Partitioning of benthic biodiversity in boreal streams: contributions of spatial, inter-annual and seasonal variability

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27   11   Kaisa-Leena Huttunen[1], Leif O. S. Väisänen[1], Riku Paavola[2] and Timo Muotka[1,3]
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33   13   [1] University of Oulu, Department of Ecology and Genetics, PO Box 3000, 90014 Oulu, Finland
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36   14   [2] Oulanka Research Station, University of Oulu Infrastructure Platform, Liikasenvaarantie 134,
37
38   15   Kuusamo 93900, Finland
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41   16   [3] Finnish Environment Institute, Natural Environment Centre, P.O. Box 413, FI-90014 Oulu, Finland
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47   18   Corresponding author: Kaisa-Leena Huttunen, kaisa-leena.huttunen@oulu.fi
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53   20   *Key words: beta diversity, community structure, intra-annual, stream invertebrates, temporal variation*
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21   ABSTRACT

22   1. Studies on biodiversity patterns should optimally relate different scales of temporal community

23   variability to spatial variability. Although temporal biodiversity variability is often negligible

24   compared to spatial variation, it may still constitute a substantial source of overall community

25   variability in stream ecosystems. Boreal streams exhibit seasonally recurring environmental

26   periodicity which can be expected to induce synchronous dynamics of abiotic variables among

27   sites, and consequently, to produce spatial synchrony of deterministically controlled biological

28   communities with higher intra- than inter-annual community variability.

29   2.   We sampled benthic macroinvertebrates in 10 near-pristine boreal streams on three different

30   seasons (spring, summer, autumn) across four consecutive years in northern Finland. We aimed

31   to identify the relative contributions of spatial, inter-annual and seasonal variability to overall

32   benthic biodiversity; and relate variation in benthic invertebrate communities to key

33   environmental factors, particularly in-stream habitat diversity.

34   3. Among-site spatial variability was clearly the most important source of variation for both

35   species richness and community dissimilarity. Of the two temporal scales, inter-annual

36   variability contributed more to variation in taxonomic richness and seasonal variability slightly

37   more to variability in community composition.

38   4. Only inter-annual variation differed systematically from random expectation, indicating strong

39   stability (low variability) of stream macroinvertebrate communities across years, with less

40   variation at sites with higher substrate heterogeneity. Considering the distinct seasonality of the

41   boreal stream environment, seasonal variability accounted for an unexpectedly low amount of

42   total community variability.

5. Although differences between seasons were small, autumnal sampling is likely the least

susceptible to climatic vagaries, thus providing the most consistent and predictable conditions

for benthic sampling in boreal streams, particularly for bioassessment purposes. Exceptional

climatic conditions are becoming more frequent in northern Europe, likely causing substantial

and largely unpredictable changes in benthic community composition. As a result, the

importance of temporal (relative to spatial) community variability may increase.

INTRODUCTION

The structure of stream macroinvertebrate communities varies across spatial extents from patch-scale to

regional and continental scales, but also temporally from daily to decadal scales (Tonkin et al., 2017).

Temporal biodiversity variability is often negligible compared to spatial, among-site variation but may

still constitute a substantial source of overall variability in lotic ecosystems (Heino et al., 2004). Inter-

annual variation of benthic macroinvertebrate communities has been related to, for example, among-

year differences in broad-scale climatic variability (e.g. Bradley & Ormerod, 2002; Sarremejane et al.,

2018) and local habitat characteristics that buffer communities against flow-related disturbances (in-

stream vegetation, Huttunen et al., 2017; substratum diversity, Brown, 2003). Most lotic ecosystems

also exhibit strong, and often predictable, seasonal variability in their environment. For example, most

boreal streams flow permanently with relatively predictable seasonal periodicity with distinct changes

in water temperature, precipitation, and light (Mustonen et al., 2016).

Such seasonally recurring environmental periodicity induces community level responses due

to two, partly intertwined, reasons: (i) intrinsic changes in community structure that reflect species' life

cycle phenologies (growth, development and voltinism; Butler, 1984), each species taking advantage of

the temporally most suitable environmental conditions, or avoiding unfavorable ones (Johnson et al.,

66 2012; Shimadzu et al., 2013); and, (ii) extrinsic changes in community structure due to deterministic

67 habitat filtering and/or stochastic processes. If deterministic processes dominate, both spatial and

68 temporal beta diversity (i.e., community variability among sites at a certain time vs. variability among

69 times at a certain site, respectively) should remain low among sites and times sharing similar

70 characteristics (Chase & Myers, 2011; Van Allen et al., 2017). Also, the timing of changes in

71 community structure should be closely similar across sites sharing the same environmental filter, i.e.,

72 such communities should vary synchronously through time (Kratz et al., 1987; Rusak et al., 2008). In

73 contrast, if stochastic processes are prevailing, communities should exhibit larger, and less predictable,

74 variability (higher beta diversity) through space and time despite similar environmental conditions

75 (Chase & Myers, 2011; Van Allen et al., 2017). Furthermore, if deterministic seasonally varying filters

76 predominate, species' contrasting phenologies should result in the presence of seasonally distinct

77 species groups (Shimadzu et al., 2011), leading to high and synchronous intra-annual community

78 variability. Conversely, stochastically controlled communities are characterized by relatively random

79 colonization-extinction processes across space and time resulting in lower, and asynchronous, seasonal

80 variability (see Van Allen et al., 2017).

81   It has been suggested that seasonal variation in community composition may often be higher

82 than inter-annual variation (Korhonen et al., 2010), and this has indeed been observed in, for example,

83 monsoonal streams with regular intra-annual alternation of dry and wet seasons (Leung et al., 2012). In

84 contrast, streams in temperate regions, albeit seasonal, exhibit less pronounced seasonal environmental

85 dynamics and may therefore support less variable communities throughout the year (Dolédec et al.,

86 2017). Seasonal variability in benthic invertebrate community composition may have important

87 implications for stream bioassessment because samples collected at only one season may provide a

88 grossly biased estimate of local diversity (Tonkin et al., 2017; Van Allen et al., 2017), potentially

89 resulting in reduced precision of ecological status assessment (Mazor et al., 2009; Johnson et al., 2012).

90   Theoretically, predictably seasonal environments should support distinctly different

91   communities in different seasons, resulting in high temporal diversity. By contrast, communities in

92   aseasonal systems tend to fluctuate randomly, with little seasonal turnover (and low temporal diversity)

93   (Tonkin et al. 2017). Current understanding of intra-annual variation in macroinvertebrate communities

94   is largely based on monsoonal streams (Leung & Dudgeon, 2011; Leung et al., 2012) or comparisons

95   between intermittent and perennial streams in Mediterranean regions (Bêche & Resh, 2007;

96   Sarremejane et al., 2017), whereas boreal systems have received less attention. Studies on temporal

97   (relative to spatial) biodiversity patterns in pristine streams are needed to benchmark the level of intra-

98   and inter-annual community variability, allowing a more reliable identification of human-induced

99   community change in altered landscapes (Magurran et al., 2010). In addition, climate change is altering

100 water temperature, precipitation, and flow regimes around the globe, and certainly not the least in

101 boreal streams and rivers (Mustonen et al., 2018). Climate-change scenarios are very different for

102 different parts of the world: for example, while Mediterranean streams are expected to experience even

103 stronger seasonal flow variability in the future (Dolédec et al., 2017), boreal streams may lose much of

104 their inherent flow seasonality (Mustonen et al., 2018). Because of their small size, headwater streams

105 are particularly prone to altered flow regimes and consequent changes in benthic community

106 composition (Finn et al., 2011; Mustonen et al., 2018), with potential consequences on downstream

107 processes in riverine networks (Wipfli et al., 2007).

108   The primary goal of the present study was to identify the relative contributions of spatial,

109 inter-annual and seasonal variability to total benthic invertebrate biodiversity in boreal streams. For that

110 purpose, we sampled benthic macroinvertebrates on three different seasons (spring, summer, autumn)

111 across four consecutive years in ten near-pristine streams in NE Finland. These sites were selected from

112 a larger set of 75 streams (Huttunen et al., 2012) to represent gradients in habitat complexity (i.e.

113 substrate diversity and macrophyte cover) known to be important in-stream habitat filters regulating

114   benthic invertebrate community composition (e.g. Brown, 2003; Huttunen et al., 2017). Specifically,

115   we expected (i) invertebrate communities to vary more through space (among sites) than through time

116   (within sites) and diversity patterns to be (deterministically) controlled by local habitat factors. Due to

117   the distinct seasonality of boreal streams, we expected (ii) to detect strong and spatially synchronous

118   temporal (particularly intra-annual) variation of environmental variables, resulting in synchronous

119   variation also in biological communities. However, we expected less temporal coherence in ecological

120   than environmental variables, as has been previously reported for lake planktonic (Arnott et al., 2003;

121   Özkan et al., 2016) and stream benthic (Huttunen et al. 2014) communities. Further, owing to distinct

122   seasonal variability of the stream environment, we expected (iii) seasonal variation to outweigh inter-

123   annual variation in community composition of benthic invertebrates.

124

125   METHODS

126   *Study area*

127   Samples were collected from ten headwater streams in the Koutajoki drainage basin (4000 km^2) in

128   northeastern Finland, just south of the Arctic Circle (66-67°N, 28-30°E). Koutajoki basin is

129   geologically diverse with extensive calcareous rock deposits, and its vegetation is dominated by pine

130   forests on mineral and peatlands (Nilsson et al., in press). Our study sites are in first-to-third order

131   permanent streams with catchment sizes ranging from 4 to 33 km^2 (mean 13.5 km^2). Discharges peak

132   after spring snowmelt in early-to-middle of May, with a secondary peak in late autumn (October),

133   before the onset of winter. The study sites are within or close to Oulanka National Park, a nature

134   conservation reserve representing the westernmost remnants of pristine taiga forests. All ten streams

135   drain mixed forests, bogs, and fens with minimal anthropogenic impact (mainly forestry). They are

136 oligotrophic with circumneutral to slightly alkaline water with low humic content (Nilsson et al., in

137 press). All study streams support sparse fish populations, with brown trout (*Salmo trutta*), Alpine

138 bullhead (*Cottus poecilopus*) and Eurasian minnow (*Phoxinus phoxinus*) being the dominant species.

139

140 *Data collection*

141 We sampled benthic macroinvertebrates in 2013-2016 from ten streams three times a year: (i) late

142 spring, soon after the snowmelt-induced spring flood (late May/early June); (ii) summer (early August);

143 and (iii) autumn (early October). No sampling could be conducted during the winter months

144 (November-April) because most of the streams are inaccessible then due to snow and ice cover. Total

145 number of samples was 120 (10 sites x 4 years x 3 x seasons). Samples were collected from a riffle

146 section of about 100 m² by taking a 2-min kick-net sample covering ca. 1.3 m² of the stream bed and

147 including most microhabitats present in a riffle. Samples were preserved in the field and all individuals

148 were later sorted in the laboratory, then counted and identified to the lowest feasible level, mainly

149 species or genus. Chironomids were excluded from all analyses as they were not sorted each time. Taxa

150 that occurred in less than 3 samples (out of 120) were removed from the data before statistical analyses.

151   Study sites were selected *a priori* to represent gradients of habitat complexity, measured as

152 macrophyte cover and substrate diversity. The percentage cover of macrophytes was estimated visually

153 at 30 randomly placed 50 x 50 cm quadrats at each site 5 times during the study, whereas substrate

154 diversity index (Simpson index, 1/D) was based on measurements of substrate size distribution

155 (modified Wentworth scale) by Mykrä et al. (2011) at the same sites. To estimate whether other

156 limnological variables could be equally, or even more, important determinants of invertebrate

157 community structure than those related to in-stream habitat complexity, we also measured stream water

158 temperature, depth and water quality at each site. We installed data loggers (WT-HR 1000 mm,

159 TruTrack Ltd, New Zealand) in each stream to record water temperature and water level at 30-min

160 intervals from late May to October each year. These measurements were used to calculate daily average

161 values for each site. Water samples were collected on each visit, and analyzed for pH, specific

162 conductivity, water colour (mg Pt L^{-1}) and total P (µg L^{-1}). Total N and DOC were measured

163 sporadically (3-4 times) at each site; they were therefore not included in data analyses but are presented

164 for illustrative purposes, along with other environmental variables in Table S1. In addition, to consider

165 connectivity as a potential driver of community patterns we used availability of riffle habitat (as m^2)

166 within a 1 km circle buffer from the sample reach as a measure of relative isolation of a site within a

167 stream network (see Huttunen et al. 2017).

168

Data analyses

170 Spatial synchrony, i.e., similarity in the temporal dynamics of environmental variables (water depth,

171 temperature and chemistry) and taxonomic richness across sites was measured using Spearman rank

172 correlations. We used Spearman correlations since we were interested in similar highs and lows in our

173 response variables rather than in their absolute values. Mean level of synchrony for each variable was

174 calculated as average across all site pairs. We used bootstrapped 95% confidence intervals to explore

175 whether the observed level of synchrony differed from zero, indicating similarity (or dissimilarity) of

176 temporal patterns among study sites. Following Lillegård et al. (2005) and Huttunen et al. (2019) we

177 used moving-block resampling of segments of time instead of individual time points to account for

178 temporal autocorrelation. The block length (i.e., time lag) was set separately for each variable using the

179 autocorrelation function ('acf' in R package stats). Autocorrelation estimates were generally highest for

180 lag one (consecutive samples) or lag three (same season). Resampling with replacement was conducted

181 1000 times and spatial synchrony was interpreted as statistically significant if the obtained 95% CI did

182 not overlap zero.

183   Linear mixed effects models (function 'lme' in R package nlme; Pinheiro et al. 2017) were

184   used to test whether species richness differed among sites and across time, with the aim of identifying

185   the relative importance of spatial, inter-annual and seasonal variability to benthic invertebrate diversity.

186   This was done by using years, seasons, or seasons within years as random factors and site as a fixed

187   factor. Each temporal scale was interpreted as having a significant role if it improved model fit

188   compared to a model without it (function 'gls' in R package nlme) based on AIC_c values.

189   To analyze variation in community composition among sites at a certain time, or among times

190   at a certain site (i.e., spatial and temporal beta diversity, respectively), we used Bray-Curtis

191   dissimilarity on $\log(x+1)$ transformed data. Nonmetric multidimensional scaling (NMS) and

192   permutational multivariate analysis of variance (function 'adonis' in R package vegan; Oksanen et al.,

193   2014) were used to visualize changes in community composition in space and time and to partition

194   variation to different sources (spatial, inter-annual, seasonal), respectively. To quantify the level of beta

195   diversity for different sources of community variability, we calculated dissimilarity i) as divergence of

196   a site from all other sites, separately for each sampling time (spatial β); ii) among all years, separately

197   for each season at each site (inter-annual β); and iii) among all seasons, separately for each year and

198   site (seasonal β).

199   Next, we used a null model approach to explore whether assembly mechanisms were mainly

200   stochastic or deterministic (Chase & Myers, 2011; Chase et al., 2011). We used "temporally local" null

201   models for spatial community variability and "spatially local" null models for temporal variability to

202   focus purely on spatial or temporal aspects of beta diversity, respectively. In practice, null models were

203   constructed separately for each sampling time (spatial variability) or for each site (temporal variability),

204   the potential species pool then consisting of either taxa observed on a given sampling time at any of the

205   sites or taxa observed at a given site on any sampling time, respectively. Both types of null models

206   were quantitative and were constructed using function *nullmodel* and algorithm *swsh_both_r* in vegan

207 package (Oksanen et al., 2014). In this algorithm, species presences are randomly shuffled while

208 keeping sample-specific taxa richness (α diversity), species frequencies and γ diversity constant.

209 Individuals are then randomly distributed to non-zero cells for each sample, retaining sample-specific

210 total abundances. Expected community variability (β_{exp}) was calculated across 1000 iterations.

211 Departure of the observed variability from random expectation (β_{dep}) is presented as standard effect

212 size (SES = (β_{obs}- β_{exp})/$SD_{\beta exp}$) where negative β_{dep} values indicate lower and positive values higher

213 than expected dissimilarity.

214 Finally, we explored the influence of habitat complexity (substrate diversity; macrophyte

215 abundance) and other potentially important environmental correlates (connectivity, water temperature,

216 water depth and among-site differences in water chemistry (Euclidean distance of water chemistry

217 variables; function *vegdist* in vegan (Oksanen et al., 2014)) of spatial community variability.

218 Explanatory variables for temporal community variability (both annual and seasonal) were otherwise

219 the same, but instead of mean values for water temperature and depth, we used their daily variability

220 from late May to early October. Similarly, temporal variability in water chemistry (site specific

221 Euclidean distance through time) was used instead of among-site differences in mean values. We

222 initially used multimodel inference (Burnham & Anderson, 2002) in multiple linear regressions for this

223 purpose but as the best models included only one variable, we opted on using ordinary least-squares

224 regressions. In all regressions, standardized effect size (SES) of departure from null (β_{dep}) was used as

225 dependent variable, a significant relationship referring to deterministic control by the environmental

226 variable in question (Stegen et al., 2013).

227

228 RESULTS

229   Our study period did not include climatically exceptional years, except summer 2016 with higher-than-

230   average summertime precipitation (Figure S1). Water temperature and depth exhibited strong

231   seasonality despite large differences between sites in absolute values (Figure 1). The mean level of

232   synchrony across sites (r_s) was 0.76 for water depth and 0.91 for water temperature. For water

233   chemistry variables, the level of synchrony varied more, ranging from 0.14 (pH) to 0.65 (conductivity),

234   but spatial synchrony was still significant for all measured variables (Table 1, Figure S2).

235   We collected altogether 244 114 individuals in our samples, representing 123 invertebrate taxa

236   (102 after removal of taxa occurring in < 3 samples). The overall number of taxa detected at a site

237   during the whole study period, i.e., temporal γ diversity, ranged from 63 to 88 (mean 73), whereas the

238   site-specific number of taxa per sampling occasion (temporal α diversity) varied from 14 to 50 (mean

239   35). Taxonomic richness (i.e. α diversity) varied greatly between sites ($F_{9,107}$ = 9.12, p<0.01; Figure 2).

240   Compared to the model with only the main effect of 'site', the random effect 'season' did not improve

241   the fit whereas 'season within year' and 'year' did. Variance component for 'year' was 31 % whereas it

242   was only 3% for 'season within year', further indicating differences in species richness between years

243   but not between seasons. However, despite among-site and among-year differences, temporal dynamics

244   in taxonomic richness were spatially synchronous among sites (mean r_s=0.34) (Table 1).

245   Spatial variation among study sites was clearly the most important source of beta diversity, as

246   indicated by the clustering of samples in the NMS ordination space (Figure 3), permutational

247   multivariate analysis of variance (adonis: spatial: $F_{9,105}$ = 18.37, R^2=0.517; annual: $F_{3,105}$ = 6.84,

248   R^2=0.064; seasonal: $F_{2,105}$ = 14.33, R^2=0.090), and the highest Bray-Curtis dissimilarity values (Figure

249   4a). Among-site dissimilarity (spatial β), measured as mean divergence of each site from all the others,

250   was 0.52, with low variability among time points (mean SD = 0.052). Inter-annual and seasonal

251   community variability (temporal β) were of about the same order, and clearly lower than spatial

252   variability (mean 0.34 for inter-annual, 0.36 for seasonal beta diversity; Figure 4a). Only a few taxa

253 occurred at only one season, most of the taxa (88%) being observed at least once in every season. The

254 riffle beetle *Elmis aenea*, blackfly larvae (Simuliidae) and the mayflies *Baetis rhodani* and *B. muticus*

255 were the most common and abundant taxa, occurring in all (or almost all) samples, each comprising

256 more than 10 %, and all four together 52%, of total benthic abundance.

257   Only inter-annual beta diversity was lower than expected by chance at all study sites (mean

258 β_{dep} = -7.34; Figure 4b), indicating that deterministic processes control community assembly, resulting

259 in high community stability across years for each season (mean $\beta_{dep:}$ spring = -5.97, summer = -4.94,

260 autumn = -6.77). By contrast, seasonal variability in community composition did not differ from

261 random expectation (mean β_{DEP} = -0.195), referring to stochastic assembly processes (see Methods).

262 Similarly, spatial beta diversity did not, on average, differ systematically from random expectation

263 (mean β_{dep} = 1.50), but sites were divided in two groups: those that differed from the others more than

264 expected by chance (n=4) and those (n=6) that did not (Figure 4b).

265   In linear regressions (with SES of β_{dep} as the response variable), spatial dissimilarity (beta

266 diversity) increased with dissimilarity in water chemistry (R^2= 0.35, p=0.07, Figure 5a). This was

267 mostly due to total P concentrations spatial divergence increasing with increasing total P (R^2=0.43,

268 p=0.04). Inter-annual beta diversity was related to substrate diversity, with temporally more stable

269 communities being associated with diverse benthic substrates (R^2= 0.40, p=0.05, Figure 5b). Null-

270 model controlled seasonal community variability could not be explained by any of the measured

271 variables.

272

273 DISCUSSION

274 All biological communities vary through space and time and this change is manifested across multiple

275 hierarchical scales. The most relevant scale of temporal community variability depends on the life

276   cycles of the constituent species, yet a great majority of studies have focused entirely on inter-annual

277   variation. However, in strongly seasonal environments, community variability across seasons can be

278   expected to be profound, reflecting the life histories of the species involved and/or their responses to

279   seasonally changing environmental filters (Tonkin et al., 2017). For example, boreal freshwater insects

280   typically go through an intensive period of growth in late summer and autumn, followed by a period of

281   quiescence in the winter and a new burst of growth in spring and early summer; however, even closely

282   related species may have contrasting patterns of seasonal phenology (Nilsson, 1996). It might therefore

283   be expected that benthic macroinvertebrates in boreal streams occurred as relatively distinct temporal

284   guilds (or seasonal clusters; Shimadzu, et al. 2013), with seasonal variability contributing substantially

285   to overall community variability. It is therefore somewhat unexpected that we did not observe much

286   seasonal variation in our benthic communities, particularly as the stream environment did exhibit

287   strong seasonality. Although season contributed slightly more to temporal beta diversity than did inter-

288   annual variability, spatial beta diversity was by far the most important source of overall community

289   variability in the stream invertebrate communities.

290   Several studies have shown that the level of spatial synchrony in lentic ecosystems decreases

291   from physical to chemical, and further to biological, variables (Magnuson et al., 1990; Rusak et al.,

292   2008). We observed a similar range of responses, contingent upon the type of the variable, but even the

293   biological variable (taxonomic richness) showed significant spatial synchrony despite wide among-site

294   variation in absolute species numbers (see also Huttunen et al., 2014). Such regionally similar temporal

295   dynamics of alpha diversity indicates shared mechanisms of deterministic control of invertebrate

296   communities induced by the spatially correlated dynamics of environmental variables (here, climate

297   and water chemistry). Of the two temporal scales, among-year variability was a much more important

298   component of alpha diversity than was seasonality. Furthermore, seasons did not differ appreciably in

299   how large a proportion of the total diversity they represented (on average 65%, 69% and 69% for

300 spring, summer, and autumn, respectively). This difference between temporal scales was due mainly to

301 one specific year (2014) with somewhat lower species richness at most of the sites and seasons.

302 Summer 2016 with higher-than-average precipitation had no effect on richness, either at seasonal or

303 inter-annual scale, supporting previous studies showing that excess of water might not be such a strong

304 environmental filter for stream macroinvertebrates, at least if compared to drought (Woodward et al.,

305 2016; Huttunen et al., 2018).

306   Spatial variability (dissimilarity) among study sites was clearly the key component of benthic

307 macroinvertebrate beta diversity, with temporal variability contributing much less. Opposite to alpha

308 diversity, seasonal variability was a slightly more important component of community composition

309 than was inter-annual variability. In Van Allen et al.'s (2017) study on dragonfly communities along a

310 gradient of predation intensity in lakes, spatial and temporal variability were controlled by the same

311 local factor. The size of the top predator (invertebrate vs. fish) imposed a key habitat filter for

312 dragonfly communities, resulting in a highly predictable pattern of community variability among lakes

313 with differing top predator size and identity (Van Allen et al., 2017). In our study, spatial variability

314 was mainly associated with differences in water chemistry, i.e., sites supporting invertebrate

315 communities that differed most from the others were also the ones with most deviating water chemistry

316 conditions, particularly higher phosphorus concentrations. Such a key role of water chemistry as a

317 correlate of spatial beta diversity has indeed been frequently reported for stream invertebrates (e.g.

318 Thompson & Townsend, 2006; Astorga et al., 2012).

319   While seasonal community variability was stochastic, and unrelated to any of the measured

320 environmental factors, inter-annual variability was clearly lower than expected by chance at all study

321 sites, indicating strong environmental control (i.e., deterministic habitat filtering) of inter-annual

322 community variability. Communities varied less across years at sites with more diverse substrates, as

323 was previously observed by Brown (2003) who reported a decrease in invertebrate community

324   variability along a gradient of increasing spatial heterogeneity. The mechanism by which substrate

325   diversity enhances community stability is likely related to a greater number of refugia from predation

326   and flow disturbance afforded by more diverse stream substrates (see also Brown, 2003).

327   We expected that the seasonally variable environment of boreal streams would allow species

328   to coexist on an annual scale by occupying different temporal niches. This would result in relatively

329   distinct seasonal guilds (sensu Van Allen et al., 2017) and substantial community variability across

330   seasons (see Tonkin et al., 2017). However, community change between seasons was gradual and

331   largely the same taxa dominated the invertebrate community at all seasons. While this partly reflects

332   our relatively coarse taxonomic resolution for some groups (e.g., Simuliidae), most of the dominant

333   taxa were identified at species level. For example, the mayflies *Baetis rhodani* and *B. muticus* occurred

334   in differing body sizes in all samples and each season, as did also another ubiquitous species, the

335   coleopteran *Elmis aenea*, which is aquatic at all life stages. Our observation from these boreal streams

336   is consistent with the predictions by Korhonen et al. (2010) and Tonkin et al. (2017) that intra-annual

337   variation in aquatic ecosystems should exhibit a latitudinal gradient with seasonal community changes

338   contributing less to beta diversity at high-latitude streams.

339   One of our goals was to explore if any of the three seasons contributed disproportionately to

340   benthic biodiversity, indicating that sampling effort should be concentrated on that particular season for

341   the highest gains relative to the limited resources available for benthic sampling. Our results on species

342   richness suggest that if the goal of a study is to capture as large a proportion of total benthic

343   biodiversity as possible, no season does clearly better than the others. It might, however, be advisable

344   to avoid midsummer samples as most individuals are then quite small, resulting in a much longer

345   sample processing time compared to autumn and spring samples. In addition, inter-annual community

346   variability was lowest in autumn and highest in spring, which suggests that autumnal sampling is likely

347   the least susceptible to climatic vagaries, thus providing the most consistent and predictable conditions

348   for benthic sampling in boreal streams. However, biological differences between seasons were

349   relatively small, and it seems therefore that the seasonal timing of sampling may not be a critical

350   consideration in boreal stream bioassessment. While our results are only applicable to boreal systems,

351   we suggest that the same pattern may also hold for high-altitude streams which typically exhibit similar

352   strongly seasonal environmental variability as our high-latitude streams.

353   Our data are correlative by nature which obviously prohibits detailed examination of the

354   mechanisms underlying the patterns detected. Nevertheless, the few earlier studies that have directly

355   compared spatial vs. temporal components of variability in freshwater assemblages have also suggested

356   that spatial beta diversity outweighs its temporal counterpart (e.g., Suurkuukka et al., 2012; Van Allen

357   et al., 2017). However, spatial variability is always study-specific, depending on the geographical and

358   environmental configuration of the study sites. Another set of sites, even within the same region, could

359   have exhibited lower (or higher) community variability, depending on the type and intensity of the key

360   environmental filters. Our study sites span a fairly limited spatial extent and it is very likely that

361   another study extending across several watersheds and ecoregions would have encompassed wider

362   environmental gradients and therefore might have detected an even stronger contribution of spatial

363   relative to temporal community variability (see Mykrä et al. 2007). Furthermore, the predicted

364   alteration of the flow regimes of boreal streams (Veijalainen et al. 2010; Mustonen et al. 2018) is likely

365   to modify benthic biodiversity along both spatial and temporal dimensions. Exceptional climatic

366   conditions, especially severe droughts, are becoming more frequent in North European streams with the

367   changing climate (Spinoni et al. 2018), with potentially substantial changes in community composition,

368   and not always in a predictable manner (Nilsson et al., 2015; Sarremejane et al., 2021). Depending on

369   the timing and duration of the disturbance, this may then increase the relative importance of temporal,

370   either seasonal or inter-annual (or both), component of the overall community variability.

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377   CONFLICT OF INTEREST

378   The authors declare that the research was conducted in the absence of any commercial or financial

379   relationships that could be construed as a potential conflict of interest.

380

381   AUTHOR CONTRIBUTIONS

382   K.-L.H. and T.M. initiated the study and carried out the field work in co-operation with R.P.; L.O.S.V.

383   processed and identified macroinvertebrate samples; K.-L.H. analyzed the data; K.-L.H. and T.M. led

384   the writing of the manuscript. All authors commented critically on the final manuscript.

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524   FIGURE LEGENDS

525   **Figure 1.** Temporal variation across the study period (from late May to early October each year) in

526   water depth (mm) and water temperature (°C) at each study site.

527   **Figure 2.** Variation in taxonomic richness per sample across sites (A), years (B) and seasons (C).

528   Boxes represent median values (horizontal lines), and upper and lower quartiles; whiskers indicate the

529   range of nonoutliers.

530   **Figure 3.** NMS ordination based on Bray-Curtis dissimilarity, describing clustering of samples in

531   relation to A) site identity (i.e. spatial dissimilarity), B) study years (inter-annual dissimilarity) and C)

532   study seasons (seasonal dissimilarity). Ellipses represent standard deviation around group centers.

533   **Figure 4.** Partitioning of beta diversity to different sources of community variability at each study site.

534   A) Bray-Curtis dissimilarity on abundance data was used to quantify observed beta diversity. Spatial

535   beta diversity was calculated as divergence of a site from all other sites, separately for each sampling

536   time; inter-annual beta diversity as dissimilarity among years, separately for each season at each site;

537   and seasonal beta diversity as dissimilarity among seasons, separately for each year and site. B) A null

538   model approach was used to explore whether the observed levels of community variability differed

539   from random expectation. The greater the divergence from standard effect size -2 or +2 (dashed lines),

540   the lower or higher, respectively, community dissimilarity is compared to that expected by chance.

541   Between the dashed lines community dissimilarity does not differ from random expectation.

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542 **Figure 5.** Spatial (A) and inter-annual (B) community dissimilarity (beta diversity) as departure from

543 null (SES) in relation to the best explanatory variables, i.e. dissimilarity in water chemistry (Euclidian

544 distance among sites) and substrate diversity (Simpson index), respectively. Departure from null

545 describes how much the observed dissimilarity differs from random expectation, with negative values

546 indicating lower and positive values higher than expected dissimilarity, i.e. low spatial divergence/high

547 inter-annual stability, or high spatial divergence/low inter-annual stability, respectively.
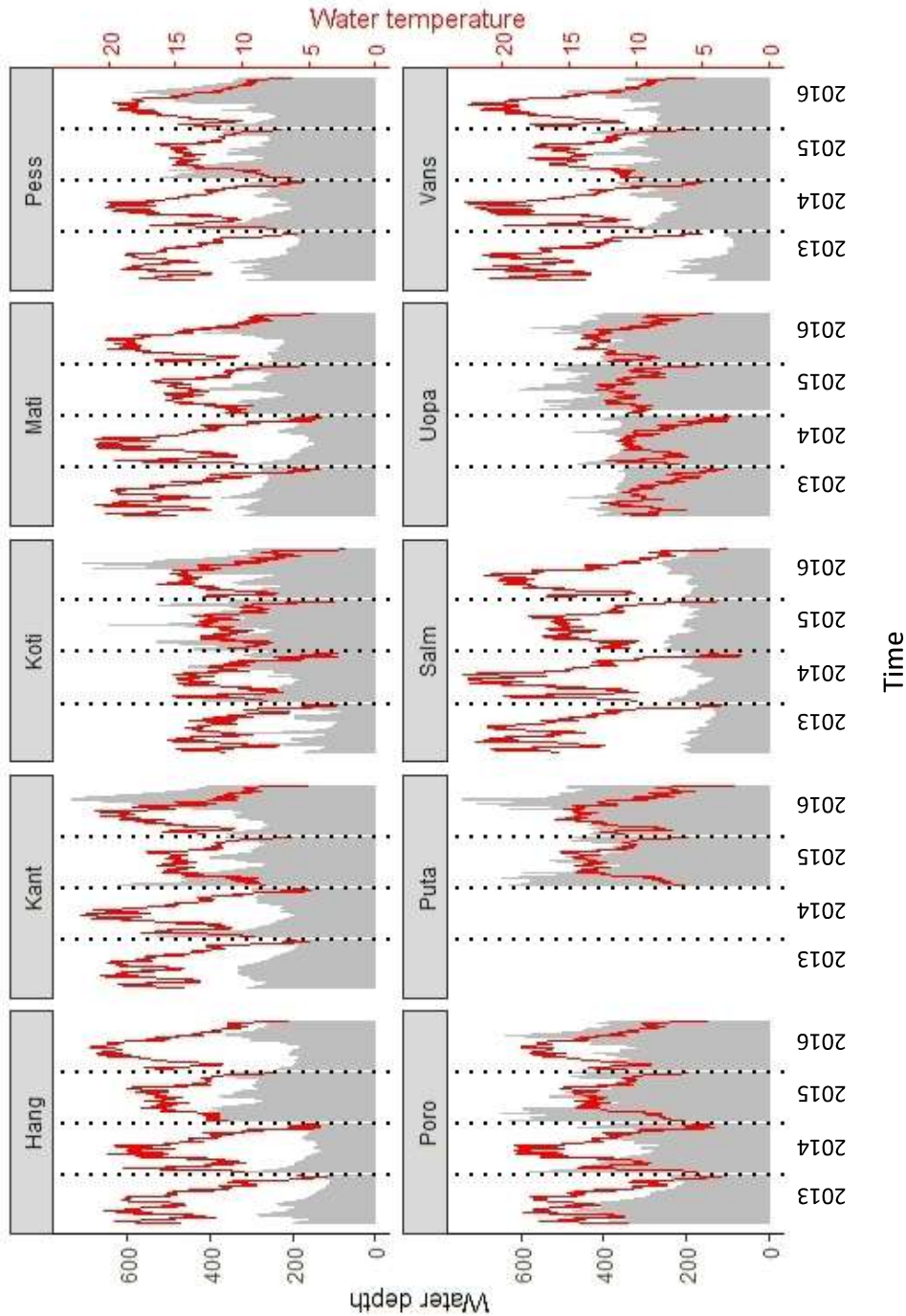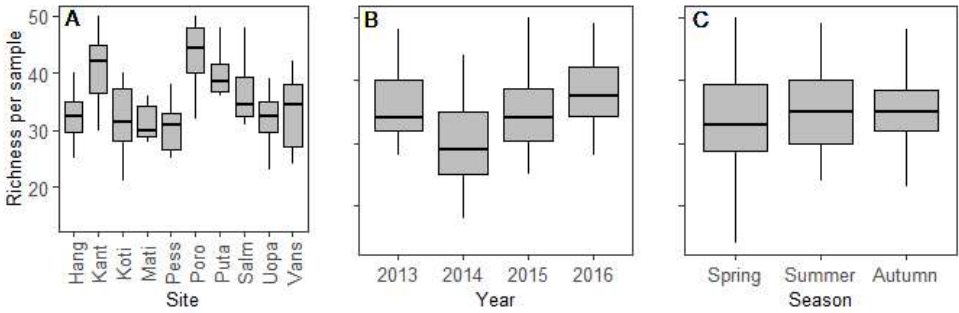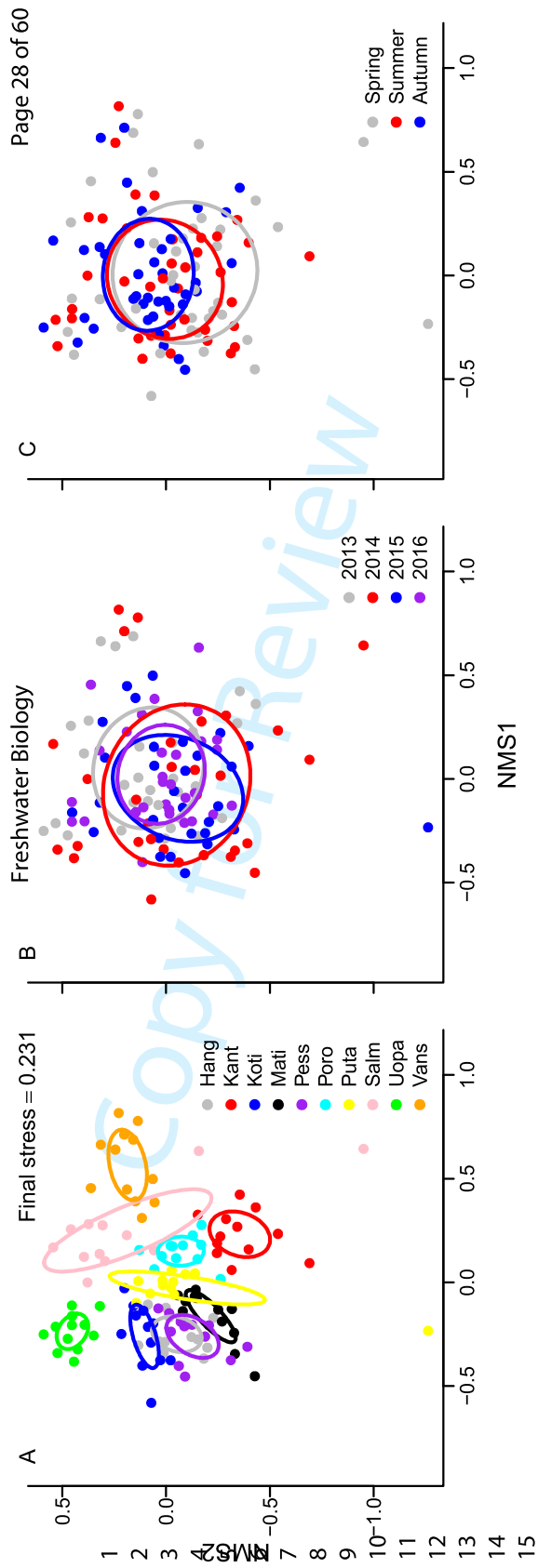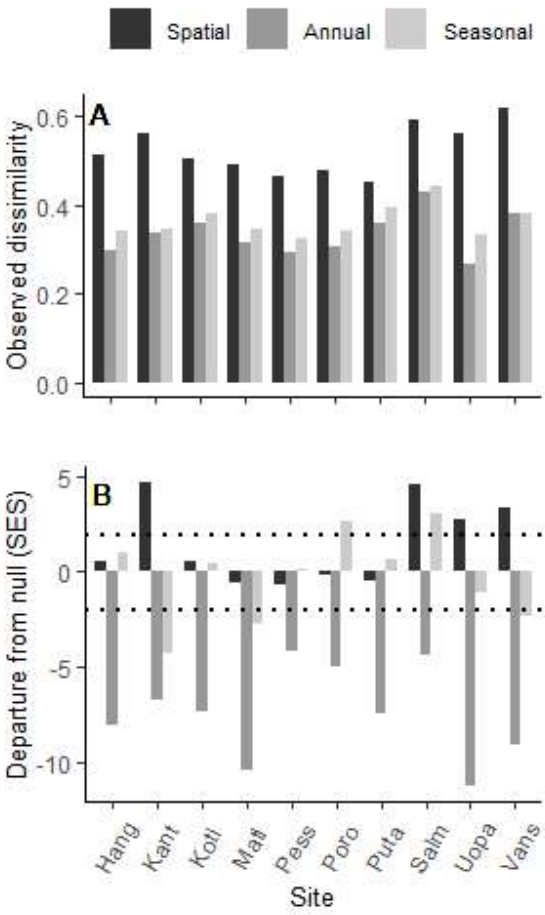
Freshwater Biology

Figure 1. Temporal variation across the study period (from late May to early October each year) in water depth (mm) and water temperature (°C) at each study site.

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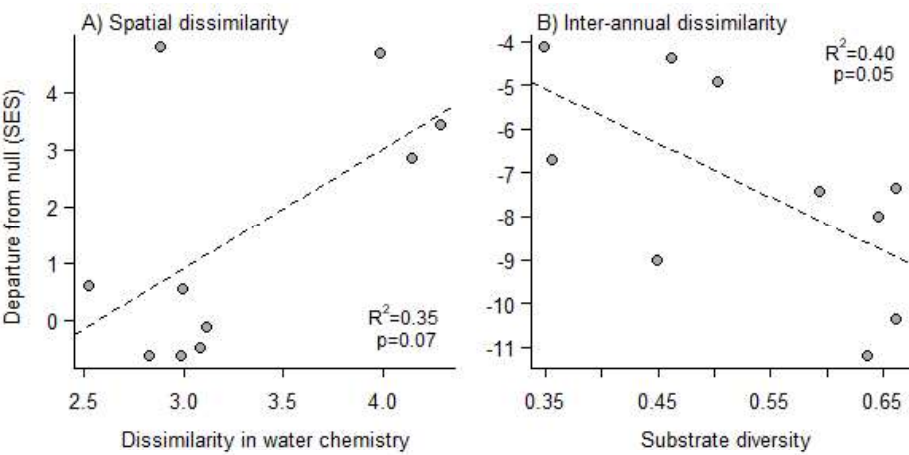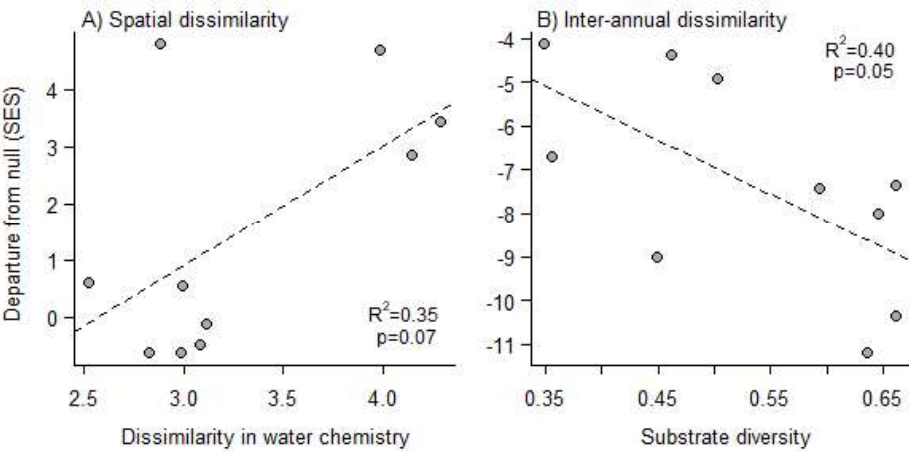102x171mm (72 x 72 DPI)

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Table 1. Spatial synchrony (mean, range and 95% confidence intervals) in physical, chemical, and biological

variables across the study period. Lag represents the time lag used in calculating the bootstrapped

synchrony values. Synchrony is interpreted as statistically significant if the bootstrapped 95% CI do not

overlap zero.

	Observed r_s			Bootstrapped r_s		
	Mean	Min	Max	2.50 %	97.50 %	Lag
Water depth (mm)	0.76	0.31	0.93	0.72	0.79	1
Water temperature (°C)	0.91	0.67	0.98	0.89	0.92	1
pH	0.14	-0.61	0.83	0.03	0.27	1
Conductivity (mS/m)	0.65	0.28	0.95	0.29	0.79	3
Total P (mg/l)	0.35	-0.48	0.90	0.23	0.57	3
Colour (mg Pt/l)	0.59	0.07	0.96	0.50	0.72	3
Taxonomic richness	0.34	0.25	0.84	0.08	0.57	1

Table S1. Means of environmental variables for each study stream. Temporal variation (CV) is presented for variables which were measured several times over the study period (see Methods). For mean water temperature and depth seasonal values are calculated as a mean over 14 days period (week before and after the sampling date). Daily values are presented in Figure 1.

|		Hang	Kant	Koti	Mati	Pess	Poro	Puta	Salm	Uopa	Vans
Catchment area (km2)		8.2	29.7	11.0	4.0	5.2	21.9	33.0	4.1	11.4	6.7
Substrate diversity		0.646	0.356	0.662	0.661	0.349	0.503	0.594	0.462	0.636	0.449
Connectivity (m^2)		2500	750	3300	60	350	900	4200	750	3000	1000
DOC (mg/l)		4.9 (0.09)	3.1 (0.03)	5.2 (0.18)	4.5 (0.13)	2.9 (0.13)	4.2 (0.09)	5.6 (0.37)	3.7 (0.17)	2.7 (0.50)	8.6 (0.03)
Tot N (mg/l)		193 (0.08)	170 (0.10)	303 (0.10)	239 (0.09)	167 (0.07)	170 (0.10)	268 (0.24)	277 (0.18)	114 (0.44)	280 (0.04)
Macrophyte cover (%)	Spring	7.2 (0.41)	57.4 (0.04)	6.2 (0.31)	2.3 (0.34)	15.7 (0.18)	59.6 (0.13)	40.1 (0.17)	27.6 (0.34)	59.1 (0.57)	4.8 (0.13)
	Summer	x	x	x	x	x	x	x	x	x	x
	Autumn	9.2 (0.18)	81.9 (0.12)	5.1 (0.02)	2.6 (0.05)	18.9 (0.19)	83.9 (0.04)	44.7 (0.14)	46.6 (0.16)	83.2 (0.21)	6.0 (0.08)
pH	Spring	7.8 (0.01)	7.6 (0.01)	7.8 (0.02)	7.8 (0.02)	7.7 (0.03)	7.6 (0.02)	7.8 (0.02)	7.6 (0.02)	7.9 (0.01)	7.6 (0.04)
	Summer	7.8 (0.03)	7.8 (0.03)	7.8 (0.03)	7.8 (0.02)	7.6 (0.05)	7.5 (0.03)	7.8 (0.02)	7.7 (0.02)	7.9 (0.02)	7.8 (0.01)
	Autumn	7.6 (0.03)	7.8 (0.04)	7.9 (0.01)	7.9 (0.02)	7.6 (0.02)	7.5 (0.03)	7.9 (0.01)	8.5 (0.12)	8.0 (0.01)	7.5 (0.03)
Conductivity$_{25°C}$ (mS/m)	Spring	5.7 (0.02)	5.3 (0.02)	14.6 (0.17)	13.6 (0.02)	4.8 (0.02)	4.7 (0.03)	14.3 (0.22)	4.3 (0.07)	18.6 (0.07)	6.0 (0.03)
	Summer	5.8 (0.03)	5.3 (0.07)	15.0 (0.20)	14.0 (0.08)	4.6 (0.07)	5.0 (0.10)	12.9 (0.17)	4.4 (0.10)	20.5 (0.08)	6.2 (0.10)
	Autumn	6.1 (0.05)	5.5 (0.04)	17.2 (0.16)	14.4 (0.06)	5.0 (0.01)	5.4 (0.12)	20.2 (0.31)	5.1 (0.06)	21.3 (0.04)	6.4 (0.10)
Tot P (mg/l)	Spring	6.0 (0.10)	8.0 (0.22)	8.0 (0.29)	5.3 (0.04)	5.7 (0.22)	6.7 (0.12)	10.1 (0.78)	15.0 (0.47)	5.2 (0.33)	9.5 (0.25)
	Summer	9.2 (0.26)	16.6 (0.40)	8.2 (0.47)	5.5 (0.56)	6.6 (0.24)	9.6 (0.15)	9.0 (0.38)	16.0 (0.27)	5.4 (0.24)	7.4 (0.16)
	Autumn	5.9 (0.42)	5.0 (0.21)	7.0 (0.30)	4.0 (0.31)	4.6 (0.17)	5.4 (0.13)	4.7 (0.13)	12.7 (0.18)	3.3 (0.27)	8.5 (0.35)
Colour (mg Pt/l)	Spring	40 (0)	24 (0.21)	43 (0.23)	34 (0.14)	23 (0.13)	35 (0.16)	58 (0.22)	39 (0.06)	26 (0.18)	88 (0.06)
	Summer	40 (0.01)	43 (0.29)	70 (0.39)	31 (0.27)	48 (0.77)	70 (0.62)	108 (0.33)	48 (0.38)	26 (0.42)	83 (0.25)
	Autumn	30 (0.38)	21 (0.35)	38 (0.26)	25 (0.49)	23 (0.53)	40 (0.44)	46 (0.54)	33 (0.29)	16 (0.63)	92.5 (0.36)
Mean water temperature (°C)	Spring	12.3 (0.09)	11.0 (0.15)	9.7 (0.06)	11.8 (0.13)	9.8 (0.19)	8.5 (0.20)	9.4 (0.07)	12.7 (0.08)	8.7 (0.15)	11.6 (0.13)
	Summer	18.1 (0.09)	17.9 (0.12)	13.4 (0.07)	17.0 (0.13)	17.3 (0.11)	16.3 (0.11)	13.4 (0.11)	18.6 (0.12)	11.5 (0.13)	18.7 (0.14)
	Autumn	10.3 (0.19)	10.7 (0.24)	7.8 (0.21)	10.1 (0.22)	10.7 (0.20)	9.1 (0.18)	7.1 (0.30)	10.0 (0.31)	7.2 (0.15)	10.6 (0.23)
Mean water depth (mm)	Spring	281 (0.30)	418 (0.25)	324 (0.30)	313 (0.15)	391 (0.21)	486 (0.16)	443 (0.10)	218 (0.10)	576 (0.51)	270 (0.28)
	Summer	216 (0.42)	307 (0.25)	302 (0.41)	270 (0.35)	298 (0.29)	369 (0.22)	518 (0.04)	181 (0.19)	414 (0.21)	254 (0.41)
	Autumn	196 (0.41)	284 (0.28)	249 (0.41)	238 (0.16)	252 (0.22)	310 (0.23)	446 (0.02)	165 (0.16)	382 (0.11)	242 (0.47)
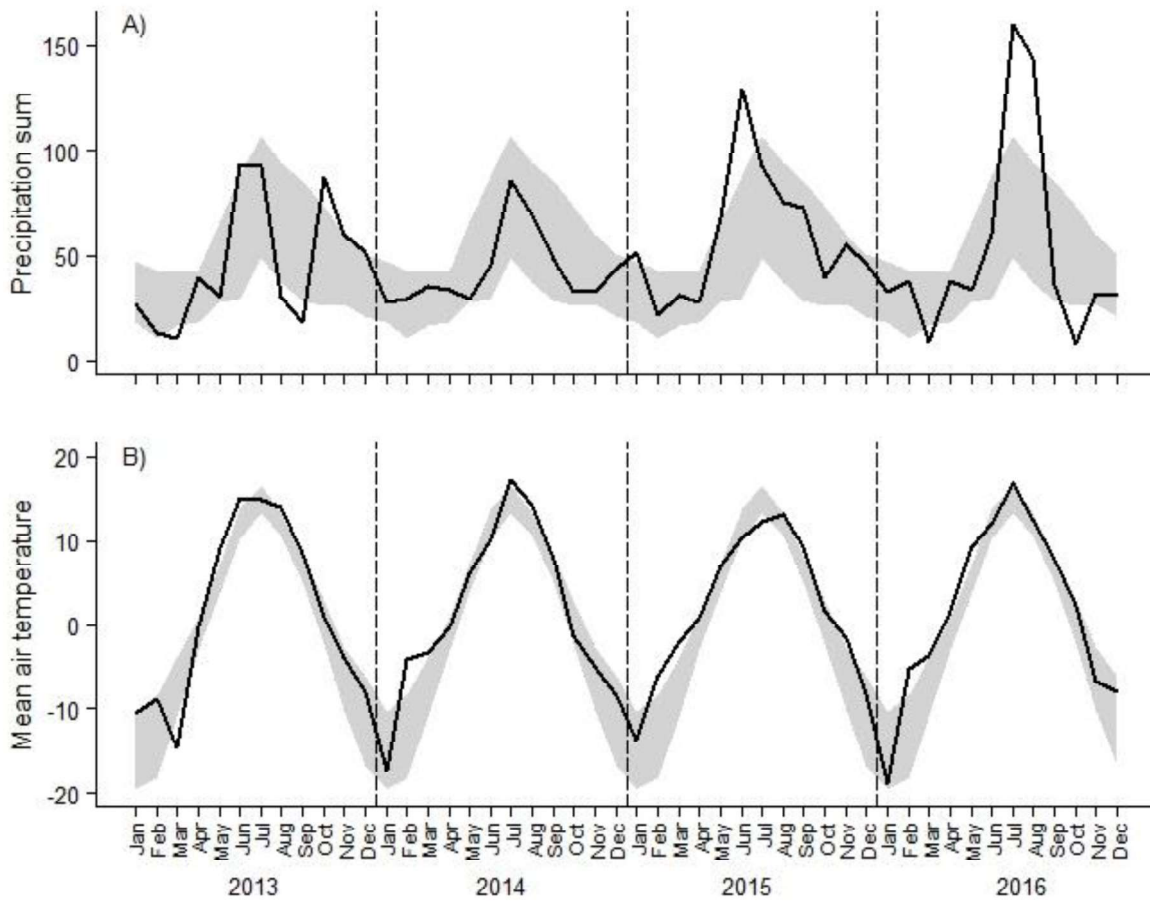
Figure S1. A) Monthly sum of precipitation (mm of water or snow) and B) average air temperature (°C)

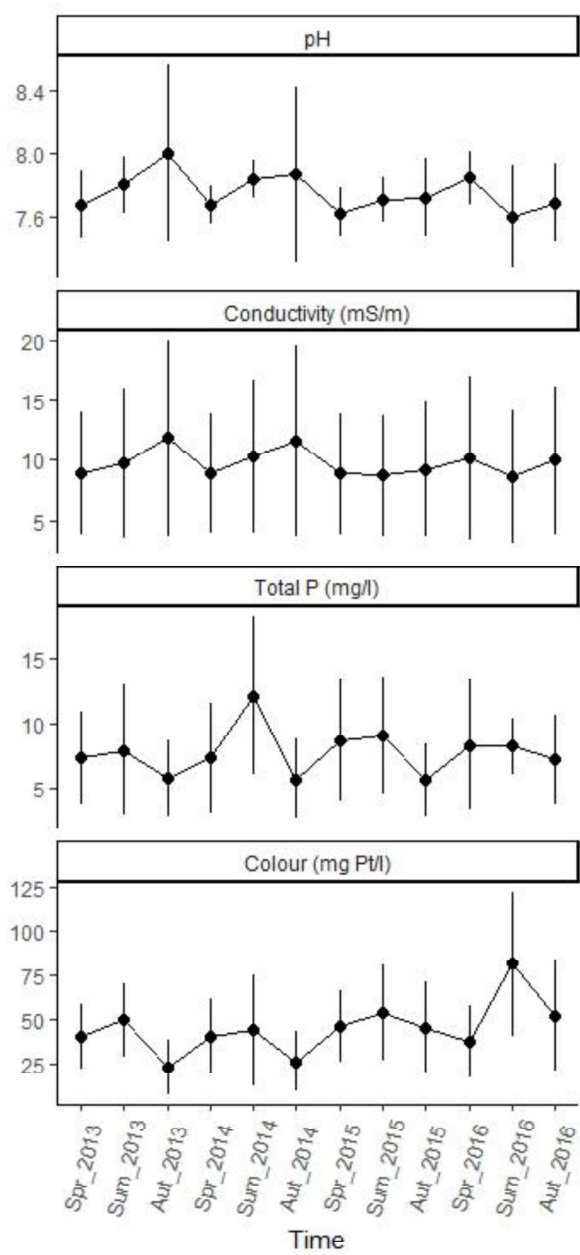at a nearby weather station. Grey areas represent long-term (1969-2016) standard deviation.

Figure S2. Variation in water chemistry variables across time. Error bars show variation among sites (±1SD).