. In our study, this was not the case, as the local  
369 environmental component explained best the variation in the low-profile guild. It has been also suggested that the  
370 degree of attachment and the mobility of micro-organisms can affect the extent of dispersal (Vilmi et al., 2017).  
371 This can partly explain the importance of spatial-related processes to planktic guild species in our study.  
372 Unfortunately, dispersal capacities of diatom species and what traits determine them—at least in terms of long-  
373 distance dispersal—is a subject that has not been studied much (Kristiansen, 1996; Vyverman et al., 2007;  
374 Casteleyn et al., 2010; Souffreau et al. 2013; Rimet et al., 2014). However, the use of guild division can give us  
375 some indirect indications of dispersal processes.

376

377 *The factors affecting different groups of ecological specialization*

378 Our results showed that generalists and specialists differ strongly in responses to environmental and spatial  
379 variables (supports H<sub>4</sub>; Pandit et al., 2009; Székely & Langenheder, 2014). We thought that generalists would be  
380 structured by spatial-related processes because they can tolerate a wide range of environmental conditions  
381 (Devictor et al., 2010). However, the variation in the generalist species was explained mostly by catchment  
382 environmental factors (contradicts with H<sub>6</sub>). According to the hierarchical environmental filtering model (Poff,  
383 1997), regional processes determine the species reaching the local habitat. Thus, it is possible that regional  
384 processes are limiting factors to generalist species. Our results also indicated that spatial processes are important  
385 to specialist species (contradict H<sub>5</sub>). Dispersal can be more challenging to specialist species because there are  
386 fewer suitable environments for them (Kolasa & Romanuk, 2005). However, it is unlikely that dispersal limitation  
387 would explain these spatial patterns due to the relatively small spatial extent of our study area and the fact that  
388 this study was conducted within one drainage basin (see Mouquet & Loreau, 2003; Leibold et al., 2004; Heino et  
389 al., 2017).

390 Our results are slightly inconsistent with previous studies (e.g. Pandit et al., 2009). With rock pool  
391 invertebrates, habitat generalists respond mainly to spatial factors and habitat specialists mostly to environmental  
392 factors (Pandit et al., 2009). On the other hand, community composition of generalist bacteria was best explained  
393 by environmental factors (Székely & Langenheder, 2014). In addition, for dragonflies, dispersal restricted the  
394 distributions of habitat specialist species (McCauley, 2007). In Alahuhta et al.'s (2014) study, the community  
395 compositions of both common and rare macrophyte species were explained by environmental factors, suggesting  
396 environmental filtering to be more dominant regardless of the degree of rarity.

397 In our study, the amount of explained variation was much higher for the generalists than for the specialists.  
398 This is not surprising, as specialist species have a narrower niche breadth, and environmental factors can affect  
399 different specialist species in different ways (Pandit et al., 2009). Overall, some species can be strongly specialized  
400 or clearly generalists, but generally, species are something in between these extreme ends (Heino & Soininen,  
401 2006; Pandit et al., 2009). Thus, the generalist and specialist division in our study is rather coarse. However, our  
402 results suggest that even this coarse division can be useful when studying the effects of ecological specialization  
403 on community structure.

404

#### 405 *Spatial processes and scale dependency*

406 Our results showed that spatial variables had a much larger effect on diatom metacommunity organization than  
407 we thought based on the relatively small spatial extent of our study area (Verleyen et al., 2009; Bennett et al.,  
408 2010). However, Astorga et al. (2012) have found that diatom communities are spatially structured in very similar  
409 environments at small scale (<200 km) but not at larger spatial extents. In studies concerning microbial  
410 communities, spatial patterns have been found at the small spatial scale in systems of high connectivity (Lear et  
411 al., 2014; Vilmi et al., 2016; Vilmi et al., 2017). Connectivity probably can also play a role in stream diatom  
412 metacommunities. Historical factors are important in explaining geographical patterns found in diatom genus  
413 richness at regional to global scales, indicating the vital roles of dispersal limitation in structuring diatom  
414 communities (Vyverman et al., 2007). Thus, as the spatial variables used in this study can portray also the  
415 historical factors and dispersal (Dray et al., 2012), this could explain the importance of these variables also in our  
416 study, although the scale in our study is much smaller. However, spatial structures found in small spatial extent  
417 and within a region (i.e. Tenojoki drainage basin) are usually mainly related to homogenizing effects rather than  
418 dispersal limitations (Mouquet & Loreau, 2003; Leibold et al., 2004; Heino et al., 2017), even though both can  
419 produce spatial patterns (Ng et al., 2009). These homogenizing effects can take place via mass-effects (Mouquet  
420 & Loreau, 2003). In the Tenojoki drainage basin, diatom communities seem to be structured by processes active  
421 at multiple spatial scales, as they have been in comparable studies (Göthe et al., 2013; Vilmi et al., 2016; Vilmi et  
422 al., 2017). However, interpretation of spatial variables is always dependent on the size and connectivity of the  
423 study system (Dray et al., 2012).

424

#### 425 *Concluding remarks*

426 The results of this study should be interpreted with caution, as the amounts of unexplained variation were  
427 relatively high. This was partly due to the statistical methods used (adjusted coefficient of determination; Peres-  
428 Neto et al., 2006), and low amount of explained variation is common in these kind of studies (e.g. Pandit et al.,  
429 2009; Algarte et al., 2014). Moreover, it is possible that some important explanatory variables are missing from  
430 the analysis (e.g. Algarte et al., 2014). For example, this study did not include biotic interaction, e.g. grazing.  
431 However, previous studies have shown that grazing has no apparent effects, at least on the structure of diatom  
432 guilds (e.g. Göthe et al., 2013; Vilmi et al., 2017). Yet, biotic and trophic interactions would be an interesting  
433 addition to the study of northern, nutrient-poor environments. According to Berthon et al. (2011), grazing pressure  
434 may be higher in nutrient-poor rivers than in nutrient-rich rivers because biofilms are rare. However, a more likely  
435 reason for the low amounts of explained variations is the occurrence of stochastic processes (Vellend et al., 2014),  
436 as biological communities are formed through very complex processes and interactions. The guild and ecological  
437 specialization information were not available for all species and this can have implications on results. However,  
438 we believe that our results are representative, because the reduced overall guild and ecological specialization  
439 matrices showed patterns similar to those of the entire community matrix.

440 Our findings suggested that dividing the whole community into different groups by species traits indeed  
441 increases understanding of metacommunity organization. Our study showed that diatom communities in subarctic  
442 streams are a result of both environmental filtering and spatial-related processes. Future studies should focus on  
443 measuring grazing pressure, especially in nutrient-poor subarctic streams, and dispersal rates of diatom species to  
444 acquire more reliable knowledge of the processes structuring diatom communities. Focusing on these biological  
445 processes would, however, necessitate experimental approaches, which may be complicated at spatial extents  
446 comprising entire drainage basins. Hence, large-scale observational studies offer necessary background  
447 information for guiding more detailed experimental work and provide important information for biodiversity  
448 assessment research.

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450

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637 **Tables and figures**

638 **Table 1** Summary of local and catchment variables across the study sites in the River Tenojoki drainage basin.

639 N = 52 streams.

<b>Variable</b>	<b>Min</b>	<b>Max</b>	<b>Mean</b>	<b>SD</b>
<b>Local scale</b>				
Total nitrogen (µg/l)	62	260	132.08	43.8
Color (mg Pt/l)	10	50	27.40	9.62
Iron (µg/l)	8	160	69.06	41.06
Manganese (µg/l)	1	5.5	2.01	1.39
pH	6.58	7.51	6.87	0.17
Conductivity (µS/cm)	11	27	17.48	3.96
Particle size (%)				
Sand (0.25–2 mm)	0	24.5	0.88	3.48
Gravel (2–16 mm)	0	12	2.62	2.95
Pebble (16–64 mm)	0	45.67	14.40	11.17
Cobble (64–256 mm)	1	52	24.51	11.82
Boulder (256–1024 mm)	14	99	57.60	21.08
Moss cover (%)	0.3	75	17.76	20.21
Current velocity (m/s)	0.28	0.89	0.57	0.13
Depth (cm)	14.6	34.47	24.27	4.62
Mean width (m)	1.2	22	5.91	4.22
Height of the lower stream bank (cm)	0.0	117.9	32.00	24.6
Steepness (cm)	0.5	108	36.74	23.41
Shading (%)	0	100	41.46	33.58
<b>Catchment scale</b>				
Drainage basin area (km <sup>2</sup> )	1.55	135.74	24.89	29.95
Proportion of lakes (%)	0	11	1.27	2.27
Lake distance index	1.14	52.51	30.76	24.09
Length of the stream (km)	1.39	28.97	9.28	6.8
Peatlands (%)	1.17	39.78	12.70	8.13
Shrub (%)	0	93.87	45.18	31.55
Rock and cobble deposit (%)	0	26.88	2.89	4.23
NDVI, mean	-0.03	0.57	0.26	0.14
NDVI, standard deviation	0.1	0.33	0.21	0.05
Greenness, mean	0.09	0.19	0.14	0.02
Greenness, standard deviation	0.02	0.05	0.03	0.01

640 Minimum (min), maximum (max) and mean (mean) values and standard deviation (SD).

641 **Table 2** Total number of diatom species, and minimum (min), maximum (max), mean (mean) and standard  
 642 deviation (SD) of local number of species in different species matrices.

<b>Species matrix</b>	<b>Number of species</b>	<b>Min</b>	<b>Max</b>	<b>Mean</b>	<b>SD</b>
All taxa	190	19	55	32.5	8.18
Ecological guilds	117	14	40	24.98	5.93
High-profile guild	46	3	17	8.75	3.03
Low-profile guild	33	5	15	9.88	2.53
Motile guild	27	1	9	3.42	1.96
Planktic guild	11	1	5	2.92	0.97
Generalists and specialists	57	10	31	19.21	4.37
Generalist	33	7	23	13.96	3.37
Specialist	24	1	10	5.25	2.25

643

644 **Table 3** The selected variables according to the forward selection procedure and their rank order.

	<b>Local</b>	<b>Catchment</b>	<b>Spatial</b>
<b>All taxa</b>	Moss cover	Lake distance index	PCNM2
	Boulder	Greenness, standard deviation	PCNM3
	Color	Shrub	PCNM1
	Gravel	Rock and cobble deposit	PCNM6 PCNM8
<b>Ecological guilds</b>	Moss cover	Lake distance index	PCNM2
	Gravel	Greenness, standard deviation	PCNM3
	Manganese	Rock and cobble deposit	PCNM8
	Iron		PCNM1
	Current velocity		PCNM9
	Shading		PCNM6
<b>High-profile</b>	Moss cover	Lake distance index	PCNM3
	Conductivity	Greenness, mean	PCNM13
	Manganese		
	Color		
<b>Low-profile</b>	Moss cover	Lake distance index	PCNM2
	Gravel	Greenness, standard deviation	PCNM3
	Current velocity	Shrub	PCNM8
	Shading		
<b>Motile</b>	Boulder	Lake distance index	PCNM3
	Moss cover	Shrub	PCNM15
	Iron		PCNM11
	Current velocity		
<b>Planktic</b>	Moss cover	Lake distance index	PCNM3
	Conductivity	Peatlands	PCNM9
	Boulder		PCNM2
<b>Generalists and specialists</b>	Moss cover	Lake distance index	PCNM2
	Gravel	Greenness, standard deviation	PCNM3
	Current velocity	Rock and cobble deposit	PCNM8
	Manganese		PCNM6
	Iron		PCNM1 PCNM9
<b>Generalist</b>	Moss cover	Lake distance index	PCNM2
	Gravel	Greenness, standard deviation	PCNM8
	Current velocity	Rock and cobble deposit	PCNM3
<b>Specialist</b>	Moss cover	Lake distance index	PCNM3
	Manganese	Drainage basin area	PCNM13 PCNM9

646 **Table 4** A summary of variation partitioning results. The significance of each fraction explained is indicated in the table (\*p<0.05, \*\*p<0.01).

	<b>Generalists</b>																	
	<b>All taxa</b>		<b>Ecological guilds</b>		<b>High-profile guild</b>		<b>Low-profile guild</b>		<b>Motile guild</b>		<b>Planktic guild</b>		<b>plus specialists</b>		<b>Generalists</b>		<b>Specialists</b>	
	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>	<b>Df</b>	<b>Adj. R<sup>2</sup></b>
Local [a+d+f+g]	4	0.119	6	0.161	4	0.099	4	0.189	4	0.095	3	0.136	5	0.156	3	0.143	2	0.063
Catchment [b+d+e+g]	4	0.121	3	0.119	2	0.055	3	0.149	2	0.055	2	0.109	3	0.128	3	0.154	2	0.043
Spatial [c+e+f+g]	5	0.151	6	0.159	2	0.062	3	0.155	3	0.076	3	0.143	6	0.158	3	0.120	3	0.096
[a+b+d+e+f+g]	8	0.190	9	0.212	6	0.121	7	0.279	6	0.132	5	0.177	8	0.217	6	0.249	4	0.085
[a+c+d+e+f+g]	9	0.213	12	0.252	6	0.139	7	0.281	7	0.134	6	0.240	11	0.249	6	0.210	5	0.138
[b+c+d+e+f+g]	9	0.212	9	0.233	4	0.118	6	0.252	5	0.115	5	0.206	9	0.243	6	0.260	5	0.120
[a+b+c+d+e+f+g]	13	0.238	15	0.288	8	0.161	10	0.351	9	0.159	8	0.266	14	0.295	9	0.319	7	0.147
<b>Individual fractions</b>																		
[a] Pure local	4	0.026*	6	0.055*	4	0.043*	4	0.099*	4	0.044*	3	0.060*	5	0.052*	3	0.058*	2	0.027*
[b] Pure catchment	4	0.025*	3	0.036*	2	0.023*	3	0.070*	2	0.025*	2	0.025*	3	0.046*	3	0.109*	2	0.009
[c] Pure spatial	5	0.049*	6	0.076*	2	0.040*	3	0.072*	3	0.026	3	0.088*	6	0.078*	3	0.070*	3	0.062*
[d] Local + catchment	0	0.036	0	0.037	0	0.034	0	0.028	0	0.014	0	0.037	0	0.039	0	0.032	0	0.015
[e] Catchment + spatial	0	0.046	0	0.015	0	0	0	0.020	0	0.013	0	0.016	0	0.015	0	-0.003	0	0.014
[f] Local + spatial	0	0.042	0	0.037	0	0.023	0	0.032	0	0.034	0	0.009	0	0.037	0	0.036	0	0.015
[g] Shared	0	0.014	0	0.031	0	0.001	0	0.031	0	0.003	0	0.030	0	0.028	0	0.016	0	0.005
Residuals [h]		0.762		0.712		0.839		0.649		0.841		0.735		0.705		0.681		0.853

648 **Fig. 1** Map showing the location of the Tenojoki drainage basin, the study sites and the catchments of those sites  
649 (green). Only the streams from the Finnish side of the Tenojoki drainage basin are presented, with the exception of the  
650 main stem of River Tenojoki and the most north-eastern part of the map. Note that all 52 study sites are located in  
651 tributary streams and there are no sites in the main stem of the River Tenojoki. Only sites included in the data analyses  
652 are visible on the map

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654

655 **Fig. 2** A schematic diagram showing the methodology used. The analyses were done separately for each species data  
656 matrix

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658

659 **Fig. 3** Venn-diagrams showing the fractions of diatom community structure explained by the local variables (Local), the  
660 catchment variables (Catchment) and spatial variables (Spatial). All fractions are based on adjusted  $R^2$  values shown as  
661 percentages of total variation. Values  $<0$  are not shown. A = all taxa, B = ecological guilds, C = high-profile guild, D =  
662 low-profile guild, E = motile guild, F = planktic guild, G = generalist and specialist, H = generalist, I = specialist