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1 **Multiple stressors shape invertebrate assemblages and reduce their trophic niche: a case**  
2 **study in a regulated stream**

3

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14

15 **Abstract**

16 Few studies have addressed how the diversity of basal resources change with stream regulation  
17 and the potential consequences on river biota. We sampled invertebrates above and below a  
18 series of dams, over two years, at both downwelling and upwelling zones. In each zone, we  
19 recorded the daily temperature and flow variations, estimated the algal development, measured  
20 the available resources, and analysed carbon and nitrogen stable isotope compositions of the  
21 invertebrate community. The number of hydrological pulses were typically higher below the  
22 dams than above the dams especially during high-flow periods whereas the groundwater outlets  
23 had minor effects on invertebrate assemblages. Invertebrate abundance, richness and diversity  
24 tended to decrease below the dams. Co-inertia analysis showed that flow and temperature  
25 variations, and eutrophication explained most of the variance in the invertebrate assemblages,

26 which comprised a higher number of resilient taxa below than above the dams. The proportions  
27 of pesticide-sensitive invertebrates were lower below the dams and ovoviviparous and more  
28 generalist taxa were prominent. We did not observe the expected CPOM decrease and FPOM  
29 increase downstream. Accordingly, the proportions of each functional feeding group were  
30 remarkably similar above and below the dams despite the long distance between the sectors  
31 (>100 kms). The diversity of basal resources used within assemblages progressively increased  
32 downstream above dams. In contrast, the diversity of resources used by organisms below the  
33 dams decreased from upstream to downstream suggesting a significant influence of flow  
34 regulation on aquatic food webs. Finally, the shorter trophic chains for the invertebrate  
35 assemblages below the dams suggests that the effects of stream regulation and eutrophication  
36 induced a simplification of food webs. To our knowledge, this study is the first to connect  
37 taxonomic and functional trait changes in response to multiple stressors with the associated  
38 modifications in isotopic niches within aquatic invertebrate assemblages.

39

40 **Context:** Understanding how stream regulation and associated anthropogenic pressures act on  
41 aquatic assemblages and trophic niches is necessary to guide management actions.

42

43 **Goal:** We aimed to investigate the functional responses (traits and trophic niches) of aquatic  
44 invertebrate assemblages to stream regulation and eutrophication.

45

46 **Methods:** We used univariate and multivariate analyses to compare the invertebrate  
47 assemblages above and below the dams and to assess the contributions of hydrology (including  
48 groundwater supplies to the river), temperature and eutrophication to the variability in the  
49 composition of invertebrate assemblages. We also considered the relative utilization of a  
50 selected set of traits describing invertebrate resilience, resistance and specialization to address

51 the potential functional effects of stream regulation on invertebrate assemblages. Finally,  
52 carbon and nitrogen isotope analyses allowed us to characterize the length and width of  
53 invertebrate assemblage food webs as related to the availability and diversity of basal  
54 resources.

55

56 **Results:** Invertebrate abundance and richness generally decreased below the dams, with the  
57 highest impacts on insect taxa. Co-inertia analysis showed that stream regulation and  
58 eutrophication were main drivers of the aquatic invertebrate assemblages. The analysis  
59 separated the sites above and below the dams according to flow and temperature variation,  
60 whereas eutrophication appeared as a secondary stressor that separated the sites within each  
61 sector. Furthermore, the series of dams resulted in (i) a higher proportion of resilient (e.g.,  
62 multivoltine) and resistant (ovoviviparous) taxa and a majority of generalists in assemblages  
63 below dams, (ii) an impact on the classical dynamics of CPOM (decrease) and FPOM  
64 (increase) sources from upstream to downstream, and (iii) a reduction in the diversity of  
65 resource use and in the trophic chain length of invertebrate assemblages below dams. The  
66 cooler and less oxygenated upwelling zones had lower invertebrate abundance; however,  
67 contrary to our expectation, the variation in the groundwater supply did not affect the  
68 composition of epigeal invertebrate assemblages.

69

70 **Conclusion:** This study provides insights about the impacts of flow regime alteration and  
71 eutrophication on food webs that may have been caused by regulation of permanent streams.  
72 To our knowledge, this is the first to connect taxonomic and functional trait changes in response  
73 to multiple stressors with the associated modifications in energy fluxes in aquatic invertebrate  
74 assemblages. This study suggests that bed stability, which is associated with a reduction in  
75 channel mobility below the dams and with moderate eutrophication, may provide the shelter

76 and resources that can locally favour invertebrate assemblage dynamics and lessen the effects  
77 of flow regulation. In addition, the study suggests that the biological trait-based approach and  
78 isotope analysis are complementary approaches for addressing ecosystem functioning. The  
79 relative utilization of traits indicates the functional potential of aquatic invertebrate  
80 assemblages to face multiple stressors whereas isotope analysis is an expression of the actual  
81 effect of the stressors on the trophic structure of aquatic invertebrate assemblages.

82

### 83 **Key words**

84 benthic invertebrates – biological traits – aquatic food web – stream regulation

85

### 86 **1. Introduction**

87 Flowing waters are dynamic ecosystems whose functioning depends closely on the continuity  
88 of energy and material flows through longitudinal, transversal, vertical and temporal  
89 dimensions (Amoros and Petts, 1993). However, most of the flowing water worldwide has been  
90 massively modified by impoundments to meet different objectives such as flood protection,  
91 river navigation, recreation, and water supplies; these modifications represent an important  
92 threat to aquatic communities in the context of climate change (Nilsson *et al.*, 2005). In  
93 addition, in response to the rapid development of human populations, the demand for energy  
94 has greatly increased in recent decades and has resulted in the construction of many  
95 hydropower dams, making the threat even more prevalent (Zarfl *et al.*, 2014).

96

97 The abiotic effects of damming and more generally the effects of anthropogenic disruption of  
98 the river continuum have been studied for many years (e.g. Baxter, 1977; Ward and Stanford,  
99 1983a; Ligon *et al.*, 1995; Rosenberg *et al.*, 2000). Apart from changes in the flow regime, they  
100 include pronounced changes in the temperature, dissolved oxygen concentrations, and

101 chemical composition of water. In addition, the fragmentation of the rivers by dams prevents  
102 the transport of sediment downstream, which may deeply modify the channel structure and  
103 dynamics by causing river incision and bed armouring (Brenna *et al.*, 2019). These changes  
104 generally result in a loss of aquatic diversity and in river homogenization (e.g. Poff *et al.*, 2007;  
105 Rolls *et al.*, 2012; Mbaka and Mwaniki, 2015; Mellado-Diaz *et al.*, 2019). The alteration of the  
106 channel dynamics may also modify the exchanges between the hyporheic zone and surface  
107 flow (Caschetto *et al.*, 2014) whereas local hydrological exchanges greatly contribute to stream  
108 functioning (Boulton *et al.*, 1998, 2010). For example, groundwater outlets provide a supply  
109 of cooler water (White *et al.*, 1987) that is rich in nutrients (Valett *et al.*, 1994). In addition, in  
110 natural situations benthic invertebrates may migrate within the sediment to escape flow  
111 disturbances (Dole-Olivier and Marmonier, 1992; Maazouzi *et al.*, 2017; Vander Vorste *et al.*,  
112 2017). However, less is known about the direct effect of groundwater supply and the associated  
113 water quality on the benthos. Damming has also been shown to affect leaf litter decomposition  
114 and the distribution of functional feeding groups (Martinez *et al.*, 2013) as well as functional  
115 richness (Laini *et al.*, 2019) and to cause profound changes in food webs (Power *et al.*, 1996;  
116 Mor *et al.*, 2018). For example, damming in Mediterranean streams can increase hydrological  
117 and sedimentological stability downstream dams, leading to a modification of available  
118 resources and a change from a detritus-based to an algae-based food web (Mor *et al.*, 2018).  
119 Finally, apart from the direct effects of low flows or changes in flow timing associated with  
120 stream regulation, nutrient effluents from the catchment combined with low flows (damming  
121 and water abstraction for agriculture) and the higher transparency associated with a lack of fine  
122 sediment transport may exacerbate primary production, ultimately leading to eutrophication  
123 (Biggs, 2000). Moreover, chemical releases associated with agricultural or industrial activities  
124 or with contaminants accumulated in the reservoir may interact with flow alteration (Colas *et*  
125 *al.*, 2013).

126

127 As a result, stream regulation involves multiple stressors that constrain the resilience and  
128 resistance capabilities of aquatic invertebrate assemblages, which can potentially be assessed  
129 through a multiple trait-based approach (Statzner *et al.*, 2010). According to the literature, the  
130 disturbances associated with frequent flow fluctuations may favour small size invertebrates  
131 (higher resilience capability; Townsend *et al.*, 1997), and/or invertebrates with short  
132 development periods (life duration <1 y.) and/or with more than one generation per year  
133 (multivoltine). Apart from the specific hydraulic effects of stream regulation, the  
134 eutrophication that frequently occurs below dams results in selection for organisms with traits  
135 that allow them to resist the potential degradation of the water quality (e.g. offspring protection  
136 by ovoviviparity, less sensitivity to oxygen depletion). As a consequence, by modifying the  
137 composition of assemblages, stream regulation may lead to simplified food webs. Food webs  
138 can be also affected by dams and associated reservoirs which act as powerful retention  
139 structures in river networks by burying particulate organic matter in sediments (Vörösmarty *et*  
140 *al.*, 2003). This retention process decreases the availability of particulate organic matter to  
141 downstream benthic food webs, affecting the secondary production of consumers (Ward and  
142 Stanford, 1983b; Power *et al.*, 1996; Kominoski and Rosemond, 2012). Moreover, reduction  
143 of POM below dams would lead to dominant algae-based food webs characterized by a lower  
144 complexity than food webs based on both algae and detritus (Power *et al.*, 1996). Indeed,  
145 Layman *et al.* (2007) showed that a reduction of food diversity (as expected below dams) would  
146 strongly reduce the trophic niche width of primary consumers and predators, reflecting a  
147 homogenization of energy flow pathways to top predators. This reduction of trophic niche  
148 width could be critical for ecosystem structure and functioning as it destabilizes food webs and  
149 increases the extinction risk of top predators. With this objective, stable isotopes appear as very  
150 pertinent tools to evaluate the consequences of environmental stressors affecting food sources

151 for benthic communities (Pingram et al., 2012; Burdon et al. 2019). Understanding the  
152 combined effect of different stressors and the contribution of the different environmental  
153 parameters in the structure and function of aquatic communities remains a key question for  
154 managers to address restoration goals and mitigation measures (Azzellino *et al.*, 2015).  
155 Therefore, integrated approaches that consider various physical and chemical compartments  
156 and biological processes in a single study are required. The Ain River, which rises in the Jura  
157 Mountains from a karstic emergence at approximately 680 metres above sea level, is a major  
158 tributary of the Upper Rhône. It is 190 km long and has 3765 km<sup>2</sup> drainage area. Five  
159 hydroelectric power plants were built on its main course between 1928 and 1968. Among them,  
160 the Vouglans dam, built in 1968, forms a 35-km long reservoir of more than 600 million m<sup>3</sup> of  
161 water. This large reservoir is followed by a series of four other dams in succession along the  
162 river course that strongly influence water flow and generate a significant sediment deficit  
163 (Rollet *et al.*, 2013; Dole-Olivier *et al.*, 2019). This river thus represents a good experimental  
164 situation for addressing the complex effects of stream regulation and its associated stressors on  
165 the taxonomic composition, functional responses and potential changes in food web  
166 complexity.

167

168 In this study, we hypothesize that the combination of thermal, hydraulic and land use  
169 disturbances below the dams is likely to (i) decrease the abundance and richness of invertebrate  
170 assemblages, (ii) modify their taxonomic composition, by favouring organisms with resilience  
171 and resistance traits as well as generalists, and (iii) alter the balance among functional feeding  
172 groups, and (iv) modify the resource use by invertebrates and in turn the complexity of the  
173 invertebrate food web by reducing the niche width of primary consumers and predators. At the  
174 same time, we evaluate the potential of upwelling zones, which are characterized by thermally  
175 buffered groundwater supplies and are rich in nutrients to modulate the impacts of dams on



176 benthic invertebrates. More precisely, we hypothesize that the groundwater upwellings below  
177 the dams may (i) locally limit the negative thermal impacts of stream regulation on invertebrate  
178 assemblages and (ii) stimulate primary production with potential consequences on food webs.

179

## 180 **2. Material and Methods**

### 181 *2.1. Study locations*

182 We selected three sites (A1 to A3; Fig. 1A) above the series of dams to represent environmental  
183 situations that are not or moderately subjected (by passed section in A3) to hydrological  
184 alterations and three sites below the series of dams (A4 to A6; Fig. 1A). According to a  
185 preliminary study, the six sites were assumed to be influenced by various alterations in land  
186 use, and the differences in temperature and trophic status among the three sites within each  
187 sector allowed us to consider the possible confounding effects of these factors (Table 1). In  
188 addition, at each of the six sites, groundwater supply zones were mapped using the method of  
189 Dole-Olivier *et al.* (2019). This mapping permitted the identification of one zone that was  
190 supplied with groundwater (upwelling; Fig. 1B) and one zone that was supplied with surface  
191 water only (downwelling; Fig. 1B) for each site.

192

### 193 *2.2. Environmental characterization*

#### 194 *2.2.1. Water level and temperature*

195 Two Mini-Diver sensors (Schlumberger, Water Services, Waterloo, Canada) were installed per  
196 site to monitor pressure (corresponding to the water level after correction for atmospheric  
197 pressure) and temperature dynamics during the experiment (from August 10, 2014 to July 08,  
198 2016). One sensor was installed in the streambed sediments in a zone influenced by  
199 groundwater outlets (upwelling) and the other in a downwelling zone (no influence of  
200 groundwater) in order to assess the relative importance of these zones for the epigean benthic

201 invertebrates (Fig. 1B). Water levels (cm) were further transformed into hourly discharge ( $\text{m}^3 \cdot \text{s}^{-1}$ )  
202 <sup>1</sup>) by using the relationship between the measured discharges and the water levels at each site.  
203 We used the water level series to compute, at each site and each date, four metrics related to  
204 the prevailing hydrological conditions for the 15 days preceding the invertebrate sampling: (i)  
205 the number of extreme ecological events, which was measured by the number instances of an  
206 increase of >50% in less than 1 day, (ii) the average discharge ( $\text{m}^3 \cdot \text{s}^{-1}$ ), (iii) the standard  
207 deviation of the discharge, and (iv) the coefficient of variation of the discharge. Similarly, we  
208 used the water temperature series to compute for each site, each zone and each date, three  
209 metrics considering the prevailing water temperature conditions for the 15 days preceding the  
210 invertebrate sampling: (i) the average temperature ( $^{\circ}\text{C}$ ), (ii) the standard deviation of the  
211 temperature, and (iii) the temperature range ( $^{\circ}\text{C}$ ).

212

### 213 2.2.2. *Chemical parameters*

214 Sampling was performed at six times (August 2014, October 2014, April 2015, July 2015,  
215 October 2015, and June 2016; arrows on Fig. 2) to cover all environmental conditions  
216 (hydrology and temperature) in three seasons (spring, summer and fall) twice. To assess the  
217 influence of ground waters on water quality, we considered 3 sampling points under the direct  
218 influence of upwelling and 3 sampling points in the downwelling zone. Chemical parameters  
219 were measured at these sampling points sampling time, with the exception of October 2014  
220 due to a device malfunction. The dissolved oxygen concentration ( $\text{mg} \cdot \text{L}^{-1}$ ) and electrical  
221 conductivity ( $\mu\text{S} \cdot \text{cm}^{-1}$ ) were measured directly in the field using portable EC (electric  
222 conductivity) and DO-meter (HQ20, HACH, Dusseldorf, Germany) probes. Inorganic nutrients  
223 ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and  $\text{PO}_4^{3-}$ ) were measured in previously filtered (glass fibre membrane GF/F,  
224 porosity:  $0.7 \mu\text{m}$ ) water samples by standard colorimetric methods (Grasshoff *et al.*, 1999)  
225 using an automatic analyser (SmartChem200, AMS, Frepillon, France).

226

### 227 2.3. Basal resources and stable isotope analyses

228 To allow a temporal and spatial comparison of the availability of nutrient resources and their  
229 ability to provide energy (in the form of carbon) to organisms, we collected and quantified the  
230 basal nutrient resources available for the invertebrates at each site and in the upwelling and  
231 downwelling zones for the three sampling occasions in 2015. Following the approach of  
232 François *et al.* (2020), this sampling consisted of collecting all available resources occurring  
233 within a standardized area (256 cm<sup>2</sup>) at a depth of 1 cm at the six points selected in the  
234 upwelling and downwelling zones of each site. The nutritional resources sampled were sorted  
235 in the laboratory, dried, and weighed, and the quantity of organic carbon in each resource (g.  
236 of C. m<sup>-2</sup>) was assessed by elemental analysis (Thermo FlashEA 1112; Thermo Electron). The  
237 seven quantified nutrient sources found were: (i) sedimentary biofilm (biofilm), (ii) algal  
238 biofilm developing on stones (perilithon), (iii) coarse particulate organic matter (CPOM,  
239 organic matter particles > 1 mm), (iv) fine particulate organic matter (FPOM, organic matter  
240 particles < 1 mm), (v) aquatic mosses (moss), (vi) filamentous algae (algae) and (vii) aquatic  
241 macrophytes (macrophyte).

242

243 In addition, during these three sampling occasions in 2015, additional benthic invertebrate  
244 samples (Surber net mesh size: 500 µm) were collected to estimate the size of the trophic niche  
245 of organisms and assemblages at each site and each zone (upwelling and downwelling).  
246 Invertebrates were sorted and identified at the lowest possible taxonomic level (see Appendix  
247 1 and 2 for identification level used) and 5 individuals of each taxon were used for isotopic  
248 analyses for each date, site and zone. When possible, we avoided using parts of the animals  
249 that contained the digestive tracts, as gut contents may affect the isotope ratio of the sample  
250 (Mateo *et al.*, 2008). Invertebrates were weighed individually (dry mass between 0.1 and

251 0.5mg) in tin capsules. The basal resources were acidified using 1 M HCl to remove carbonates  
252 before carbon isotope analysis, and an amount of 2 to 20 mg of basal resources, depending on  
253 the carbon and nitrogen content, was encapsulated in tin capsules. The isotopic compositions  
254 of carbon ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) of the different invertebrates selected and of the  
255 basal resources described above were measured using an isotope ratio mass spectrometer  
256 (Isoprime 100, Elementar) coupled to an elementary analyser (Vario PyroCube, Elementar).  
257 In-house standards calibrated against IAEA-N1, IAEA-N2, IAEA-CH6 and IAEA-C3  
258 reference materials were analysed with the samples, and the standard deviations of the replicate  
259 analyses were lower than 0.20‰. The carbon and nitrogen stable isotope compositions were  
260 expressed as  $\delta$  in ‰ with V-PDB ( $\delta^{13}\text{C}$ ) and air ( $\delta^{15}\text{N}$ ) as standards.

261

#### 262 *2.4. Primary production*

263 To cover a maximum range of environmental conditions over the width of each zone (up and  
264 downwelling), 2 transects, separated by a few metres and parallel to each other, were defined  
265 per site. Three points corresponding to different substrates (sand, gravel, pebbles) were selected  
266 at random on each of the transects over an area of approximately 0.025 m<sup>2</sup>. Six samples were  
267 thus taken in each zone on each sampling occasion. In each sample, the biofilm was scraped  
268 with a brush, and the substrate was rinsed several times to obtain a complete collection of the  
269 biofilm. The sample was transferred into a propylene bottle, after removing any  
270 macroinvertebrates, leaves and stones. The sample was then homogenized and divided into two  
271 equal subsamples. The first subsample was used for chlorophyll-*a* measurement. The second  
272 subsample was fixed with Lugol solution for further identification of the different groups of  
273 algae. On the same day, the chlorophyll-*a* was quantified in the laboratory by filtering each  
274 biofilm sample on a glass fibre membrane GF/C (pore diameter 1.2  $\mu\text{m}$ ). Pigment extraction  
275 was carried out with 90% acetone. After centrifugation, the absorbance of the supernatant was

276 measured at 630, 645, 663 and 750 nm wavelengths, using a spectrophotometer. The  
277 concentrations in chlorophyll-*a* were obtained by applying the Lorenzen formula (according to  
278 the NF T90-117 French standard) and used as a proxy for algal biomass. For each benthic  
279 biofilm subsample, the individuals were classified into the main functional groups, i.e.  
280 cyanobacteria, chlorophytes and diatoms, and counted under a microscope as the number of  
281 cells per m<sup>2</sup> (Bourrely, 1968, Prescott *et al.*, 1978). Given the high densities observed, we used  
282 a Nageotte chamber to count the cells in small volumes.

283

## 284 2.5. *Benthic invertebrates*

### 285 2.5.1. *Sampling*

286 Three Surber samples (area 0.05 m<sup>2</sup>, mesh size 500 µm) were taken from each zone (upwelling  
287 and downwelling), at each site on each sampling occasion. In addition, at each site and each  
288 sampling occasion, we collected three additional Surber samples in the vicinity of the  
289 upwelling and the downwelling zones to cover the different hydraulic and substrate conditions.  
290 Individuals were identified at the genus level using Tachet *et al.* (2010), with the exception of  
291 Diptera, which were identified at the family level. The community matrix data are available in  
292 Appendix 1 and 2.

293

### 294 2.5.2. *Biological traits metrics*

295 The biological traits used in this study were extracted from a European database constructed  
296 from the literature that contains information on life history, resilience and resistance potential,  
297 morphology, physiology and feeding behaviour for European freshwater invertebrate genera  
298 (Tachet *et al.*, 2010). In this public database, available on the web (see Schmidt-Kloiber and  
299 Hering, 2015), traits are usually divided into categories and are quantified using affinity scores  
300 between 0 and 3 (maximal size, voltinism, reproduction types, locomotion and relation to

301 substrate) or 0 and 5 (food and feeding habits) (Chevenet *et al.*, 1994). This quantification,  
302 which enables the compilation of information from various sources, also (i) captures the  
303 variability in traits that often occurs in an organism at different life stages and (ii) accounts for  
304 within-taxon variations in responses. We computed metrics describing (i) the relative  
305 utilization of fuzzy-coded traits such as multi-voltinism, small size, short life span,  
306 ovoviviparity, and oligotrophy (Table 2; see Mondy and Usseglio-Polatera, 2013) to address  
307 the response of organisms in terms of resilience and resistance abilities, (ii) food Rao diversity  
308 and community specialization (Table 2; Mondy and Usseglio-Polatera, 2014) in terms of food  
309 and trophic status, and (iii) the ‘Species at Risk’ index to consider a potential additional stress  
310 associated to agricultural activities (SPEAR pesticide relative abundance index; Liess and von  
311 der Ohe, 2005). Selected metrics are available in Appendix 3.

312

### 313 2.6. Data analyses

314 To assess temporal and spatial effects on the above selected abiotic parameters and biological  
315 metrics, we used mixed ANOVAs with zones (upwelling and downwelling), sectors (above  
316 and below dams) and sampling dates as fixed effects, and the sampling sites as random effects.  
317 When the normality assumption was not met, we used the Box-Cox transformation (Box and  
318 Cox, 1964). We used co-inertia analysis (CoiA) to assess the contributions of parameters  
319 describing hydrology, temperature and eutrophication, for explaining the variance in  
320 invertebrate assemblage composition. Since algal variables (eutrophication) were taken on  
321 transects whereas benthic invertebrate samples were taken at sampling point, we summed  
322 samples by zones (upwelling vs. downwelling) within each site at each season, thus ending up  
323 with 72 sampling units. CoiA provides factorial axes from each dataset that are the most  
324 covariant, i.e., they simultaneously depict the highest possible variance of each dataset and  
325 optimize their correlation (Dolédec and Chessel, 1994; Dray *et al.*, 2003), and we considered

326 the loadings of variables to assess the relative contribution of each of them to the covariance  
327 between benthic invertebrates and environmental variables. The strength of the relationship  
328 was measured by means of the  $Rv$  coefficient, a multidimensional equivalent for two tables of  
329 the regression coefficient for two variables (Robert and Escoufier, 1976). We tested the  
330 statistical significance of the  $Rv$  coefficient by a Monte Carlo permutation test and by  
331 comparing the distribution of 999 replicated matches of the two datasets (after random  
332 permutations of their rows) with the observed  $Rv$  coefficient.

333

334 To evaluate the changes in the trophic diversity of the benthic invertebrate assemblages, we  
335 used community-wide metrics based on the carbon and nitrogen isotope compositions. The  
336 isotopic space area was used to quantify the trophic diversity (Newsome *et al.*, 2007; Jackson  
337 *et al.*, 2011). The  $\delta^{13}\text{C}$  (CR) and  $\delta^{15}\text{N}$  (NR) ranges in the  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  biplot space were calculated  
338 using the mean isotope composition of each taxon following the approach developed by  
339 Laymann *et al.* (2007). These ranges provide, respectively, an integrative measure of the  
340 diversity of the basal resources that are exploited by the assemblage (noted CR) and of the  
341 trophic level diversity (NR). Because the convex hull approach emphasizes the weight of  
342 species with extreme positions in the  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  biplot space, we used the standard ellipse  
343 approach (SEAnr), which was calculated using a Bayesian framework with  $2 \times 10^4$  iterations,  
344  $10^3$  burning-in and 10% of thinning (Jackson *et al.*, 2011). Since the variability in the isotope  
345 composition of the basal resources among sampling sites and dates explained a part of the  
346 variation in the isotope space area, we normalized values by the standard ellipse area of the  
347 resources (knowing that all resources were recovered from all sites, zones and dates).

348

349 Statistics and graphical outputs were performed and generated with R freeware (R  
350 Development Core Team, 2020) including the *ade4* and *adegraphics* (Thioulouse *et al.*, 2018),  
351 *lme4* (Bates *et al.*, 2015), and *siber* (Jackson *et al.*, 2011) packages.

352

### 353 **3. Results**

#### 354 *3.1. Environmental characterization*

##### 355 *3.1.1. Water level and temperature*

356 According to the flow variation, 2015 was the driest year, 2016 was the wettest year, and 2014  
357 fell in between (Fig. 2). On average, the number of pulses was lower above the dams than  
358 below the dams (Table 3A). Despite stream regulation, the discharge was obviously higher  
359 below the dams than above the dams (Table 3A) but the significant interaction with the  
360 sampling date was associated with the very low difference in discharge in summer 2015, i.e.,  
361 the driest period. Finally, coefficient of variation of the discharge values were significantly  
362 lower below the dams than above the dams in summer and fall 2015, and the opposite trend  
363 was observed for the 4 other sampling dates (Table 3A). Similarly, the water temperature varied  
364 across the years. The highest temperatures occurred in the summer of 2015, and the lowest  
365 occurred in the winter of 2014, and 2016 was slightly cooler (Fig. 3). Apart from the obvious  
366 effect of the sampling date (Table 3A), the average temperature preceding each sampling  
367 occasion below the dams was significantly higher than that above the dams (Table 3A). In  
368 contrast, the temperature range did not significantly change between sectors located below and  
369 above the dams (Table 3A). There was a statistical interaction between the presence of  
370 groundwater outlets and the sampling date (Table 3A), i.e., water temperature was significantly  
371 lower in the upwelling zone ( $20.3\pm 2.2^{\circ}\text{C}$ ) than in the downwelling zone ( $23.0\pm 1.6^{\circ}\text{C}$ ) in  
372 summer 2015. The variations in water temperature were buffered in the upwelling zones in



373 comparison with the more pronounced variations in the downwelling zones (1.6°C more on  
374 average; Fig. 3).

375

### 376 *3.1.2. Water chemistry*

377 Apart from interaction between sector and sampling date and site effect, the dissolved oxygen  
378 concentration and nitrate concentrations varied significantly among zones (Table 3B). On  
379 average, the concentrations of dissolved oxygen and nitrate measured in upwelling zones were  
380 respectively lower (-0.5 mg.L<sup>-1</sup> of oxygen) and higher (+0.056 mg.L<sup>-1</sup> of nitrogen) than  
381 concentrations measured in the downwelling zones. Electrical conductivity was on average 20  
382 µS.cm<sup>-1</sup> lower below the dams than above the dams, but the magnitude of the difference  
383 changed with the sampling date (Table 3B). Ammonium concentrations ranged from 4.0 to  
384 65.2 µg.L<sup>-1</sup> and from 0.7 to 57.0 µg.L<sup>-1</sup> above and below the dams, respectively (Table 3B).  
385 Similarly, orthophosphate concentrations ranged from 0.8 to 25.1 µg.L<sup>-1</sup> and from 1 to 17.3  
386 µg.L<sup>-1</sup> above and below the dams, respectively (Table 3B). Most measured concentrations were  
387 very low (<20 µg.L<sup>-1</sup>) and significant differences between sectors or zones would be of low  
388 biological relevance. Thus, the ammonium and orthophosphate concentrations did not allow us  
389 to make any further inferences.

390

### 391 *3.1.3. Primary production*

392 The chlorophyll-*a* concentration and the densities of cyanobacteria, chlorophytes and diatoms  
393 showed similar spatial patterns including a high variability among sites in each sector and with  
394 the highest values reported at site A4 below dams (Table 4A). Cyanobacteria had the greatest  
395 development with densities generally higher on both sides of the dams (especially at sites A3  
396 and A4; Table 5A). As expected, seasonal changes in algal development also explained the  
397 variability in the algal dataset for all algal metrics (Table 4A).

398

### 399 3.2. *Invertebrate assemblage responses*

#### 400 3.2.1. *Spatial and temporal patterns*

401 With the exception of spring 2015, the total abundance of benthic invertebrates was generally  
402 lower below the dams than above the dams ( $497\pm 460$  vs.  $415\pm 582$  individuals; Table 4B) and  
403 lower in the upwelling zones than in downwelling zones ( $401\pm 436$  vs.  $511\pm 598$  individuals).  
404 The total richness was not significantly lower below the dams than above the dams (Table 4B).  
405 Nevertheless, as for the total abundance, the richness values below the dams at the last two  
406 sites were significantly lower than those at the other sites (Table 4B). No significant difference  
407 in richness was observed between the upwelling and downwelling zones. Shannon diversity  
408 was significantly lower below the dams than above the dams ( $1.8\pm 0.1$  vs.  $2.1\pm 0.4$ ; Table 4B)  
409 and highlighted significantly lower values in upwelling than in downwelling zones at three  
410 sampling dates (fall 2014, spring and summer 2015).

411

#### 412 3.2.2. *Main drivers of invertebrate assemblage responses*

413 The co-inertia analysis between the invertebrate assemblage composition and environmental  
414 metrics showed a significant correlation ( $R_v=0.318$ , simulated- $P<0.001$ ,  $n=72$ ). The first-three  
415 axes depicted 83% of the co-variability between the invertebrate assemblage composition and  
416 the environmental metrics (46%, 20.9% and 16.1% for the first, second and third co-inertia  
417 axes, respectively; Fig. 4). The first two co-inertia axes depicted 96% and 72.6% of the  
418 environmental and faunal variance, respectively. The first co-inertia axis clearly separated the  
419 two sectors suggesting that invertebrate composition responded significantly to the  
420 environmental context above and below the dams (Fig. 4A). This separation was associated  
421 with the higher temperature range ( $T_r$  in Fig. 4B) and standard deviation ( $T_s$ ) above the dams,  
422 and with the higher discharge ( $Q_m$ ), flow pulse ( $Q_p$ ) and algal development below the dams

423 (E1-E4; Fig. 4B). The second co-inertia axis separated sites within sectors according to the  
424 higher flow variation ( $Q_c$  in Fig. 4B) above the dams and the higher temperature ( $T_m$ ) and  
425 algal development (E1) at the moderately regulated above-dam site (A3; Fig. 4A) and the  
426 regulated below-dam site (A4; Fig. 4A). The apparent proximity of sites A5 and A6 with A1  
427 and A2 (Fig. 4A) was a consequence of the multivariate analysis projection, and the third co-  
428 inertia axes clearly separated them according to their discharge values ( $Q_c$ ,  $Q_m$ ; Fig. 4D).  
429 Noticeably, algal development appeared again as a driver at the moderately regulated above-  
430 dam site (A3; Fig. 4C) and the regulated below-dam site (A4; Fig. 4C).

431

432 Accordingly, taxa responsible for these differences above and below the dams included  
433 Ephemeroptera such as *Torleya* sp. (expressed in average % of individuals collected in sites:  
434  $1.18\% \pm 1.75$  vs.  $0.003\% \pm 0.015$  above and below dams respectively; supplementary  
435 information, Fig. S1E), *Serratella* sp. ( $4.65\% \pm 6.20$  vs.  $2.86\% \pm 3.39$ ), *Rhithrogena* sp.  
436 ( $0.85\% \pm 1.56$  vs.  $0.10\% \pm 0.21$ ) and *Ecdyonurus* sp. ( $0.75\% \pm 0.58$  vs.  $0.20\% \pm 0.45$ ); various  
437 Plecoptera including *Leuctra* sp. ( $2.45\% \pm 2.65$  vs.  $1.31\% \pm 2.34$ ; Fig. S1G), Perlodidae  
438 ( $0.13\% \pm 0.26$  vs.  $0.01\% \pm 0.05$ ), *Nemoura* sp. ( $0.04\% \pm 0.08$  vs.  $0.00\% \pm 0.00$ ), *Protonemura* sp.  
439 ( $0.07\% \pm 0.20$  vs.  $0.00\% \pm 0.00$ ), *Dinocras* sp. ( $0.01\% \pm 0.03$  vs.  $0.00\% \pm 0.00$ ) and *Perla*  
440 ( $0.07\% \pm 0.11$  vs.  $0.00\% \pm 0.00$ ); Coleoptera such as *Stenelmis* sp. ( $0.08\% \pm 0.22$  vs.  $0.03\% \pm 0.05$ ;  
441 Fig. S1C); and Trichoptera such as *Hydropsyche* sp. ( $6.09\% \pm 7.19$  vs.  $3.85\% \pm 4.47$ ), *Micrasema*  
442 sp. ( $0.21\% \pm 0.39$  vs.  $0.00\% \pm 0.00$ ) and *Odontocerum* sp. ( $0.22\% \pm 0.7$  vs.  $0.00\% \pm 0.00$ ) (Fig.  
443 S1H). The taxa having higher proportions below the dams included the Ephemeroptera  
444 *Heptagenia* sp. ( $0.00\% \pm 0.02$  vs.  $0.69\% \pm 1.04$  above and below dams respectively; Fig. S1E)  
445 and *Potamanthus* sp. ( $0.00\% \pm 0.00$  vs.  $0.22\% \pm 0.53$ ), *Dreissena* sp. ( $0.00\% \pm 0.00$  vs.  
446  $0.02\% \pm 0.04$ ; Fig. S1A), triclads such as *Dugesia* sp. ( $0.15\% \pm 0.39$  vs.  $0.67\% \pm 1.31$ ; Fig. S1A),  
447 various taxa belonging to the Trichoptera Leptoceridae family (*Athripsodes* sp. ( $0.18\% \pm 0.27$

448 vs.  $0.76\% \pm 1.00$ ), *Setodes* sp. ( $0.18\% \pm 0.27$  vs.  $0.76\% \pm 1.00$ ), *Mystacides* sp. ( $0.00\% \pm 0.01$  vs.  
449  $0.07\% \pm 0.20$ ); Fig. S1H); Crustacea such as *Gammarus* sp. ( $13.1\% \pm 10.9$  vs.  $29.9\% \pm 18.8$ ; Fig.  
450 S1A) and Asellidae sp. ( $0.58\% \pm 1.49$  vs.  $2.34\% \pm 3.82$ ; Fig. S1A); Hirudinea such as *Piscicola*  
451 sp. ( $0.00\% \pm 0.00$  vs.  $0.04\% \pm 0.09$ ; Fig. S1A); and lentic Coleoptera such as *Dryops* sp.  
452 ( $0.00\% \pm 0.00$  vs.  $0.03\% \pm 0.12$ ) and *Haliphus* sp. ( $0.00\% \pm 0.01$  vs.  $0.02\% \pm 0.05$ ; Fig. S1C).

453

### 454 3.2.3. Assemblage resilience and resistance

455 The relative utilization of some life history traits demonstrated significant changes between  
456 sectors (i.e. above vs. below the dams). For example, the proportion of multivoltine individuals  
457 was significantly higher below dams than above dams (Table 5A; Fig. 5A). This proportion  
458 was significantly and positively correlated with the proportion of short-lived organisms  
459 ( $n=432$ ,  $r=0.165$ ,  $P<0.0001$ , not shown) but not with small-sized organisms. The proportion of  
460 multivoltine organisms was also negatively related to the proportion of individuals with aerial  
461 dispersal ( $n=432$ ,  $r=-0.694$ ,  $P<10^{-16}$ , not shown) and positively related to the proportion of  
462 drifting organisms ( $n=432$ ,  $r=0.300$ ,  $P<10^{-10}$ , not shown). In addition, the proportion of small  
463 and short life duration organisms were slightly lower in the upwelling than in downwelling  
464 zones ( $0.64 \pm 0.07$  vs.  $0.66 \pm 0.09$  and  $0.69 \pm 0.09$  vs.  $0.71 \pm 0.08$  respectively), especially below  
465 dams (Table 5, Se:UD interaction). The reverse occurred for the proportion of drifting  
466 organisms ( $0.38 \pm 0.04$  vs.  $0.37 \pm 0.04$ ).

467

468 These changes in resilience traits mirrored in the proportions of individuals sensitive to  
469 pollution, which decreased from upstream to downstream. The sites below the dams exhibited  
470 slightly lower proportions of organisms that are sensitive to eutrophication (Fig. 5C) and  
471 sensitive to pesticide as measured by the SPEAR index (Fig. 5D), though overall differences  
472 below and above dams were marginally statistically significant (Table 5A). Likewise, the

473 proportion of ovoviviparous organisms was higher below the dams than above the dams (Table  
474 5A; Fig. 5B) and was higher in the upwelling in comparison to the downwelling ( $0.154\pm 0.09$   
475 vs.  $0.132\pm 0.06$ ).

476

### 477 *3.3. Assemblage trophic responses*

#### 478 *3.3.1. Functional feeding groups*

479 The proportions of each functional group generally differed across sites (Fig. 5E-H). A within-  
480 sector decreasing trend from upstream to downstream was observed for shredders (Fig. 5F),  
481 scrapers (Fig. 5G), and predators (Fig. 5H), whereas the opposite trend was observed for  
482 filtering feeders (Fig. 5E). As this trend occurred in both sectors, there were no significant  
483 differences above and below the dams in the average proportion of each functional feeding  
484 group (Table 5B). In addition, the proportions of filter feeders and scrapers were slightly lower  
485 in the upwelling than in downwelling zones ( $0.10\pm 0.05$  vs.  $0.11\pm 0.06$  and  $0.34\pm 0.06$  vs.  
486  $0.36\pm 0.06$  respectively). The reverse occurred for the proportion of shredders ( $0.29\pm 0.06$  vs.  
487  $0.26\pm 0.07$ ). Even statistically significant, these differences in proportions were too low to be  
488 further interpreted.

489

490 Finally, food specialization showed no statistically significant difference above and below  
491 dams (Table 5B). Nevertheless, sites A5 and A6 located below the dams tended to have fewer  
492 food-specialized taxa (Fig. 6A). Trophic status specialization also differed significantly across  
493 sites (Fig. 6B) with a trend towards more generalists below the dams but again the difference  
494 between above and below dams was hardly statistically significant (Table 5C). Finally, food or  
495 trophic status specialization did not differ between the upwelling and downwelling zones  
496 located at each site (Table 5C).

497

498 3.3.2. *Isotope analysis*

499 3.3.2.1. *Basal resources*

500 The resource diversity available to benthic invertebrates did not significantly differ above and  
501 below the dams (Table 6A). Neither, the amount of FPOM (Table 6A; supplementary  
502 information Fig. S2), sedimentary biofilm (Table 6A; Fig. S2), mosses (Table 6A; Fig. S2) and  
503 more generally the total amount of carbon (Table 6A; Fig. S2). A within-sector decreasing  
504 trend from up to downstream occurred for sedimentary biofilm, whereas FPOM and mosses  
505 peaked at site A4 (Fig. S2), below the dams. Finally, the total organic carbon content decreased  
506 from upstream sites to downstream sites within each sector and peaked at site A4 (Fig. S2).

507

508 3.3.2.2. *Isotopic niche*

509 The isotope space area determined as the standard ellipse area normalized to the isotope  
510 composition of the basal resource (SEAnr) differed significantly among sampling dates (Table  
511 6B) and between sectors (Table 6B) (supplementary information, Fig. S3). SEAnr generally  
512 increased from upstream to downstream in the sites above the dams, reaching its highest value  
513 at A3 (Fig. 7A); however, this tendency was weaker during summer. Below the dams, SEAnr  
514 decreased from sites A4 to A6, except in fall, when the maximum value was measured at site  
515 A5. The diversity in the basal resource use, quantified by the  $\delta^{13}\text{C}$  range (CR in Fig. 7C),  
516 showed an increase from sites A1 to A3 but no difference between above and below dams  
517 could be detected (Table 6B). Finally, the diversity of trophic levels quantified by the  $\delta^{15}\text{N}$   
518 range again showed an increase from upstream to downstream above the dams and a decrease  
519 below the dams (Table 6B). At all sampling occasions, the most downstream site, A6, displayed  
520 the lowest trophic diversity (SEAnr), with a low diversity in the exploitation of the basal  
521 resources (CR) and a low diversity in trophic levels (NR). Regardless of the index used, no  
522 significant influence of surface water-groundwater exchanges on the invertebrate food web

523 was detected (e.g. average values of SEAnr were  $41.9 \pm 16.2$  vs.  $39.6 \pm 19.1$  for the upwelling  
524 and downwelling zones, respectively).

525

526 The calculation of linear correlations allowed the detection of the potential influences of  
527 environmental conditions (hydrology, temperature, basal resources) on invertebrate food web  
528 indexes (SEAnr, CR, and NR values). Interestingly, there was a positive linear relationship  
529 between the organic carbon quantity in food sources and the isotope space area in summer (Fig.  
530 8), when the hydrological conditions (cf. Fig. 2) were not disturbed by dramatic flood events.  
531 No correlation was found in summer between SEAnr and hydrological parameters, whereas  
532 SEAnr displayed a negative correlation with the variation in the discharge in spring ( $r = -0.70$ ,  
533  $P < 0.015$ ) and fall ( $r = -0.70$ ,  $P < 0.012$  and  $r = -0.65$ ,  $P < 0.025$ , respectively).

534

#### 535 **4. Discussion**

536 To our knowledge, this study is the first to simultaneously compare the taxonomic and  
537 functional spatial and temporal responses of aquatic invertebrate assemblages and the  
538 associated modifications in the isotopic metrics describing food webs in a regulated river. On  
539 the one hand, our hypotheses about the effects of the alteration of the hydrological regime and  
540 temperature and the potential eutrophication associated with stream regulation on the  
541 invertebrate assemblages are generally supported by the results of the study. The overall  
542 abundance and richness, resilience and resistance potential, sensitivity to pollution and food  
543 specialization in invertebrate assemblages were found to be lower below the dams than above  
544 the dams. The aquatic invertebrate assemblages above and below the dams significantly  
545 responded to the combined effects of hydrology, temperature, and algal development. Even  
546 moderate stream regulation seemed to promote eutrophication locally above the dams (site A3).  
547 The reduction in basal resource use that occurred in the downstream sites (A5 and A6) below

548 the dams was found to narrow the isotopic niche (i.e. isotopic space that describes food web)  
549 of invertebrates but local eutrophication (algal development) sometimes modified this scheme  
550 (A4). Finally, the balance among functional feeding groups was unexpectedly found to be  
551 similar below and above the dams. On the other hand, our hypotheses concerning groundwater  
552 supplies are not supported because groundwater outlets only marginally influenced benthic  
553 invertebrate assemblages and food web complexity despite their buffering effect on  
554 temperature during summer and the stimulation of primary production by nutrient (especially  
555 nitrate) supplies.

556

#### 557 *4.1. Main drivers of benthic invertebrate assemblages between sectors and among sites*

558 The co-inertia analysis suggested that hydrological (flow pulses) and thermal (temperature  
559 variations) conditions were the main drivers explaining changes in the invertebrate assemblage  
560 structure between sectors. The damming conditions generated a global reduction in invertebrate  
561 density and diversity at the sites below the dams. This reduction, which is expected in theory  
562 for rivers of the same stream order as the Ain River (Ward and Stanford, 1983a), has generally  
563 been observed elsewhere (e.g. Fleituch, 2003; Kjærstad *et al.*, 2017; Mellado-Diaz *et al.*, 2019).  
564 As observed in other studies (Krajenbrink *et al.*, 2019), the number of Ephemeroptera and  
565 Plecoptera taxa was especially affected due to their sensitivity to habitat alteration. However,  
566 this reduction was especially observed at the two downstream sites (A5 and A6). Even if the  
567 dams similarly affected discharge dynamics and thermal changes, eutrophication (dense algal  
568 development) and high quantities of basal food sources (e.g., CPOM) seemed to buffer the  
569 effects of stream regulation at site A4. This interpretation was supported by the wider isotopic  
570 niche of invertebrate food web measured in site A4 than in sites A5 and A6. Indeed, this result  
571 highlighted that food webs were mainly fuelled by algal sources in A5 and A6 sites whereas  
572 food webs were based on more diversified food sources (algae and detritus) in site A4. In



573 addition, the fact that sites A3 and A4, characterized by the highest algal growth, had the  
574 highest density and diversity of invertebrates suggests that algal development on cobbles and  
575 stones was an important local condition favouring benthic invertebrates. Indeed, it has been  
576 demonstrated in the literature that biofilms (including bryophytes) that develop on hard  
577 substrates act as both a preferential habitat (Linhart *et al.*, 2002) and a food source (Suren,  
578 1992) for a wide range of benthic invertebrates (Wulf and Pearson, 2017). Local nutrient  
579 enrichment and eutrophication could thus have a positive influence on the biological  
580 compartment of the Ain River. Nevertheless, this interpretation cannot be extended to all lotic  
581 systems because the water flow dynamics in the Ain River facilitate the oxygenation of water  
582 and prevent the occurrence of low-oxygen conditions associated with eutrophication in the  
583 water column (Table 2). Indeed, eutrophication may generate water column anoxia that can  
584 markedly damage the benthic life when hydrological conditions are not strong enough to  
585 efficiently reoxygenate the water column (see Parr and Mason, 2004 and Pardo and Garcia,  
586 2016 for examples in lowland streams).

587

#### 588 *4.2. Biological traits of the invertebrates above and below the dams*

589 The invertebrate taxa found below the dams were generally more resilient and resistant than  
590 the taxa found above the dams. These results fit well with observations from the literature  
591 showing that hydrological disturbances such as those generated by dam functioning can select  
592 for small, multivoltine species with short life spans (Wallace, 1990). A higher number of  
593 generations per year is expected to occur under unstable conditions, as it allows rapid  
594 population growth and an increase in resilience capacity in invertebrates (Townsend and  
595 Hildrew, 1994) as observed elsewhere (e.g. Usseglio-Polatera and Beisel, 2002; Statzner *et al.*,  
596 2010; Feio and Dolédec, 2012). The biological trait approach thus appears as highly relevant  
597 for highlighting the hydrological impacts on benthic invertebrate assemblages; resilience traits

598 were apparently not affected by trophic resources or eutrophication at each site, which suggests  
599 some specificity in their responses (see e.g. Mondy *et al.*, 2016). We did not find significant  
600 differences in traits associated with tolerance to eutrophication between the two sectors. This  
601 result is coherent with the analyses performed on algae, which did not indicate any differences  
602 in eutrophication status between the two sectors. In contrast, we observed a higher proportion  
603 of biological traits associated with tolerance to pesticides at sites below the dams than at sites  
604 above the dams suggesting a difference in pesticide exposure. In addition, ovoviviparity, a  
605 parental care strategy that may prevent high egg mortality in harsh environmental conditions,  
606 was prominent below the dams. This egg protection trait has been shown to increase in the  
607 presence of pesticides (Kuzmanovic *et al.*, 2017). The higher pesticide resistance of  
608 invertebrates sampled below the dams is consistent with the surrounding land use patterns  
609 because crop production occurred predominantly in sites below the dams (see Table 1), and  
610 this agricultural practice is often associated with pesticide use (e.g., Papadakis *et al.*, 2018).  
611 Under these conditions, it is thus not surprising that the eutrophication response traits of species  
612 were not tightly linked with algal development at the sites because herbicides might have  
613 impaired algae growth at sites below the dams (especially in sites A5 and A6, which had low  
614 algal development). An additional explanation for the biological trait distribution among the  
615 sites could be linked to the physical disturbances that change channel morphodynamics below  
616 the dams (e.g., Brenna *et al.*, 2020). Indeed, Rollet *et al.* (2013) showed that changes in  
617 sediment transport in the Lower Ain River resulted in bed coarsening and sediment instability,  
618 and their pavement index, measuring river bed alteration, was high in one reach (corresponding  
619 to our site A4) and low in another reach (corresponding to our two last sites, A5 and A6). Such  
620 sediment instability may also favour resilient traits (e.g. multivoltine taxa see Fig. 5B;  
621 Townsend and Hildrew, 1994). Thus, the responses of invertebrate biological traits below the  
622 dams may result from both physical disturbances and chemical stresses. To evaluate whether

623 the chemical impacts of pesticides on algae and invertebrates are a relevant explanation of the  
624 benthic invertebrate assemblages' structure and functioning, the content of pesticides and  
625 herbicides in the sediment are needed to assess the contamination levels at the six studied sites.

626

627 Another set of traits addresses invertebrate functional feeding groups of invertebrates (FFGs).  
628 According to the river continuum concept (RCC; Vannote *et al.*, 1980), FFGs along a stream  
629 should shift from a dominance of shredders upstream associated with high CPOM availability  
630 (due to dense riparian vegetation) to a dominance of grazers, scrapers and collectors  
631 downstream, where the riparian vegetation is no longer the main food source for stream  
632 invertebrates. In line with several studies and reviews highlighting the limits on the application  
633 of the RCC (e.g. Statzner and Higler, 1985), dams seem to modify the natural stream zonation  
634 of food sources and their associated FFGs from the upstream sector to the downstream sector  
635 in the Ain River. Indeed, the balance in functional feeding groups was unexpectedly similar  
636 below and above the dams; for example, site A4, below the dams presented the same proportion  
637 of shredders as site A1 above the dams. Relatedly, in terms of organic matter resources, site  
638 A4 was characterized by a CPOM content (6.03 mg/m<sup>2</sup> of organic carbon) comparable to that  
639 observed at site A1 (7.83 mg/m<sup>2</sup> of organic carbon). As suggested by Sanchis-Ibor *et al.*  
640 (2018), the changes in channel morphodynamics caused by dams can favour the presence of a  
641 riparian vegetation made up of pioneering tree species (e.g. *Salix*, which are prominent trees  
642 on the Lower Ain, see Rollet *et al.*, 2013). Tree installation on gravel bars may in turn both  
643 reduce sediment mobility and feed the river with leaf litter and woody debris. Thus, the bed  
644 artificialization associated with dams can also affect the availability of resources at each site  
645 and the FFG distribution along the river course.

646

647 *4.3. Food web responses to environmental factors*

648 Above the dams, we observed an increase in the isotope space area from upstream to  
649 downstream that was mainly driven by an increase in the basal resource diversity used by the  
650 invertebrate assemblages. Such an increase has been observed in unregulated rivers and  
651 generally suggests a structural change in the food web along the longitudinal gradient  
652 (Winemiller *et al.*, 2011; Hette-Tronquart *et al.*, 2016). Indeed, the increase of food web  
653 diversity from site A1 to site A3 above dams highlighted modifications of food sources used  
654 by invertebrate communities: a detritus-based food web dominated in site A1 whereas a food  
655 web based on both algae and detritus occurred in site A3. The decrease in the isotope space  
656 area below the dams (from site A4 to site A6) indicates a decrease in the diversity of resource  
657 use and in the number of trophic levels. This decrease could be explained by the wide diversity  
658 of resources (algae and detritus) fuelling invertebrate food web in site A4 whereas food web in  
659 site A6 was uniquely based on algae. Thus, changes in food sources may have caused the  
660 reduction in the prey diversity, which is potentially corroborated by the trend of decrease in  
661 taxonomic diversity and invertebrate abundance at the last two sites (Table 4A). This resource  
662 use decrease appeared to be negatively correlated with the discharge values and their rates of  
663 variation. Marty *et al.* (2009) showed comparable results in boreal rivers where high ramping  
664 rates during hydropeaking were responsible for a one-trophic-level decrease in the length of  
665 the food chain between macroinvertebrates and fish. Stream hydrodynamics thus appear to be  
666 the dominant factor in structuring the invertebrate assemblages, as positive correlations  
667 between food resources and their use by benthic invertebrates were only detected during low  
668 flow conditions (summer 2015). At this time, a positive relationship was observed between the  
669 quantity of energy (organic carbon) in the benthic environment and the area of the food web of  
670 the benthic invertebrates. According to the literature (Wright, 1983; Smith, 2007), this  
671 relationship could be due to the positive species-energy relationship encountered in many  
672 ecosystems. More precisely, an increase in energy (available resources) increases the ability of

673 trophic specialists to develop persistent populations (Evans *et al.*, 2005). Consequently, these  
674 specialist species increase the isotopic area of the food web by feeding on one or two resources  
675 without mixing isotopic signatures from several sources as generalist species would do  
676 (Layman *et al.*, 2007; Hette-Tronquart *et al.*, 2016). Increases in basal energy resources would  
677 allow the development of predatory levels (Oksanen *et al.*, 1981; Mermillod-Blondin *et al.*,  
678 2020). This pattern was observed in summer with the linear relationship between the organic  
679 carbon content and the  $\delta^{15}\text{N}$  range. Therefore, the trophic structure of benthic fauna was  
680 dominated by resources (bottom-up control) in summer. However, the same connections  
681 between the total organic carbon content and the isotopic indexes were not observed on the two  
682 other sampling dates when hydrological conditions were less stable than in summer. Indeed,  
683 significant correlations between hydrological variables and isotopic areas were observed in  
684 spring and fall, while this kind of result has not been detected in summer. We can thus conclude  
685 that hydrological disturbance appeared to be the main stressor on trophic food webs in the Ain  
686 River and that it disrupted the observed connection between food webs and basal resources  
687 (e.g. Menge *et al.*, 2002).

688

#### 689 *4.4. Upwelling zones as refuges for benthic invertebrates during harsh thermal conditions*

690 According to the literature (White *et al.*, 1987; Capderrey *et al.*, 2013), upwelling zones are  
691 cooler than downwelling zones during the summer, when water temperatures are the highest  
692 and potentially harshest for benthic invertebrates. This difference in temperature is also  
693 associated with a reduction in dissolved oxygen concentrations in upwelling zones compared  
694 with those in downwelling zones. This pattern of dissolved oxygen concentrations is due to the  
695 contrast between the highly oxygenated water of the Ain River downwelling in sediments and  
696 the moderately oxygenated groundwater upwelling from hyporheic and/or riparian zones. As  
697 aerobic microbial processes reduce the dissolved oxygen concentration in water during its

698 transfer through sediments (Jones Jr *et al.*, 1995; Boulton *et al.*, 1998), upwelling water, which  
699 is characterized by a higher retention time in sediments than downwelling water, is more  
700 depleted in dissolved oxygen. In line with the literature (Valett *et al.*, 1994; Dahm *et al.*, 1998),  
701 the groundwater supply was also richer in nitrate than the surface waters. Despite these  
702 differences in benthic conditions between the upwelling and downwelling zones, the variation  
703 in groundwater supply moderately affected the composition of benthic invertebrate  
704 assemblages and their life history traits (e.g., reduction in small and short-lived organisms).  
705 Even in summer, when the thermal conditions were the harshest for benthic fauna, the  
706 upwelling zones did not act as efficient refugia for invertebrates. This lack of an effect may be  
707 associated with the fact that (i) the thermal conditions were not very stressful for invertebrates  
708 as most taxa found in the sites below dams are generally resistant to higher temperatures and  
709 oxygen depletion, as is typical for generalists, and (ii) most epigean invertebrates are quite  
710 mobile and may not use cool upwelling zones permanently (taxa can move from one patch to  
711 another for foraging activities and can recover from damage induced by thermal stress during  
712 foraging periods by resting periods in cool habitats; see e.g. Colinet *et al.*, 2015). As observed  
713 by Capderrey *et al.* (2013), who demonstrated significant effects of surface-groundwater  
714 exchanges on hyporheic invertebrates but no effects on benthic fauna, the upwelling flow of  
715 groundwater directly into the main channel might not be sufficient to affect habitat conditions  
716 in the benthic zones of the Ain River. Supporting this interpretation, we did not find a positive  
717 influence of the nutrient enrichment associated with upwelling zones on benthic algae, whereas  
718 this influence has been observed in many streams (e.g. Grimm and Fisher, 1989; Pepin and  
719 Hauer, 2002; Hunt *et al.*, 2006). Therefore, the selected upwelling zones in the Ain River were  
720 probably too spatially restrained to allow the development and maintenance of specific benthic  
721 invertebrate assemblages.

722

723 4.5. Concluding remarks

724 Understanding the combined effects of different stressors and the contribution of each stressor  
725 to the structure and function of aquatic communities remains crucial for managers in addressing  
726 restoration goals and mitigation measures. We observed that stream hydrology is a key driver  
727 aquatic invertebrate assemblage and that the modification of the interplay between water and  
728 sediment transport may inhibit biological processes in some areas while favouring these  
729 processes in other areas. In addition, the temporal variation in the hydrological regime may  
730 have a different effect on the biological processes since, for example, the responses of the food  
731 web structure to the available resources were visible only during a certain season. These  
732 spatiotemporal changes must be considered in the design of future studies. As a second  
733 outcome of our study, combining approaches based on biological traits and stable isotope  
734 analyses provides better insights into the biological process patterns since these approaches are  
735 complementary in evaluating invertebrate assemblage changes and modifications in species  
736 feeding behaviours. On the one hand, the biological trait-based approach provides information  
737 about the substantial impacts of environmental stressors on benthic fauna and contributes to  
738 understanding the potential of an assemblage in terms of resistance and/or resilience to  
739 disturbance and in terms of trophic specialization. On the other hand, isotopic food web metrics  
740 can highlight “short” temporal changes in the structuring of benthic invertebrates, since food  
741 web characterization using isotopic analyses may reveal changes in the feeding behaviour of  
742 invertebrates due to short-term stressors. Nevertheless, repeated measurements of the isotopic  
743 niche at the downstream site (A6) demonstrated a long-term pattern. At this site, the lower  
744 diversity of the resources supporting the food web ( $\delta^{13}\text{C}$  range) and the reduced length of the  
745 trophic chains ( $\delta^{15}\text{N}$  range) in comparison with those at the other sites indicated a reduction in  
746 the trophic linkages and a simplification of the food web, which are characteristics of low-  
747 stability food webs (Post *et al.*, 2000; Rooney *et al.*, 2006). Finally, we recommend the use of

748 both biological trait-based and stable isotope-based approaches to clarify the complex impacts  
749 of multiple stressors on stream communities at different spatial and temporal scales.

750

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763

## 764 **Figure legends**

765 **Figure 1.** (A) Map showing the 6 study sites (noted A1 to A6) along the Ain river. Reservoirs  
766 are identified by light blue colour. Insert indicates the position of the catchment on the right  
767 side of the Rhône river. (B) Diagram showing the hydrological exchanges between surface  
768 flow and groundwaters (downwelling) and between groundwaters and surface flow (upwelling)  
769 within a gravel bar.

770

771 **Figure 2.** Average daily discharge variations in (A) site A3 (above the dams) and (B) site A4  
772 (below the dams). Invertebrate sampling occasions are indicated by arrows.



773

774 **Figure 3.** Average daily temperature variations in (A) site A3 (above the dams) and (B) site  
775 A4 (below the dams) and showing downwelling (black) and upwelling (dashed grey) values  
776 over the study period.

777

778 **Figure 4.** Result of a co-inertia analysis between the invertebrate assemblage composition and  
779 environmental factors depicting hydrology, temperature and eutrophication. (A) First-two co-  
780 inertia axes position of samples from the faunistic (squares) and environmental dataset (dots),  
781 respectively and green (faunistic dataset). Samples made above and below dams are coloured  
782 in blue and green respectively. Labels are positioned at the center of gravity of the samples  
783 belonging to a site (faunistic dataset). (B) Environmental factor loadings along the first-two  
784 co-inertia axis (E1: cyanobacteria density; E2: chlorophyte density; E3: diatom density; E4:  
785 Chlorophyll-a concentration; Tm: average temperature; Ts: standard deviation of the  
786 temperature; Tr: temperature range; Qp: number of extreme ecological events; Qm: average  
787 discharge; Qs: standard deviation of the discharge; Qc: coefficient of variation of the  
788 discharge). (C) Same as (A) for the second and third co-inertia axes. D. Same as B for the  
789 second and third co-inertia axes.

790

791 **Figure 5.** Violin plot showing the probability density curves of changes in the proportion of  
792 individuals being (A) multivoltine, (B) ovoviviparous, (C) sensitive to pollution (oligotrophic)  
793 and (D) to pesticides and functional feeding groups with (E) filtering feeders, (F) shredders,  
794 (G) scrapers and (D) predators in each site along the river course. Sites above dams are in grey  
795 and those below dams are in white. The dotted vertical line marks the dam separation. Large  
796 dots stand for median and small dots represent the data ( $n=72$  per site).

797

798 **Figure 6.** Violin plot showing the probability density curves of changes in (A) food and (B)  
799 trophic status specialization at each site along the river course. Sites above dams are in grey  
800 and those below dams are in white. The dotted vertical line marks the dam separation. Large  
801 dots stand for the median value and small dots represent the data ( $n=72$  per site).

802

803 **Figure 7.** Violin plot showing the probability density curves of changes in (A) the normalized  
804 isotopic areas (SEAnr), (B) the diversity of the exploited basal resources (range of  $\delta^{13}\text{C}$ , CR),  
805 and (C) the diversity of trophic levels (range of  $\delta^{15}\text{N}$ , NR) along the river course at each site.  
806 Sites above dams are in grey and those below dams are in white. The dotted vertical line marks  
807 the dam separation. Large dots stand for the median value and small dots represent the data  
808 ( $n=6$  per site).

809

810 **Figure 8.** Relationship between the amount of total organic carbon and the normalized isotopic  
811 area (SEAnr) at each sampling date.

812

### 813 **Table Captions**

814 **Table 1.** General characteristics of the study sites.

815

816 **Table 2.** A priori hypotheses and rationale of expected changes in invertebrate trait metrics  
817 selected in this study.

818

819 **Table 3.** (A) Flow ( $n=36$ ) and temperature ( $n=72$ ) characteristics in each study site  
820 (mean $\pm$ standard deviation). (B) Chemical parameters in each study site (mean $\pm$ standard  
821 deviation,  $n=432$  for oxygen and  $n=360$  for other parameters) Significance of mixed ANOVAs

822 are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects  
823 (\*\*P<0.001; \*P<0.01; . P<0.1; ns: non-significant).

824

825 **Table 4.** Algal (A) and invertebrate (B) metrics in each study site (mean±standard deviation;  
826  $n=72$  and  $n=432$  for algal and invertebrate metrics respectively). Significance of mixed  
827 ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and  
828 random effects (\*\*P<0.001; \*P<0.01; . P<0.1; ns: non-significant).

829

830 **Table 5.** Invertebrate trait metrics in each study site (mean±standard deviation,  $n=432$ )  
831 separated into resilience and resistance trait (A), functional feeding groups (B) and trophic  
832 specialization (C). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector,  
833 Da: sampling date) interactions, and random effects (\*\*P<0.001; \*P<0.01; . P<0.1;  
834 ns: non-significant).

835

836 **Table 6.** Resource (A) and niche metrics (B) in each study site (mean±standard deviation,  
837  $n=36$ ). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling  
838 date) interactions, and random effects (SEAnr: normalized isotopic area; CR: index of basal  
839 resource exploitation; NR: index of trophic level diversity) (\*\*P<0.001; \*P<0.01; . P<0.1;  
840 ns: non-significant).

841

842

843 **Appendices**

844 **Appendix 1.** Community matrix showing the abundance of taxa summed by sampling zone  
845 ( $n=6$ ) and collected above the dams with the indication of sampling date (“1408” to “1606”),  
846 sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling).  
847 Taxa are listed in alphabetical order.

848

849 **Appendix 2.** Community matrix showing the abundance of taxa summed by sampling zone  
850 ( $n=6$ ) and collected below the dams with the indication of sampling date (“1408” to “1606”),  
851 sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling).  
852 Taxa are listed in alphabetical order.

853

854 **Appendix 3.** Trait matrix showing values for (a) maximum size, (b) life duration, (c) number  
855 of generations per year, (d) reproduction type, (e) dispersal, (f) food types, (g) feeding habits,  
856 (h) trophic status, and (i) SPEAR pesticide sensitivity. Values in (a-h) represent affinity scores  
857 (fuzzy coding). Values in (i) equal "1" if the taxon is sensitive to pesticide, "0" otherwise (NA:  
858 not available) (extracted from Tachet *et al.* (2010) and Schmidt-Kloiber and Hering (2015)).

859

860 **Supplementary information**

861 **Figure S1.** First-two axes taxon scores yielded by the co-inertia analysis between the  
862 invertebrate assemblage composition and the environmental variables depicting hydrology,  
863 temperature and eutrophication. Scores are separated by taxonomic groups with (A) Mollusca,  
864 Hirudinea and Tricladida; (B) Crustacea, Hydracarina and Heteroptera; (C) Coleoptera; (D)  
865 Diptera; (E) Ephemeroptera; (F) Odonata; (G) Plecoptera; (H) Trichoptera.

866

867 **Figure S2.** Changes in the amount of total carbon and five main basal resources along the river  
868 course. Sites above dams are in grey and those below dams are in white. The dotted vertical  
869 line marks the dam separation.

870

871 **Figure S3.** Carbon and Nitrogen isotope compositions of invertebrate taxa (open dots) and  
872 resources (see legend) in spring (A), summer (B) and fall (C). The ellipse corresponds to the  
873 SIBER ellipse without normalisation by the composition of the resources.

874

## 875 **References**

876 Azzellino, A., Canobbio, S., Çervigen, S., Marchesi, V., Piana, A., 2015. Disentangling the  
877 multiple stressors acting on stream ecosystems to support restoration priorities. *Water*  
878 *Sci. Technol.* 72, 293–302. <https://doi.org/10.2166/wst.2015.177>.

879 Amoros, C., Petts, G.E., 1993. *Hydrosystèmes fluviaux*. Masson, Paris.  
880 <https://doi.org/10.7202/033016ar>.

881 Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models  
882 using lme4. *J. Stat. Softw.* 67, 1–48. doi:10.18637/jss.v067.i01.

883 Baxter, R.M., 1977. Environmental effects of dams and impoundments. *Annu. Rev. Ecol. Syst.*  
884 8, 255–283. <https://doi.org/10.1146/annurev.es.08.110177.001351>.

885 Biggs, B.J.F., 2000. Eutrophication of streams and rivers: dissolved nutrient-chlorophyll  
886 relationships for benthic algae. *J. North Am. Benthol. Soc.* 19, 17–31.  
887 <https://doi.org/10.2307/1468279>.

888 Boulton, A.J., Datry, T., Kasahara, T., Mutz, M., Stanford, J.A., 2010. Ecology and  
889 management of the hyporheic zone: stream-groundwater interactions of running waters  
890 and their floodplains. *J. North Am. Benthol. Soc.* 29, 26–40. [https://doi: 10.1899/08-](https://doi:10.1899/08-017.1)  
891 017.1.

892 Boulton, A.J., Findlay, S., Marmonier, P., Stanley, E.H., Valett, H.M., 1998. The functional  
893 significance of the hyporheic zone in streams and rivers. *Annu. Rev. Ecol. Syst.* 29, 59–  
894 81. <https://doi.org/10.1146/annurev.ecolsys.29.1.59>.

895 Bourrelly, P., 1968. *Les algues d'eau douce. Tome I - Les Algues Vertes*, Ed. Boubée, Paris.  
896 <https://doi.org/10.1002/iroh.19740590219>.

897 Box, G.E.P., Cox, D.R., 1964. An analysis of transformations (with discussion). *J. R. Stat. Soc.*  
898 *Series B* 26, 211–252. <https://doi.org/10.1007/BF02595868>.

899 Brenna, A., Surian, N., Mao, L., 2020. Response of a gravel-bed river to dam closure: insights  
900 from sediment transport processes and channel morphodynamics. *Earth Surf. Process*  
901 *Landf.* 745, 756–770. <https://doi.org/10.1002/esp.4750>.

902 Burdon, F.J., McIntosh, A.R., Harding, J.S., 2020. Mechanisms of trophic niche compression:  
903 Evidence from landscape disturbance. *J. Anim. Ecol.* 89, 730–744.  
904 <https://doi.org/10.1111/1365-2656.13142>

905 Capderrey, C., Datry, T., Foulquier, A., Claret, C., Malard, F., 2013. Invertebrate distribution  
906 across nested geomorphic features in braided-river landscapes. *Freshw. Sci.* 32, 1188–  
907 1204. <https://doi.org/10.1899/12-188.1>.

908 Chevenet, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-  
909 term ecological data. *Freshw. Biol.* 31, 295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>.

911 Colas, F., Baudoin, J.M., Danger, M., Usseglio-Polatera, P., Wagner, P., Devin, S., 2013.  
912 Synergistic impacts of sediment contamination and dam presence on river functioning.  
913 *Freshw. Biol.* 58, 320–336. <https://doi.org/10.1111/fwb.12060>.

914 Colinet, H., Sinclair, B.J., Vernon, P., Renault, D., 2015. Insects in fluctuating thermal  
915 environments. *Annu. Rev. Entomol.* 60, 123–140. <https://doi.org/10.1146/annurev-ento-010814-021017>.

917 Dahm, C., Grimm, N., Marmonier, P., Valett, M., Vervier, P., 1998. Nutrient dynamics at the  
918 interface between surface waters and groundwaters. *Freshw. Biol.* 40, 427–451.  
919 <https://doi.org/10.1046/j.1365-2427.1998.00367.x>.

920 Dolédec, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying  
921 species–environment relationships. *Freshw. Biol.* 31, 277–294.  
922 <https://doi.org/10.1111/j.1365-2427.1994.tb01741.x>.

923 Dole-Olivier, M.J., Marmonier, P., 1992. Patch distribution of interstitial communities:  
924 prevailing factors. *Freshw. Biol.* 27, 177–191. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2427.1992.tb00532.x)  
925 [2427.1992.tb00532.x](https://doi.org/10.1111/j.1365-2427.1992.tb00532.x).

926 Dole-Olivier, M.J., Wawzyniak, V., Creuzé des Chatelliers, M., Marmonier, P., 2019. Do  
927 thermal infrared (TIR) remote sensing and direct hyporheic measurements (DHM)  
928 similarly detect river-groundwater exchanges? Study along a 40 km-section of the Ain  
929 River (France). *Sci. Total Environ.* 646, 1097–1110.  
930 <https://doi.org/doi.org/10.1016/j.scitotenv.2018.07.294>.

931 Dray, S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecological  
932 data tables. *Ecology* 84, 3078–3089. <https://doi.org/10.1890/03-0178>.

933 Evans, K.L., Warren, P.H., Gaston, K.J., 2005. Species-energy relationships at the  
934 macroecological scale: a review of the mechanisms. *Biol. Rev.* 80, 1–25.  
935 <https://doi.org/10.1017/s1464793104006517>.

936 Feio, M.J., Dolédec, S., 2012. Integration of invertebrate traits into predictive models for  
937 indirect assessment of stream functional integrity: A case study in Portugal. *Ecol. Indic.*  
938 15, 236–247. <https://doi.org/10.1016/j.ecolind.2011.09.039>.

939 Fleituch, T., 2003. Structure and functional organization of benthic invertebrates in a regulated  
940 stream. *Int. Rev. Hydrobiol.* 88, 332–344. <https://doi.org/10.1002/iroh.200390029>.

941 Francois, C.M., Simon, L., Malard, F., Lefébure, T., Douady, C.J., Mermillod-Blondin, F.,  
942 2020. Trophic selectivity in aquatic isopods increases with the availability of resources.  
943 *Funct. Ecol.* 34, 1078–1090. <https://doi.org/10.1111/1365-2435.13530>.

944 Grimm, N.B., Fisher, S.G., 1989. Stability of periphyton and macroinvertebrates to  
945 disturbance by flash floods in a desert stream. *J. North Am. Benthol. Soc.* 8, 293–307.  
946 <https://doi.org/10.2307/1467493>.

947 Hunt, R.J., Strand, M., Walker, J.F., 2006. Measuring groundwater–surface water interaction  
948 and its effect on wetland stream benthic productivity, Trout Lake watershed, northern  
949 Wisconsin, USA. *J. Hydrol.* 320, 370–384.  
950 <https://doi.org/10.1016/j.jhydrol.2005.07.029>.

951 Hette-Tronquart, N., Belliard, J., Tales, E., Oberdorff, T., 2016. Stable isotopes reveal food  
952 web modifications along the upstream-downstream gradient of a temperate stream.  
953 *Aquat. Sci.* 78, 255–265. <https://doi.10.1007/s00027-015-0421-8>.

954 Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths  
955 among and within communities: SIBER-Stable Isotope Bayesian Ellipses in R. *J. Anim.*  
956 *Ecol.* 80, 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.

957 Jones Jr, J.B., Fisher, S.G., Grimm, N.B., 1995. Nitrification in the hyporheic zone of a desert  
958 stream ecosystem. *J. North Am. Benthol. Soc.* 14, 249-258.  
959 <https://doi.org/10.2307/1467777>.

960 Kjærstad, G., Arnekleiv, J.V., Speed, J.D.M., Herland, A.K., 2018. Effects of hydropeaking on  
961 benthic invertebrate community composition in two central Norwegian rivers. *River Res.*  
962 *Appl.* 34, 218–231. <https://doi.org/10.1002/rra.3241>.

963 Kominoski, J.S., Rosemond, A.D., 2012. Conservation from the bottom up: forecasting effects  
964 of global change on dynamics of organic matter and management needs for river  
965 networks. *Freshw. Sci.* 31, 51–68. <https://10.1111/j.1600-0706.2009.17904.x>.



966 Krajenbrink, H.J., Acreman, M., Dunbar, M.J., Hannah, D.M., Laizé, C.L.R., Wood, P.J., 2019.  
967 Macroinvertebrate community responses to river impoundment at multiple spatial scales.  
968 *Sci. Total Environ.* 650, 2648–2656. <https://doi.org/10.1016/j.scitotenv.2018.09.264>.

969 Kuzmanovic, M., Dolédec, S., de Castro-Catala, N., Ginebreda, A., Sabater, S., Muñoz, I.,  
970 Barceló, D., 2017. Environmental stressors as a driver of the trait composition of benthic  
971 macroinvertebrate assemblages in polluted Iberian rivers. *Environ. Res.* 156, 485–493.  
972 <https://doi.org/10.1016/j.envres.2017.03.054>.

973 Laini, A., Viaroli, P., Bolpagni, R., Cancellario, T., 2019. Taxonomic and functional responses  
974 of benthic macroinvertebrate communities to hydrological and water quality variations  
975 in a heavily regulated river. *Water* 11, 1478.  
976 <https://doi.org/https://doi.org/10.3390/w11071478>.

977 Layman, C.A., Arrington, D.A., Montana, C.G., Post, D.M., 2007. Can stable isotope ratios  
978 provide for community-wide measures of trophic structure? *Ecology* 88, 42–48.  
979 [https://doi.org/10.1890/0012-9658\(2007\)88\[42:csirpf\]2.0.co;2](https://doi.org/10.1890/0012-9658(2007)88[42:csirpf]2.0.co;2).

980 Liess, M., von der Ohe, P.C., 2005. Analyzing effects of pesticides on invertebrate  
981 communities in streams. *Environ. Toxicol. Chem.* 24, 954–965.  
982 <https://doi.org/10.1897/03-652.1>.

983 Ligon, F.K., Dietrich, W.E., Trush, W.J., 1995. Downstream ecological effects of dams.  
984 *Bioscience* 45, 183–192. <https://doi.org/10.2307/1312557>.

985 Linhart, J., Vlčková, Š., Uvíra, V., 2002. Bryophytes as a special mesohabitat for meiofauna in  
986 a rip-rapped channel. *River Res. Appl.* 18, 321–330. <https://doi.org/10.1002/rra.671>.

987 Maazouzi, C., Galassi, D., Claret, C., Cellot, B., Fiers, F., Martin, D., Marmonier, P., Dole-  
988 Olivier, M.J., 2017. Do benthic invertebrates use hyporheic refuges during streambed  
989 drying? A manipulative field experiment in nested hyporheic flow paths. *Ecohydrology*  
990 10, e1865. <https://doi.org/10.1002/eco.1865>.

- 991 Martinez, A., Larranaga, A., Basaguren, A., 2013. Stream regulation by small dams affects  
992 benthic macroinvertebrate communities: from structural changes to functional  
993 implications. *Hydrobiologia* 711, 31–42. <http://doi.10.1007/s10750-013-1459-z>.
- 994 Marty, J., Smokorowski, K., Power, M., 2009. The influence of fluctuating ramping rates on  
995 the food web of boreal rivers. *River Res. Appl.* 25, 962–974. doi:10.1002/rra.1194.
- 996 Mateo, M.A., Serrano, O., Serrano, L., Michener, R.H., 2008. Effects of sample preparation on  
997 stable isotope ratios of carbon and nitrogen in marine invertebrates: implications for food  
998 web studies using stable isotopes. *Oecologia* 157, 105–115.  
999 <https://doi.org/10.1007/s00442-008-1052-8>
- 1000 Mbaka, J.G., Mwaniki, M.W., 2015. A global review of the downstream effects of small  
1001 impoundments on stream habitat conditions and macroinvertebrates. *Environ. Rev.* 23,  
1002 257–262. <https://doi.org/10.1139/er-2014-0080>.
- 1003 Mellado-Díaz, A., Sánchez-González, J.R., Guareschi, S., Magdaleno, F., Toro, M., 2019.  
1004 Exploring longitudinal trends and recovery gradients in macroinvertebrate communities  
1005 and biomonitoring tools along regulated rivers. *Sci. Total Environ.* 695, 133774.  
1006 <https://doi.org/https://doi.org/10.1016/j.scitotenv.2019.133774>.
- 1007 Menge, B.A., Olson, A.M., Dahlhoff, E.P., 2002. Environmental stress, bottom-up effects, and  
1008 community dynamics: integrating molecular-physiological and ecological approaches.  
1009 *Integr. Comp. Biol.* 42, 892–908. <https://doi.org/10.1093/icb/42.4.892>.
- 1010 Mermillod-Blondin, F., Marmonier, P., Tenaille, M., Lemoine, D. G., Lafont, M., Vander  
1011 Vorste, R., Simon, L., Volatier, L., 2020. Bottom-up processes control benthic  
1012 macroinvertebrate communities and food web structure of fishless artificial wetlands.  
1013 *Aquat. Ecol.* 54, 575–589. <https://doi.org/10.1007/s10452-020-09760-2>.

1014 Mondy, C.P., Usseglio-Polatera, P., 2013. Using conditional tree forests and life history traits  
1015 to assess specific risks of stream degradation under multiple pressure scenarios. *Sci.*  
1016 *Total Environ.* 461, 750–760. <https://doi.org/10.1016/j.scitotenv.2013.05.072>.

1017 Mondy, C.P., Usseglio-Polatera, P., 2014. Using fuzzy-coded traits to elucidate the non-  
1018 random role of anthropogenic stress in the functional homogenisation of invertebrate  
1019 assemblages. *Freshw. Biol.* 59, 584–600. <http://doi.org/10.1111/fwb.12289>.

1020 Mondy, C.P., Muñoz, I., Dolédec, S., 2016. Life-history strategies constrain invertebrate  
1021 community tolerance to multiple stressors: A case study in the Ebro basin. *Sci. Total*  
1022 *Environ.* 572, 196–206. <https://doi.org/10.1016/j.scitotenv.2016.07.227>.

1023 Mor, J., Ruhí, A., Tornés, E., Valcárcel, H., Muñoz, I., Sabater, S., 2018. Dam regulation and  
1024 riverine food-web structure in a Mediterranean river. *Sci. Total Environ.* 625, 301–310.  
1025 <https://doi.org/doi.org/10.1016/j.scitotenv.2017.12.296>.

1026 Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation  
1027 of the world's large river systems. *Sciences* 308, 405–409.  
1028 <https://doi.org/10.1126/science.1107887>.

1029 Newsome, S.D., Martinez del Rio, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic  
1030 ecology. *Front. Ecol. Environ.* 5, 429–436. <https://doi.org/10.1890/060150.1>

1031 Oksanen, L., Fretwell, S. D., Arruda, J., Niemelä, J., 1981. Exploitation ecosystems in  
1032 gradients of primary productivity. *Am. Nat.* 118, 240–261.  
1033 <https://doi.org/10.1086/283817>.

1034 Papadakis, E., Tsaboula, A., Vryzas, Z., Kotopoulou, A., Kintzikoglou, K., Papadopoulou-  
1035 Mourkidou, E., 2018. Pesticides in the rivers and streams of two river basins in northern  
1036 Greece. *Sci. Total Environ.* 624, 732–743.  
1037 <https://doi.org/https://doi.org/10.1016/j.scitotenv.2017.12.074>.

1038 Pardo, I., García, L., 2016. Water abstraction in small lowland streams: unforeseen hypoxia  
1039 and anoxia effects. *Sci. Total Environ.* 568, 226–235.  
1040 <https://doi.org/10.1016/j.scitotenv.2016.05.218>.

1041 Parr, L.B., Mason, C.F., 2004. Causes of low oxygen in a lowland, regulated eutrophic river in  
1042 Eastern England. *Sci. Total Environ.* 321, 273–286.  
1043 <https://doi.org/doi.org/10.1016/j.scitotenv.2017.12.296>.

1044 Pepin, D.M., Hauer, F.R., 2002. Benthic responses to groundwater–surface water exchange in  
1045 2 alluvial rivers in northwestern Montana. *J. North Am. Benthol. Soc.* 21, 370–383.  
1046 <https://doi.org/10.2307/1468476>.

1047 Pingram, M.A., Collier, K.J., Hamilton, D.P., David, B.O., Hicks, B.J., 2012. Carbon sources  
1048 supporting large river food webs: a review of ecological theories and evidence from  
1049 stable isotopes. *Freshw. Rev.* 5, 85–103. <https://doi.org/10.1608/frj-5.2.476>.

1050 Poff, N.L., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river  
1051 dynamics by dams and global biodiversity implications. *Proc. Natl. Acad. Sci. USA* 104,  
1052 5732–5737. <https://doi.org/10.1073/pnas.0609812104>.

1053 Post, D.M., Connors, D.M., Goldberg, D.S., 2000. Prey preference by a top predator and the  
1054 stability of linked food chains. *Ecology* 81, 8–14. [https://doi.org/10.1890/0012-9658\(2000\)081\[0008:ppbatp\]2.0.co;2](https://doi.org/10.1890/0012-9658(2000)081[0008:ppbatp]2.0.co;2).

1056 Power, M.E., Dietrich, W.E., Finlay, J.C., 1996. Dams and downstream aquatic biodiversity:  
1057 Potential food web consequences of hydrologic and geomorphic change. *Env. Manag.*  
1058 20, 887–895. <https://doi:10.1007/BF01205969>.

1059 Prescott, G.W., Barrick, J., Cawley, E.T., Jaques, G. 1978. How to know the freshwater algae?  
1060 McGraw-Hill Higher Education, New York.

1061 R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation  
1062 for Statistical Computing, Vienna, Austria.

1063 Robert, P., Escoufier, Y., 1976. A unifying tool for linear statistical methods: the RV-  
1064 coefficient. *J. Appl. Stat.* 25, 257–265. <https://doi.org/10.2307/2347233>.

1065 Rollet, A.J., Piégay, H., Dufour, S., Bornette, G., Persat, H., 2014. Assessment of consequences  
1066 of sediment deficit on a gravel river bed downstream of dams in restoration perspectives:  
1067 application of a multicriteria, hierarchical and spatially explicit diagnosis. *River Res.*  
1068 *Appl.* 30, 939–953. <https://doi.org/10.1002/rra>.

1069 Rolls, R. J., Leigh, C., Sheldon, F., 2012. Mechanistic effects of low-flow hydrology on  
1070 riverine ecosystems: ecological principles and consequences of alteration. *Freshw. Sci.*  
1071 31, 1163–1186. <https://doi.org/10.1899/12-002.1>.

1072 Rooney, N., McCann, K., Gellner, G., Moore, J.C., 2006. Structural asymmetry and the  
1073 stability of diverse food webs. *Nature* 442, 265–269.  
1074 <https://doi.org/10.1038/nature04887>.

1075 Rosenberg, D.M., McCully, P., Pringle, C.M., 2000. Global-scale environmental effects of  
1076 hydrological alterations: introduction. *BioScience* 50, 746–751.  
1077 [https://doi.org/10.1641/0006-3568\(2000\)050\[0746:gseeoh\]2.0.co;2](https://doi.org/10.1641/0006-3568(2000)050[0746:gseeoh]2.0.co;2).

1078 Schmidt-Kloiber, A., Hering, D., 2015. [www.freshwaterecology.info](http://www.freshwaterecology.info) – An online tool that  
1079 unifies, standardises and codifies more than 20,000 European freshwater organisms and  
1080 their ecological preferences. *Ecol. Indic.* 53, 271–282.  
1081 <https://doi.org/https://doi.org/10.1016/j.ecolind.2015.02.007>

1082 Statzner, B., Bêche, L.A., 2010. Can biological invertebrate traits resolve effects of multiple  
1083 stressors on running water ecosystems? *Freshw. Biol.* 55, 80–119.  
1084 <https://doi:10.1111/j.1365-2427.2009.02369.x>.

1085 Statzner, B., Higler, B., 1985. Questions and comments on the River Continuum Concept. *Can.*  
1086 *J. Fish. Aquat. Sci.* 42, 1038–1044. <https://doi.org/10.1139/f85-129>.

- 1087 Smith, V.H., 2007. Microbial diversity-productivity relationships in aquatic ecosystems.  
1088 FEMS Microbiol. Ecol. 62, 181–186. <https://doi.org/10.1111/j.1574-6941.2007.00381.x>.
- 1089 Suren, A.M., 1992. Enhancement of invertebrate food resources by bryophytes in New Zealand  
1090 alpine headwater streams. N. Z. J. Mar. Freshwater Res. 26, 229–239.  
1091 <https://doi.org/10.1080/00288330.1992.9516518>.
- 1092 Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2010. Invertébrés d'eau douce :  
1093 systématique, biologie, écologie, 3rd ed. CNRS éditions, Paris.
- 1094 Thioulouse, J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., Pavoine, S., 2018.  
1095 Multivariate analysis of ecological data with ade4. Springer, New York.  
1096 <https://doi.org/10.1007/978-1-4939-8850-1>.
- 1097 Townsend, C., Dolédec, S., Scarsbrook, M., 1997. Species traits in relation to temporal and  
1098 spatial heterogeneity in streams: a test of habitat templet theory. Freshw. Biol. 37, 367–  
1099 387. <https://doi.org/10.1046/j.1365-2427.1997.00166.x>.
- 1100 Usseglio-Polatera, P., Beisel, J.N., 2002. Longitudinal changes in macroinvertebrate  
1101 assemblages in the Meuse River: anthropogenic effects versus natural change. River Res.  
1102 Appl. 18, 197–211. <https://doi.org/10.1002/rra.651>.
- 1103 Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.A., Cushing, C.E. 1980. The river  
1104 continuum concept. Can. J. Fish. Aquat. Sci. 37, 130–137. [https://doi.org/10.1139/f80-](https://doi.org/10.1139/f80-017)  
1105 017.
- 1106 Valett, H.M., Fisher, S.G., Grimm, N.B., Camill, P., 1994. Vertical hydrologic exchange and  
1107 ecological stability of a desert stream ecosystem. Ecology 75, 548–560.  
1108 <https://doi.org/10.2307/1939557>.
- 1109 Vörösmarty, C.J., Meybeck, M., Fekete, B., Sharma, K., Green, P., Syvitski, J.P., 2003.  
1110 Anthropogenic sediment retention: major global impact from registered river

1111 impoundments. *Global Planet. Change* 39, 169–190. <https://doi.org/10.1016/s0921->  
1112 8181(03)00023-7.

1113 Vorste, R., Vander, Mermillod-Blondin, F., Hervant, F., Mons, R., Datry, T., 2017. *Gammarus*  
1114 *pulex* (Crustacea: Amphipoda) avoids increasing water temperature and intraspecific  
1115 competition through vertical migration into the hyporheic zone: a mesocosm experiment.  
1116 *Aquat. Sci.* 79, 45–55. <https://doi.org/10.1007/s00027-016-0478-z>.

1117 Ward, J., Stanford, J.A., 1983a. The serial discontinuity concept of lotic ecosystems, in:  
1118 Fontaine, T.D., Bartell, S.M. (Eds), *Dynamics of lotic ecosystems*, Ann Arbor. Michigan,  
1119 pp. 29–42. <https://doi.org/10.2307/2259560>

1120 Ward, J.V., Stanford, J.A., 1983b. The regulated stream as a testing ground for ecological  
1121 theory, in: Lillehammer, A., Saltveit, S.J. (Eds), *Regulated rivers*, Universitetsforlaget  
1122 AS, Oslo, pp. 23–38. [https://doi.org/10.1007/978-1-4684-8613-1\\_12](https://doi.org/10.1007/978-1-4684-8613-1_12).

1123 White, D.S., Elzinga, C.H., Hendricks, S.P., 1987. Temperature patterns within the hyporheic  
1124 zone of a northern Michigan river. *J. North Am. Benthol. Soc.* 6, 85–91.  
1125 <https://doi.org/10.2307/1467218>.

1126 Winemiller, K.O., Hoeninghaus, D.J., Pease, A.A., Esselman, P.C., Honeycutt, R.L.,  
1127 Gbanaador, D., Carrera, E., Payne, J., 2010. Stable isotope analysis reveals food web  
1128 structure and watershed impacts along the fluvial gradient of a mesoamerican coastal  
1129 river. *River Res. Appl.* 27, 791–803. <https://doi.org/10.1002/rra>.

1130 Wright, D.H., 1983. Species–energy theory: an extension of species-area theory. *Oikos* 41,  
1131 496–506. <https://doi.org/10.2307/3544109>.

1132 Wulf, P., Pearson, R.G., 2017. Mossy stones gather more bugs: moss as habitat, nurseries and  
1133 refugia for tropical stream invertebrates. *Hydrobiologia* 790, 167–182.  
1134 <https://doi.org/10.1007/s10750-016-3028-8>.

1135 Zarfl, C., Lumsdon, A.E., Tockner, K., 2014. A global boom in hydropower dam construction.

1136 Aquat. Sci. 77, 161–170. <https://doi.org/10.1007/s00027-014-0377-0>.

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**Table 1.** General characteristics of the study sites.

	<b>A1</b>	<b>A2</b>	<b>A3</b>	<b>A4</b>	<b>A5</b>	<b>A6</b>
Latitude	46°44'28.5"N	46°41'09.9"N	46°36'00.0"N	46°02'42.9"N	45°57'28.6"N	45°48'31.4"N
Longitude	5°47'39.9"E	5°45'57.0"E	5°41'52.3"E	5°19'56.1"E	5°14'58.6"E	5°11'33.3"E
Elevation (m)	469	458	436	234	216	188
Source distance (km)	47	53	67	151	170	186
Flow	Natural	Natural	Moderately regulated	Regulated	Regulated	Regulated
Land use	Mixed forest, extensive pasture	Mixed forest, extensive pasture	Mixed forest, extensive pasture	Alluvial forest, crops	Alluvial forest, crops	Alluvial forest, crops

**Table 2.** A priori hypotheses and rationale of expected changes in invertebrate trait metrics selected in this study.

<b>Metric</b>	<b>Trait category</b>	<b>Rationale</b>
Maximum size	≤10 mm	Should increase below dams due to better resilience ability in response to hydropeaking
Life cycle duration	≤1 yr	<i>idem</i>
Nb of generations per year	Multivoltine	<i>idem</i>
Dispersal	Aquatic passive	<i>idem</i>
Reproduction	Ovoviviparity	Should provide a better resistance to human disturbance though egg protection
Trophic status	Oligotrophic	Eutrophication should decrease the proportion of oligotrophic taxa below dams
Shredder	Shredders	Should decrease below dams due to the retention of CPOM in reservoirs
Scraper	Scrapers	Eutrophication and POM reduction below dams should increase proportions of algae-food scrapers
Filtering-feeder	Filtering-feeders	Should decrease below dams due to the reduction of POM below dams
Predator	Predators	Should decrease below dams due to a reduction of detritus-based food web
Food diversity (Rao)	all food types	<i>idem</i>
Food community specialization	all food types	<i>idem</i>
Trophic status community specialization	all trophic status types	<i>idem</i>
SPEAR pesticide (% abundance)	-	Should decrease in sites located in areas with high crop production

**Table 3.** (A) Flow ( $n=36$ ) and temperature ( $n=72$ ) characteristics in each study site (mean $\pm$ standard deviation). (B) Water chemistry in each study site (mean $\pm$ standard deviation,  $n=432$  for oxygen and  $n=360$  for other parameters) Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (\*\*\* $P<0.001$ ; \*\* $P<0.01$ ; \* $P<0.05$ ; .  $P<0.1$ ; ns: non-significant).

	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
<b>A</b>													
Flow ( $\text{m}^3.\text{s}^{-1}$ )	35 $\pm$ 26	37 $\pm$ 27	38 $\pm$ 27	124 $\pm$ 81	138 $\pm$ 92	133 $\pm$ 104	-	***	***	-	***	-	ns
Pulse	1-4	1-4	1-4	1-10	1-10	1-10	-	***	ns	-	-	-	ns
Flow CV	0.67	0.66	0.58	0.58	0.65	0.60	-	ns	***	-	***	-	ns
Temperature ( $^{\circ}\text{C}$ )	12.1 $\pm$ 4.6	12.4 $\pm$ 3.7	13.8 $\pm$ 5.2	13.8 $\pm$ 3.9	14.2 $\pm$ 4.3	14.2 $\pm$ 4.1	ns	*	***	ns	***	**	**
Temperature range ( $^{\circ}\text{C}$ )	5.5 $\pm$ 3.6	5.0 $\pm$ 1.0	7.7 $\pm$ 3.4	3.1 $\pm$ 3.7	4.9 $\pm$ 3.3	4.8 $\pm$ 3.0	**	ns	***	**	ns	ns	ns
<b>B</b>													
Dissolved oxygen ( $\text{mg. L}^{-1}$ )	10.8 $\pm$ 1.2	11.1 $\pm$ 2.3	11.4 $\pm$ 1.0	10.0 $\pm$ 1.8	9.5 $\pm$ 1.9	10.9 $\pm$ 1.7	**	.	***	ns	***	ns	***
Electric conductivity ( $\mu\text{S.cm}^{-1}$ )	400 $\pm$ 24	408 $\pm$ 19	383 $\pm$ 38	364 $\pm$ 27	389 $\pm$ 13	376 $\pm$ 9	ns	.	***	ns	***	ns	***
N-NO <sub>3</sub> ( $\text{mg. L}^{-1}$ )	0.87 $\pm$ 0.09	0.85 $\pm$ 0.14	0.69 $\pm$ 23	0.63 $\pm$ 0.17	0.84 $\pm$ 0.16	0.92 $\pm$ 0.13	***	ns	***	.	***	.	***
N-NH <sub>4</sub> ( $\mu\text{g. L}^{-1}$ )	20.3 $\pm$ 9.5	21.3 $\pm$ 13.6	26.0 $\pm$ 15.3	26.3 $\pm$ 13.4	19.5 $\pm$ 13.7	16.0 $\pm$ 11.1	-	-	-	-	-	-	-
P-PO <sub>4</sub> ( $\mu\text{g. L}^{-1}$ )	10.0 $\pm$ 7.9	11.3 $\pm$ 9.0	6.3 $\pm$ 6.5	8.3 $\pm$ 3.8	7.7 $\pm$ 2.8	7.4 $\pm$ 4.1	-	-	-	-	-	-	-

**Table 4.** Algal (A) and invertebrate (B) metrics in each study site (mean±standard deviation;  $n=72$  and  $n=432$  for algal and invertebrate metrics, respectively). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (\*\*\* $P<0.001$ ; \*\* $P<0.01$ ; \* $P<0.05$ ; .  $P<0.1$ ; ns: non-significant).

Station	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
<b>A</b>													
Cyanobacteria ( $10^6\text{cells.m}^{-2}$ )	1.8±2.4	1.8±21.9	2.4±3.0	5.1±4.6	0.3±0.6	1.6±2.6	ns	ns	***	ns	**	ns	***
Chlorophytes ( $10^6\text{cells.m}^{-2}$ )	0.3±0.4	0.5±0.6	0.4±0.3	0.7±0.8	0.2±0.1	0.3±0.3	ns	ns	***	ns	***	ns	***
Diatoms ( $10^6\text{cells.m}^{-2}$ )	0.6±0.8	0.8±0.7	0.7±0.6	1.2±0.7	0.2±0.3	0.8±0.9	ns	ns	***	ns	**	ns	***
Chlorophyll- <i>a</i> ( $\text{mg.cm}^{-2}$ )	1.9±92.3	2.6±2.6	2.6±2.6	4.1±2.7	0.5±0.4	1.2±1.2	ns	ns	***	ns	***	ns	***
<b>B</b>													
Total abundance	522±410	432±351	533±586	834±774	225±318	186±240	*	ns	***	ns	***	ns	***
Richness	23±6	22±9	24±7	23±5	16±6	14±6	ns	ns	***	ns	***	ns	***
Shannon diversity	2.1±0.3	2.0±0.4	2.1±0.4	1.9±0.3	1.9±0.5	1.7±0.5	ns	**	***	ns	***	*	***

**Table 5.** Invertebrate trait metrics in each study site (mean±standard deviation,  $n=432$ ) separated into resilience and resistance trait (A), functional feeding groups (B) and trophic specialization (C). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (\*\*\* $P<0.001$ ; \*\* $P<0.01$ ; \* $P<0.05$ ; .  $P<0.1$ ; ns: non-significant).

	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
<b>A</b>													
Maximal size <10 mm	0.63±0.09	0.67±0.09	0.68±0.05	0.63±0.06	0.64±0.09	0.64±0.10	**	ns	***	***	***	ns	**
Life duration <1 y.	0.69±0.06	0.75±0.06	0.71±0.06	0.67±0.08	0.68±0.11	0.71±0.12	**	ns	***	**	***	ns	***
Multivoltine	0.33±0.05	0.36±0.05	0.39±0.06	0.42±0.05	0.43±0.09	0.47±0.07	ns	*	***	ns	*	.	***
Aquatic passive dispersal	0.37±0.02	0.34±0.03	0.37±0.03	0.39±0.03	0.40±0.05	0.38±0.05	**	.	***	ns	**	ns	***
Ovoviviparity	0.11±0.04	0.08±0.04	0.13±0.05	0.19±0.05	0.19±0.09	0.17±0.10	**	*	***	***	***	ns	***
Oligotrophic	0.47±0.04	0.45±0.04	0.40±0.03	0.36±0.03	0.40±0.05	0.39±0.06	.	.	***	*	ns	ns	***
Pesticide sensitivity	10.5±3.8	9.3±4.7	8.3±3.2	7.8±2.7	5.4±2.8	4.7±3.1	ns	*	***	ns	***	ns	***
<b>B</b>													
Shredders	0.29±0.04	0.23±0.05	0.25±0.05	0.30±0.05	0.31±0.07	0.25±0.09	***	ns	***	***	***	ns	***
Scrapers	0.38±0.05	0.38±0.06	0.35±0.04	0.29±0.05	0.37±0.07	0.35±0.06	*	ns	***	ns	***	ns	***
Filter feeders	0.06±0.03	0.12±0.05	0.12±0.05	0.10±0.04	0.08±0.05	0.13±0.07	**	ns	***	*	***	ns	***
Predators	0.15±0.04	0.13±0.04	0.13±0.04	0.18±0.04	0.13±0.05	0.15±0.06	ns	ns	***	ns	***	ns	***
<b>C</b>													
Food Rao diversity	0.12±0.03	0.13±0.05	0.13±0.04	0.13±0.04	0.13±0.04	0.12±0.05	*	ns	***	***	ns	ns	*
Food specialization	0.31±0.04	0.32±0.04	0.32±0.04	0.32±0.04	0.29±0.06	0.29±0.04	ns	ns	***	ns	ns	ns	***
Trophic status specialization	0.26±0.02	0.24±0.02	0.22±0.010	0.21±0.01	0.22±0.02	0.21±0.02	ns	ns	***	**	***	ns	***

**Table 6.** Resource (A) and niche metrics (B) in each study site (mean±standard deviation,  $n=36$ ). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (SEAnr: normalized isotopic area; CR: index of basal resource exploitation; NR: index of trophic level diversity) (\*\*\* $P<0.001$ ; \*\* $P<0.01$ ; \* $P<0.05$ ; .  $P<0.1$ ; ns: non-significant).

	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
<b>A</b>													
Shannon diversity	1.06±0.26	0.96±0.20	1.09±0.26	0.99±0.54	1.05±0.19	0.96±0.24	ns	ns	.	.	ns	ns	ns
CPOM	0.56±0.76	0.06±0.08	0.09±0.08	0.43±0.61	0.31±0.33	0.07±0.07	.	ns	ns	ns	ns	.	ns
FPOM	0.08±0.02	0.11±0.09	0.30±0.41	0.65±0.74	0.12±0.06	0.04±0.06	ns	ns	ns	ns	ns	ns	**
Sedimentary biofilm	0.23±0.28	0.01±0.00	0.00±0.00	0.06±0.06	0.04±0.04	0.02±0.02	ns	ns	ns	ns	ns	ns	***
Perilithon	0.23±0.16	0.25±0.18	0.16±0.14	0.52±0.40	0.18±0.12	0.17±0.19	ns	ns	*	*	ns	ns	ns
mosses	0.16±0.36	0.43±0.51	0.16±0.18	1.89±1.56	0.42±0.85	0.14±0.25	ns	ns	ns	ns	ns	ns	.
Total C	17.7±10.8	16.1±11.5	15.7±18.2	52.9±21.9	14.9±11.8	6.0±5.2	ns	ns	ns	ns	ns	ns	**
<b>B</b>													
SEAnr	40.2±14.1	39.5±12.8	59.4±22.4	44.1±18.6	37.7±7.4	23.6±8.9	ns	*	**	ns	*	ns	*
CR	7.7±1.0	8.2±0.9	10.0±2.1	9.6±3.0	10.4±3.4	6.7±0.9	ns	ns	.	ns	ns	ns	.
NR	7.6±1.4	6.2±1.2	6.7±1.1	9.2±2.8	7.0±0.9	5.3±1.6	ns	ns	ns	ns	ns	ns	*

**Appendix 1.** Community matrix showing the abundance of taxa summed by sampling zone (n=6) and collected above the dams with the indication of sampling date (“1408” to “1606”), sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling). Taxa are listed in alphabetical order.

	1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606				
	A1d	A1u	A1d	A1u	A1d	A1u	A1d	A1u	A1d	A1u	A1d	A1u	A2d	A2u	A2d	A2u	A2d	A2u	A2d	A2u	A2d	A2u	A2d	A2u	A3d	A3u	A3d	A3u	A3d	A3u	A3d	A3u	A3d	A3u	A3d	A3u			
<i>Amphinemura</i> sp.	0	0	3	5	0	2	0	0	2	1	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0		
<i>Ancylus</i> sp.	1	0	0	1	0	0	0	0	0	0	1	0	0	0	11	7	0	2	2	4	9	9	0	0	0	1	1	8	0	0	1	1	1	0	0	0	0		
Anthomyidae	4	0	0	1	0	0	1	4	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0		
<i>Asellus</i> sp.	0	0	0	2	0	1	0	0	1	3	0	0	0	0	5	2	0	0	0	0	2	5	0	0	13	191	81	86	1	14	38	1	260	5	1	2	2		
<i>Atherix</i> sp.	3	3	1	2	1	2	20	3	4	3	1	2	10	44	14	13	0	0	35	43	8	12	0	0	1	1	3	4	0	0	53	25	18	14	0	0	0		
<i>Athripsodes</i> sp.	0	0	0	1	0	0	0	0	3	7	10	15	0	0	0	0	0	0	0	28	25	5	10	0	1	1	4	3	0	0	0	38	5	24	10	10	10		
<i>Baetis</i> sp.	154	273	150	96	32	112	129	252	72	19	43	155	559	533	143	157	92	62	48	141	21	38	14	14	196	158	33	57	199	50	50	51	16	18	40	34			
<i>Bithynia</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	23	2	0	0	0		
<i>Brychius</i> sp.	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Caenis</i> sp.	0	0	1	4	6	4	0	0	2	8	9	11	0	0	0	0	0	0	0	6	4	0	0	0	8	5	2	2	5	25	107	66	24	7	20	20			
<i>Calopteryx</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	7	1	0	0	0		
<i>Centroptilum</i> sp.	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	4	8	0	0	0	0	
<i>Ceraclea</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	24	4	2	0	0		
Ceratopogonidae	6	4	38	22	8	26	1	2	37	0	9	6	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	3	2	2	
<i>Cheumatopsyche</i> sp.	0	0	0	0	0	0	0	0	16	1	2	1	0	0	0	0	0	7	49	0	322	54	2	4	19	2	124	61	27	27	301	162	411	1901	7	14	14		
Chironomini	29	23	2	0	4	24	267	150	4	7	2	6	82	314	1	0	17	71	60	52	28	7	0	0	131	171	25	11	199	71	183	47	28	14	5	2	2		
<i>Dendrocoelum</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	
<i>Dinocras</i> sp.	0	1	0	1	0	0	5	1	3	0	0	0	2	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Dreissena</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dryops</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dugesia</i> sp.	0	0	2	2	1	0	2	3	68	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	8	3	0	4	13	2	30	108	0	0	0	0	
<i>Ecdyonurus</i> sp.	1	6	28	37	4	16	35	10	19	7	7	13	20	26	52	44	10	6	20	39	58	80	7	8	5	7	12	15	29	2	13	21	0	0	37	22	22		
<i>Elmis</i> sp.	40	43	70	100	14	95	454	69	981	66	11	10	64	165	159	127	28	20	89	66	595	751	0	3	126	65	321	380	59	22	583	94	645	522	12	7	7		
Empididae	21	24	22	27	5	73	22	9	21	7	2	8	8	13	25	11	4	3	1	2	10	14	0	0	4	3	2	5	4	2	1	1	3	2	0	0	0		
<i>Epeorus</i> sp.	0	0	9	5	1	2	0	0	0	2	0	0	1	0	14	6	8	25	0	0	1	0	0	0	0	0	7	3	3	1	0	0	0	0	0	0	0	1	
<i>Ephemera</i> sp.	3	1	5	2	0	3	0	2	1	1	0	0	0	0	0	3	0	1	7	2	6	0	0	0	0	0	2	3	1	1	1	7	12	0	0	0	0		
<i>Erbobdella</i> sp.	6	1	7	3	1	3	5	3	8	18	2	0	0	3	5	6	0	1	2	13	5	11	0	0	0	1	0	0	2	3	14	26	20	9	1	4	4		

## Appendix 1. Continued.

<i>Esolus</i> sp.	108	224	240	212	90	168	978	601	346	363	232	204	67	75	82	59	58	29	79	41	189	146	32	66	57	160	263	277	44	54	215	117	310	187	55	115		
<i>Gammarus</i> sp.	1065	549	439	896	336	584	1020	949	864	206	100	116	140	519	489	632	81	16	28	30	112	199	5	16	357	289	730	899	427	122	765	42	297	35	230	66		
<i>Glossiphonia</i> sp.	1	0	1	0	1	0	0	3	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	3	1	1	6	0	6	0	0	0	0		
<i>Habroleptoides</i> sp.	0	1	1	2	1	0	0	1	0	1	0	0	0	0	3	3	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	
<i>Habrophlebia</i> sp.	0	0	0	0	0	0	0	1	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Halipus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	
<i>Helobdella</i> sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	6	0	0	0	
<i>Hemiclepsis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	
<i>Heptagenia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	6	0	0	
Hydracarina	1	5	3	2	12	30	124	162	171	41	29	83	0	3	12	18	11	6	115	246	120	247	9	12	3	18	41	13	17	64	61	30	117	11	17	14		
<i>Hydraena</i> sp.	1	4	1	7	1	1	2	0	6	2	0	1	1	4	2	9	1	0	3	0	1	3	0	0	0	6	2	5	0	0	1	1	15	0	0	0	0	
Hydroporinae	0	0	0	0	0	0	5	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	4	1	0	0	0	0	
<i>Hydrapsyche</i> sp.	37	39	30	154	1	18	49	19	694	32	4	4	73	370	380	217	31	52	226	45	276	972	2	4	93	11	317	507	44	28	1848	256	465	1144	13	3		
<i>Hydroptila</i> sp.	0	2	22	29	0	26	16	18	14	55	7	57	1	11	29	13	0	0	81	99	244	319	6	2	6	5	48	22	4	1	8	19	689	148	42	2		
<i>Ithytrichia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	45	17	0	0	0	
<i>Lepidostoma</i> sp.	0	0	0	3	0	0	9	5	2	2	1	1	2	28	21	5	0	1	60	140	76	217	1	0	3	1	3	6	0	8	1	0	19	7	11	0	0	
<i>Leuctra</i> sp.	78	133	13	22	43	62	400	185	17	28	176	269	113	151	5	5	13	7	26	43	21	25	32	67	25	39	0	2	3	5	61	74	12	10	114	109		
Limnephilinae	1	0	1	9	10	6	1	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limnius</i> sp.	68	132	98	159	13	105	515	389	123	156	186	217	12	29	41	19	1	6	12	12	24	13	0	6	4	5	14	12	3	1	65	17	157	60	22	13		
Limoniidae	140	118	80	51	44	363	13	17	42	17	0	1	48	84	39	31	1	5	35	19	64	27	0	1	92	28	7	36	15	19	9	22	30	17	0	0	0	
<i>Metalype</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Micrasema</i> sp.	2	0	0	0	0	0	0	0	1	0	0	0	4	14	8	13	0	0	1	1	21	23	0	0	0	3	43	36	6	1	3	0	66	32	0	0	0	
<i>Micronecta</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mystacides</i> sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	2	1	0	0	0	
<i>Nemoura</i> sp.	0	0	3	3	0	0	0	0	3	6	0	0	0	6	6	0	0	0	0	0	3	3	0	0	0	0	4	0	1	1	0	0	1	1	0	0	0	0
<i>Odontocerum</i> sp.	9	5	17	23	24	15	19	16	68	10	5	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Onychogomphus</i> sp.	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Orectochilus</i> sp.	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	1	10	14	0	1	0	0	5	7	1	0	8	2	11	54	0	0	0	
Orthoclaadiinae	618	825	269	291	145	1155	167	56	1135	1083	381	1165	1894	2160	631	450	93	77	182	259	1486	1154	313	292	1287	1196	169	373	287	186	586	162	801	486	1246	632		
<i>Oulimnius</i> sp.	0	0	1	0	0	5	3	1	7	9	1	0	0	3	7	6	0	0	3	5	98	81	0	0	7	122	122	63	4	8	31	55	238	59	2	5	0	
<i>Perla</i> sp.	1	4	4	1	0	0	5	0	5	1	0	0	3	3	5	2	2	5	1	1	2	2	0	2	0	1	1	1	0	1	1	1	1	1	1	2	0	0





**Appendix 2.** Community matrix showing the abundance of taxa summed by sampling zone (n=6) and collected below the dams with the indication of sampling date (“1408” to “1606”), sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling). Taxa are listed in alphabetical order.

	1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606				
	A4d	A4u	A4d	A4u	A4d	A4u	A4d	A4u	A4d	A4u	A4d	A4u	A5d	A5u	A5d	A5u	A5d	A5u	A5d	A5u	A5d	A5u	A5d	A5u	A6d	A6u	A6d	A6u	A6d	A6u	A6d	A6u	A6d	A6u	A6d	A6u			
<i>Amphinemura</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ancylus</i> sp.	1	1	8	2	2	6	2	7	0	3	0	3	0	0	8	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Anthomyidae	1	16	0	9	0	0	0	0	6	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Asellus</i> sp.	188	417	183	206	43	282	1	74	52	119	106	285	1	2	3	7	4	1	0	13	19	180	0	2	2	0	1	4	0	0	0	0	4	84	0	3	0	3	
<i>Atherix</i> sp.	0	1	0	1	0	0	0	0	0	0	2	0	4	0	0	0	0	14	3	0	0	0	0	0	0	0	0	0	0	0	0	3	2	2	0	0	0		
<i>Athripsodes</i> sp.	2	0	6	21	49	81	16	6	5	5	40	82	0	0	2	2	20	6	1	2	6	47	24	15	0	0	0	2	7	1	0	1	6	22	3	22	0	22	
<i>Baetis</i> sp.	43	43	8	2	32	5	33	163	21	5	310	46	25	36	0	0	92	8	195	155	2	1	38	34	124	80	96	5	19	0	488	83	161	10	14	19	0		
<i>Bithynia</i> sp.	0	0	0	3	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Brychius</i> sp.	0	2	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Caenis</i> sp.	0	2	0	1	0	0	0	2	0	12	46	102	0	0	0	1	2	0	7	4	3	5	6	15	0	0	1	0	0	0	1	1	4	39	19	0	0		
<i>Calopteryx</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Centroptilum</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ceraclea</i> sp.	0	0	0	0	0	0	0	0	0	0	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Ceratopogonidae	0	1	0	0	4	5	0	1	0	3	1	0	2	1	0	0	2	1	6	4	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	
<i>Cheumatopsyche</i> sp.	19	1	29	35	33	3	752	713	62	11	15	2	75	0	9	2	71	5	68	23	3	1	8	7	70	6	9	0	13	2	92	136	153	89	1	19	0	19	
Chironomini	170	66	1	254	270	69	198	206	1	32	20	7	253	4	0	0	229	8	48	39	0	0	19	3	25	39	0	2	25	0	8	59	1	0	1	0	0		
<i>Dendrocoelum</i> sp.	0	0	0	0	0	1	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dinocras</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dreissena</i> sp.	1	2	1	0	0	2	5	0	4	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dryops</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0
<i>Dugesia</i> sp.	14	36	18	21	17	44	38	21	29	19	12	7	18	1	5	0	1	0	0	1	0	46	0	0	3	15	2	17	0	1	1	146	3	11	0	0	0	0	
<i>Ecdyonurus</i> sp.	0	0	0	0	0	0	1	0	0	0	1	1	0	0	4	8	0	4	0	3	2	1	0	2	0	1	0	0	0	0	1	0	16	6	0	4	0	4	
<i>Elmis</i> sp.	505	210	346	474	116	176	948	221	598	328	106	38	128	33	111	14	59	4	32	6	55	19	19	1	18	11	6	15	4	1	8	51	9	36	0	0	0		
Empididae	7	2	11	30	57	31	8	15	4	1	7	5	1	1	1	1	10	0	4	0	0	0	7	0	2	1	8	1	2	0	19	4	3	0	0	0	0	0	
<i>Epeorus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Ephemera</i> sp.	0	1	0	1	5	7	0	8	0	2	2	6	0	0	0	0	0	3	5	0	0	6	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	
<i>Erpobdella</i> sp.	7	12	1	4	2	7	2	2	7	0	3	3	0	1	0	2	1	0	2	2	2	2	0	2	0	0	0	1	0	0	1	1	0	3	1	0	0	0	
<i>Esolus</i> sp.	5	12	10	21	9	48	8	24	32	40	12	32	50	142	84	81	150	54	66	222	91	272	42	80	55	9	152	61	79	32	42	18	246	101	32	166	0	166	





**Appendix 3.** Trait matrix showing values for (a) maximum size, (b) life duration, (c) number of generations per year, (d) reproduction type, (e) dispersal, (f) food types, (g) feeding habits, (h) trophic status, and (i) SPEAR pesticide sensitivity. Values in (a-h) represent affinities (fuzzy coding). Values in (i) equal "1" if the taxon is sensitive to pesticide, "0" otherwise (NA: not available) (extracted from Tachet *et al.* (2010) and Schmidt-Kloiber and Hering (2015)).

Taxa	(a)	(b)	(c)	(d)	(e)	(f)						(g)				(h)			(i)	
	< 10	< 1	>1	ovoviviparity	aquatic passive	micro organisms, < 1mm	dead plant ≥ 1mm	living micro phytes	living macro phytes	dead animal ≥ 1mm	living micro inver- tebrates	large animals	shredder	scraper	filter feeder	predator	oligotrophic	mesotrophic	eutrophic	pesticides
<i>Amphinemura</i> sp.	1.00	1.00	0.00	0.00	0.40	0.25	0.50	0.25	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	1.00	0.00	0.00	1
<i>Ancylus</i> sp.	0.50	1.00	0.00	0.00	0.50	0.00	0.22	0.56	0.22	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.67	0.33	0.00	0
Anthomyidae	0.75	1.00	0.75	0.17	0.00	0.13	0.00	0.13	0.13	0.00	0.00	0.63	0.25	0.00	0.00	0.75	0.00	0.25	0.75	1
Asellidae	0.49	0.51	0.71	1.00	1.00	0.17	0.50	0.17	0.17	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.18	0.55	0.27	NA
<i>Atherix</i> sp.	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.60	0.40	0.00	1
<i>Athripsodes</i> sp.	0.50	1.00	0.00	0.00	0.29	0.00	0.00	0.20	0.80	0.00	0.00	0.00	0.75	0.25	0.00	0.00	0.25	0.75	0.00	1
<i>Baetis</i> sp.	0.75	1.00	0.60	0.00	0.33	0.18	0.18	0.45	0.09	0.09	0.00	0.00	0.00	0.75	0.00	0.00	0.33	0.33	0.33	0
<i>Bithynia</i> sp.	0.75	0.50	0.00	0.00	0.67	0.08	0.15	0.38	0.08	0.08	0.15	0.08	0.00	0.33	0.67	0.00	0.00	0.60	0.40	0
<i>Brychius</i> sp.	1.00	0.25	0.75	0.00	0.33	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.50	0.00	0.00	0.50	0.50	0.50	0.00	0
<i>Caenis</i> sp.	1.00	1.00	0.75	0.00	0.40	0.50	0.20	0.10	0.10	0.10	0.00	0.00	0.25	0.00	0.00	0.00	0.17	0.50	0.33	1
<i>Calopteryx</i> sp.	0.00	0.50	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.33	0.50	0.17	1
<i>Centroptilum</i> sp.	1.00	1.00	1.00	0.00	0.29	0.40	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.40	0.60	0.00	0
<i>Ceraclea</i> sp.	0.40	0.75	0.25	0.00	0.29	0.40	0.10	0.10	0.20	0.00	0.00	0.20	0.43	0.14	0.00	0.29	0.25	0.25	0.50	1
Ceratopogonidae	0.49	1.00	0.45	0.00	0.34	0.07	0.05	0.35	0.05	0.07	0.27	0.14	0.14	0.08	0.00	0.41	0.31	0.39	0.31	0
<i>Cheumatopsyche</i> sp.	0.75	1.00	0.40	0.00	0.38	0.33	0.00	0.33	0.00	0.00	0.33	0.00	0.00	0.00	0.75	0.25	0.00	0.60	0.40	0
Chironomini	0.17	1.00	0.75	0.20	0.29	0.45	0.00	0.18	0.18	0.00	0.09	0.09	0.20	0.10	0.20	0.20	0.00	0.40	0.60	0
<i>Dendrocoelum</i> sp.	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.40	0.60	0
<i>Dinocras</i> sp.	0.00	0.00	0.00	0.00	0.25	0.20	0.00	0.00	0.00	0.00	0.00	0.80	0.75	0.00	0.00	0.25	1.00	0.00	0.00	NA
<i>Dreissena</i> sp.	0.00	0.00	0.00	1.00	0.75	0.38	0.00	0.25	0.00	0.00	0.38	0.00	0.00	0.00	1.00	0.00	0.00	0.67	0.33	0
<i>Dryops</i> sp.	1.00	0.25	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.40	0.60	0
<i>Dugesia</i> sp.	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.20	0.40	0.40	0
<i>Ecdyonurus</i> sp.	0.00	0.75	0.00	0.00	0.38	0.38	0.38	0.25	0.00	0.00	0.00	0.00	0.40	0.60	0.00	0.00	0.40	0.60	0.00	1
<i>Elmis</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
Empididae	1.00	1.00	0.35	0.00	0.28	0.00	0.00	0.11	0.00	0.00	0.00	0.89	0.00	0.00	0.00	1.00	0.20	0.60	0.20	1
<i>Epeorus</i> sp.	0.00	1.00	0.00	0.00	0.29	0.20	0.00	0.60	0.20	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.75	0.25	0.00	1

## Appendix 3. Continued

<i>Ephemera</i> sp.	0.00	0.25	0.00	0.00	0.17	0.38	0.25	0.13	0.00	0.00	0.25	0.00	0.38	0.00	0.38	0.13	0.25	0.50	0.25	1
<i>Erpobdella</i> sp.	0.00	0.25	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.33	0.17	0.50	0.00	0.00	0.00	1.00	0.00	0.60	0.40	0
<i>Esolus</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
<i>Gammarus</i> sp.	0.00	0.25	1.00	1.00	0.60	0.07	0.36	0.14	0.07	0.14	0.14	0.07	0.75	0.25	0.00	0.00	0.50	0.50	0.00	0
<i>Glossiphonia</i> sp.	0.00	0.25	0.00	0.67	0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.75	0.25	0
<i>Habroleptoides</i> sp.	0.25	1.00	0.00	0.00	0.40	0.50	0.13	0.38	0.00	0.00	0.00	0.00	0.40	0.60	0.00	0.00	0.75	0.25	0.00	1
<i>Habrophlebia</i> sp.	1.00	1.00	0.00	0.00	0.25	0.14	0.43	0.43	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.25	0.75	0.00	1
<i>Haliphus</i> sp.	1.00	0.25	0.75	0.00	0.20	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.50	0.00	0.00	0.50	0.14	0.43	0.43	0
<i>Helobdella</i> sp.	0.75	0.75	0.25	0.67	0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.40	0.60	0
<i>Hemiclepsis</i> sp.	0.00	0.00	0.00	0.67	0.75	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.75	0.25	0
<i>Heptagenia</i> sp.	0.00	0.75	0.00	0.00	0.38	0.33	0.22	0.33	0.11	0.00	0.00	0.00	0.33	0.50	0.00	0.00	0.00	0.75	0.25	1
Hydracarina	1.00	1.00	0.75	0.20	0.50	0.17	0.00	0.08	0.17	0.08	0.17	0.33	0.20	0.00	0.00	0.70	0.33	0.33	0.33	NA
<i>Hydraena</i> sp.	1.00	0.25	0.25	0.00	0.33	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.33	0.50	0.17	0
Hydroporinae	1.00	0.25	0.75	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.40	0.60	0.50	0.00	0.00	0.50	0.25	0.47	0.29	0
<i>Hydropsyche</i> sp.	0.20	1.00	0.50	0.00	0.33	0.20	0.10	0.30	0.00	0.00	0.30	0.10	0.00	0.00	0.75	0.25	0.17	0.50	0.33	0
<i>Hydroptila</i> sp.	1.00	1.00	0.60	0.00	0.20	0.29	0.00	0.14	0.57	0.00	0.00	0.00	0.17	0.67	0.00	0.00	0.33	0.50	0.17	1
<i>Ithytrichia</i> sp.	1.00	1.00	0.00	0.00	0.20	0.29	0.00	0.57	0.14	0.00	0.00	0.00	0.20	0.60	0.00	0.00	0.75	0.25	0.00	1
<i>Lepidostoma</i> sp.	0.75	0.75	0.25	0.00	0.20	0.00	0.80	0.20	0.00	0.00	0.00	0.00	0.75	0.25	0.00	0.00	0.60	0.40	0.00	1
<i>Leuctra</i> sp.	0.75	0.75	0.00	0.00	0.40	0.14	0.14	0.29	0.29	0.14	0.00	0.00	0.60	0.20	0.00	0.00	0.75	0.25	0.00	1
Limnephilinae	0.00	0.90	0.01	0.00	0.05	0.02	0.44	0.04	0.33	0.03	0.02	0.12	0.88	0.03	0.00	0.07	0.43	0.37	0.08	1
<i>Limnius</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
Limoniidae	0.53	1.00	0.25	0.00	0.12	0.04	0.43	0.04	0.21	0.00	0.00	0.29	0.45	0.07	0.00	0.35	0.34	0.66	0.00	1
<i>Metalype</i> sp.	1.00	1.00	1.00	0.00	0.25	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.60	0.40	0.00	0.00	0.50	0.50	1
<i>Micrasema</i> sp.	1.00	0.67	0.00	0.00	0.00	0.11	0.22	0.22	0.33	0.00	0.11	0.00	0.38	0.25	0.25	0.00	0.75	0.25	0.00	0
<i>Micronecta</i> sp.	1.00	1.00	1.00	0.00	0.75	0.00	0.00	0.29	0.29	0.00	0.43	0.00	0.38	0.25	0.00	0.38	0.50	0.33	0.17	1
<i>Mystacides</i> sp.	0.75	1.00	0.00	0.00	0.20	0.22	0.00	0.22	0.44	0.00	0.00	0.11	0.50	0.33	0.00	0.00	0.14	0.43	0.43	1
<i>Nemoura</i> sp.	1.00	0.50	0.00	0.00	0.33	0.25	0.50	0.25	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.33	0.50	0.17	1
<i>Odontocerum</i> sp.	0.00	0.60	0.00	0.00	0.43	0.00	0.00	0.11	0.33	0.00	0.33	0.22	0.50	0.00	0.00	0.50	1.00	0.00	0.00	1
<i>Onychogomphus</i> sp.	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.40	0.60	0.00	0
<i>Orectochilus</i> sp.	1.00	0.25	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.25	0.75	0.50	0.00	0.00	0.50	0.25	0.75	0.00	0
Orthoclaadiinae	0.80	1.00	0.75	0.00	0.40	0.25	0.00	0.50	0.13	0.00	0.13	0.00	0.00	0.50	0.17	0.17	0.40	0.40	0.20	0
<i>Oulimnius</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0

### Appendix 3. Continued

<i>Perla</i> sp.	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.20	0.80	0.75	0.00	0.00	0.25	1.00	0.00	0.00	NA
Perlodidae	0.17	0.22	0.00	0.00	0.28	0.10	0.01	0.12	0.01	0.00	0.08	0.68	0.39	0.06	0.00	0.54	0.71	0.23	0.06	1
<i>Piscicola</i> sp.	0.00	1.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.75	0.25	0
<i>Pisidium</i> sp.	0.83	0.40	0.50	1.00	0.60	0.30	0.00	0.50	0.00	0.00	0.20	0.00	0.00	0.00	1.00	0.00	0.60	0.20	0.20	0
Planorbidae	0.70	0.87	0.03	0.00	0.63	0.09	0.26	0.31	0.18	0.16	0.00	0.01	0.45	0.55	0.00	0.00	0.26	0.44	0.30	0
<i>Polycelis</i> sp.	0.25	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.25	0.00	0.75	0.00	0.00	0.00	1.00	0.25	0.50	0.25	0
<i>Polycentropus</i> sp.	0.25	0.75	0.33	0.00	0.20	0.08	0.08	0.23	0.08	0.00	0.23	0.31	0.20	0.00	0.20	0.60	0.40	0.40	0.20	1
<i>Potamanthus</i> sp.	0.00	1.00	0.00	0.00	0.29	0.33	0.33	0.22	0.11	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.50	0.50	NA
<i>Protonemura</i> sp.	0.75	1.00	0.00	0.00	0.40	0.25	0.50	0.25	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	1
Psychodidae	1.00	1.00	0.75	0.20	0.60	0.18	0.36	0.18	0.09	0.18	0.00	0.00	0.50	0.17	0.00	0.00	0.14	0.43	0.43	0
<i>Psychomyia</i> sp.	1.00	1.00	0.75	0.00	0.25	0.13	0.00	0.63	0.13	0.00	0.13	0.00	0.00	0.50	0.33	0.00	0.25	0.75	0.00	1
<i>Radix</i> sp.	0.00	0.40	0.00	0.00	0.67	0.00	0.19	0.31	0.19	0.06	0.19	0.06	0.25	0.75	0.00	0.00	0.00	0.75	0.25	0
<i>Rhithrogena</i> sp.	0.25	0.75	0.00	0.00	0.33	0.20	0.00	0.60	0.20	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.75	0.25	0.00	1
<i>Rhyacophila</i> sp.	0.23	0.43	0.11	0.00	0.38	0.05	0.09	0.19	0.00	0.03	0.07	0.57	0.14	0.00	0.00	0.86	0.83	0.17	0.00	1
<i>Riolus</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
<i>Sericostoma</i> sp.	0.00	0.75	0.17	0.00	0.40	0.00	0.38	0.13	0.25	0.00	0.13	0.13	0.75	0.25	0.00	0.00	0.60	0.40	0.00	1
<i>Serratella</i> sp.	1.00	1.00	0.25	0.00	0.22	0.08	0.25	0.33	0.25	0.00	0.08	0.00	0.33	0.33	0.00	0.17	0.40	0.60	0.00	1
<i>Setodes</i> sp.	1.00	1.00	0.00	0.00	0.20	0.25	0.00	0.13	0.50	0.00	0.13	0.00	0.75	0.25	0.00	0.00	0.00	0.33	0.67	1
<i>Silo</i> sp.	0.75	1.00	0.00	0.00	0.20	0.17	0.17	0.67	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.50	0.33	0.17	1
Simuliidae	1.00	0.85	0.60	0.00	0.27	0.62	0.00	0.25	0.00	0.00	0.13	0.00	0.00	0.25	0.75	0.00	0.48	0.39	0.13	0
<i>Siphonoperla</i> sp.	0.60	0.67	0.00	0.00	0.40	0.18	0.18	0.09	0.00	0.00	0.09	0.45	0.50	0.17	0.00	0.17	1.00	0.00	0.00	0
<i>Stenelmis</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.40	0.60	0.00	0
Tabanidae	0.00	1.00	0.00	0.00	0.00	0.14	0.14	0.00	0.00	0.00	0.00	0.71	0.25	0.00	0.00	0.75	0.00	0.50	0.50	1
Tanypodinae	0.67	1.00	0.00	0.00	0.40	0.00	0.09	0.09	0.00	0.09	0.27	0.45	0.00	0.00	0.00	1.00	0.17	0.33	0.50	0
Tanytarsini	1.00	1.00	0.50	0.20	0.17	0.63	0.13	0.25	0.00	0.00	0.00	0.00	0.25	0.25	0.13	0.00	0.33	0.50	0.17	0
Tipulidae	0.00	0.40	0.20	0.00	0.00	0.15	0.31	0.15	0.15	0.00	0.08	0.15	0.43	0.00	0.00	0.29	0.50	0.33	0.17	1
<i>Torleya</i> sp.	1.00	1.00	0.00	0.00	0.33	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.67	0.33	0.00	1

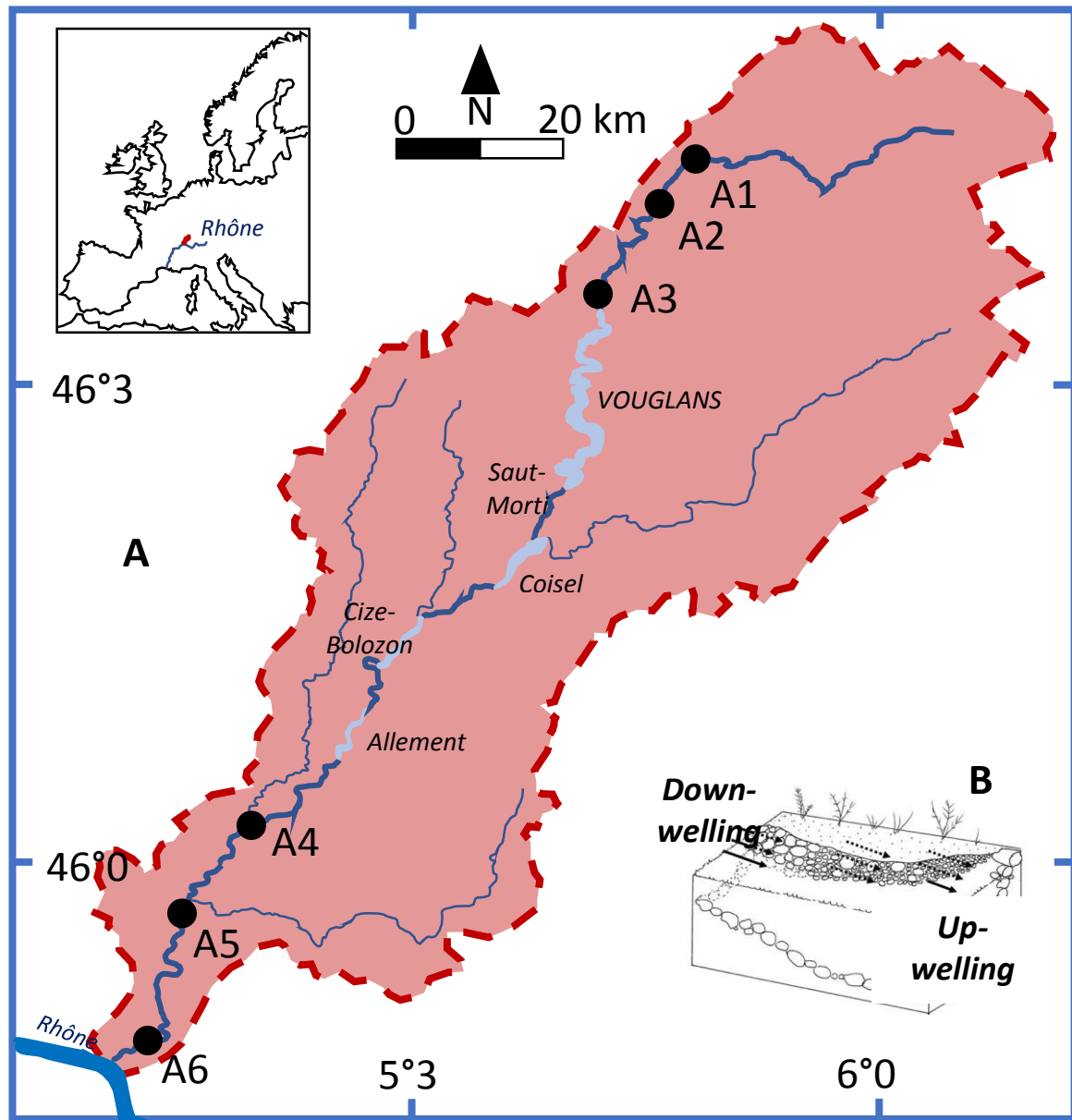
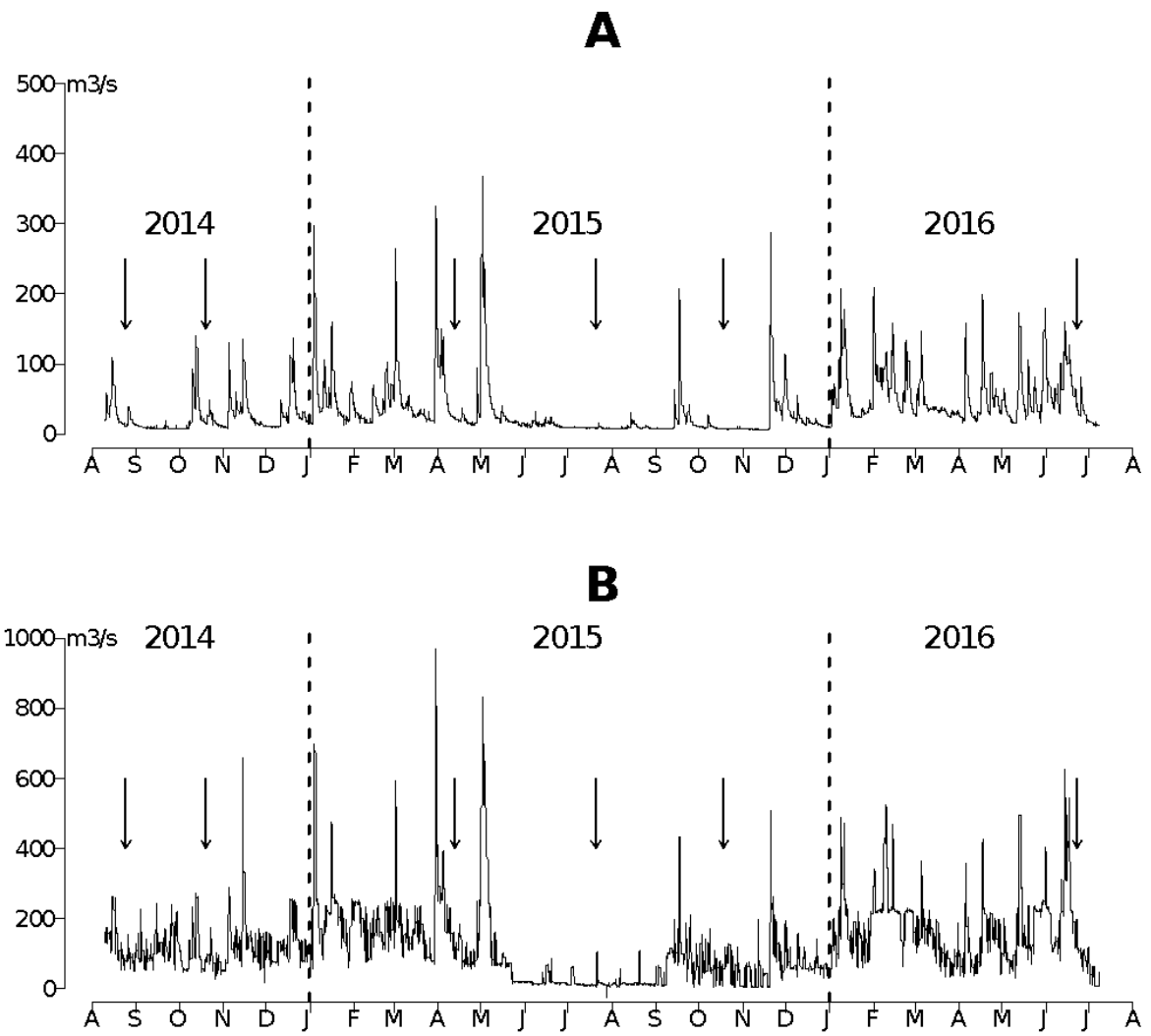
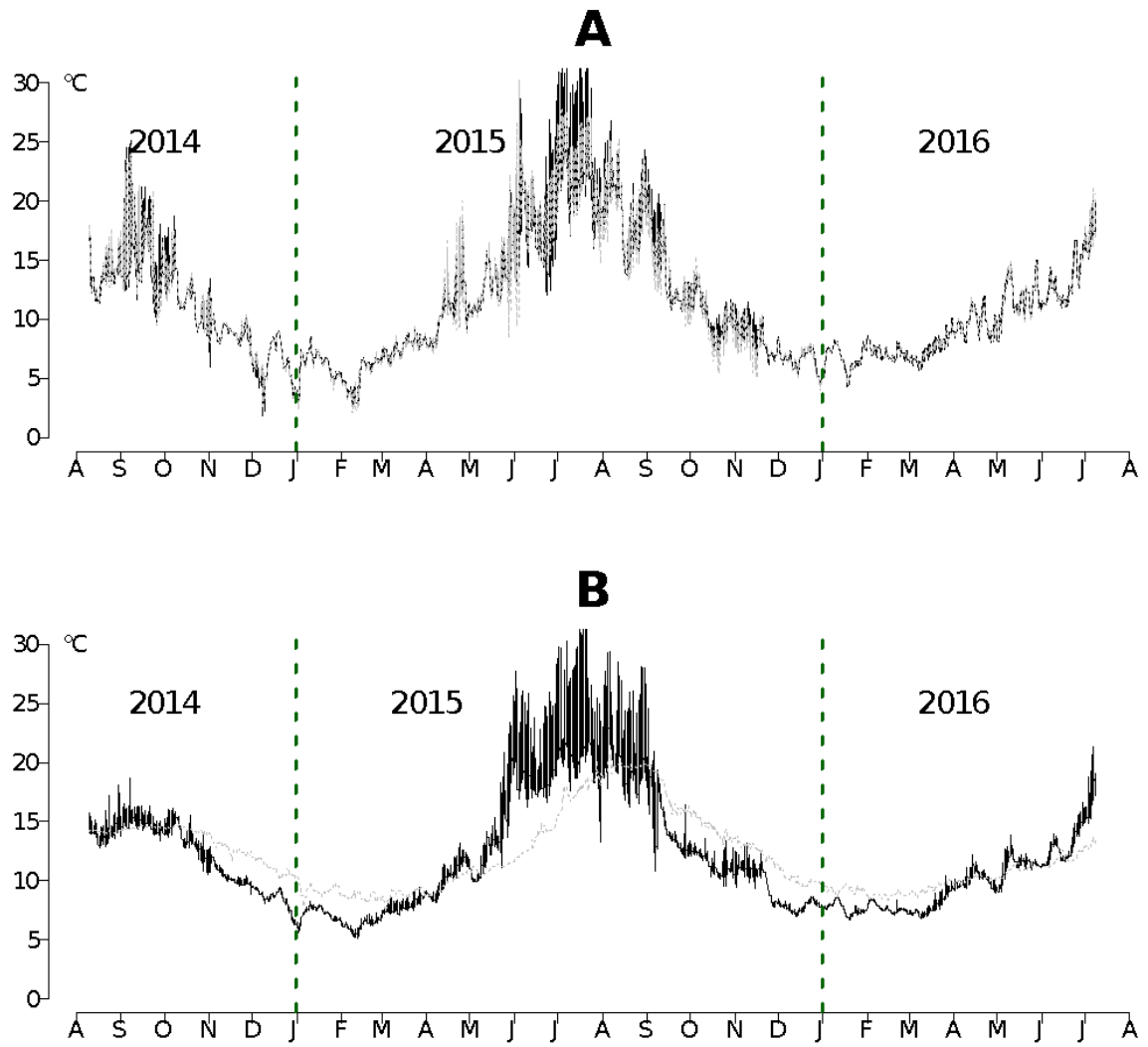


Figure 1.

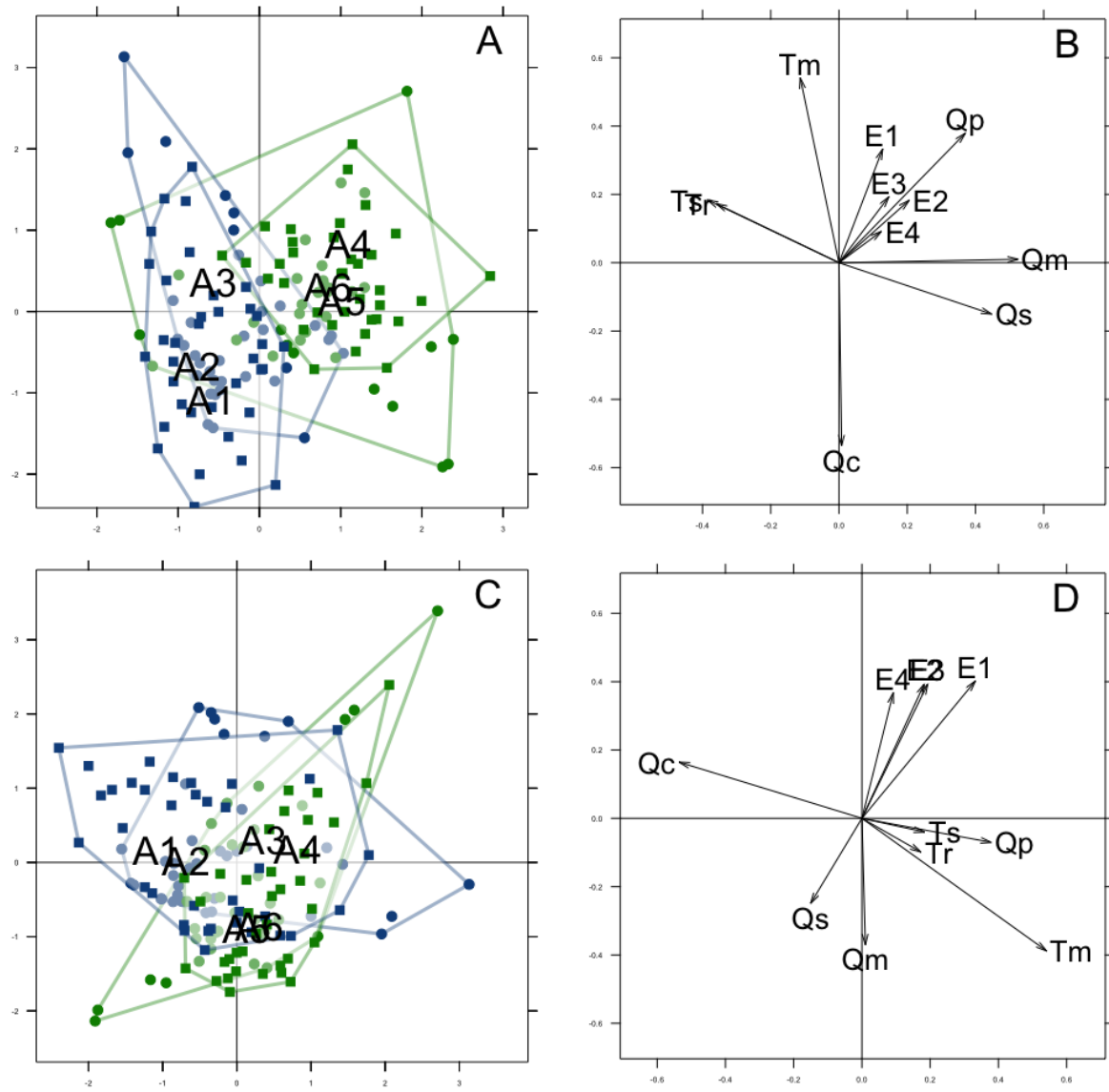




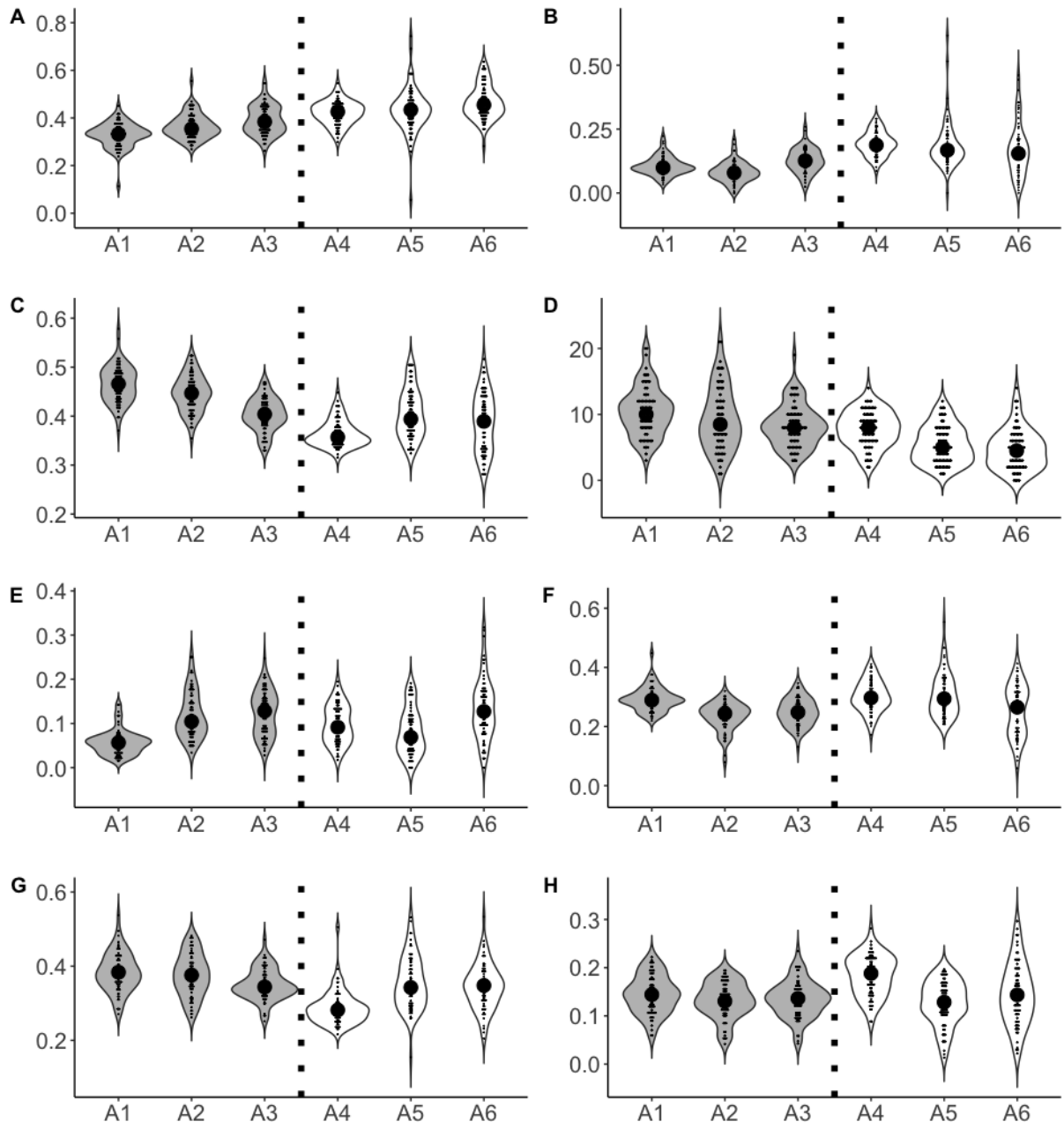
**Figure 2.**



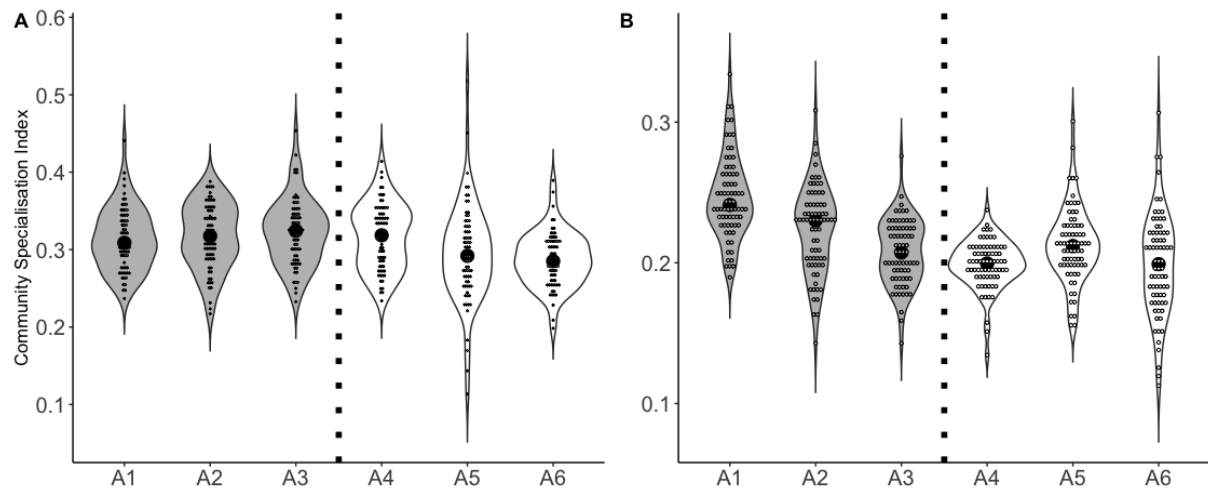
**Figure 3.**



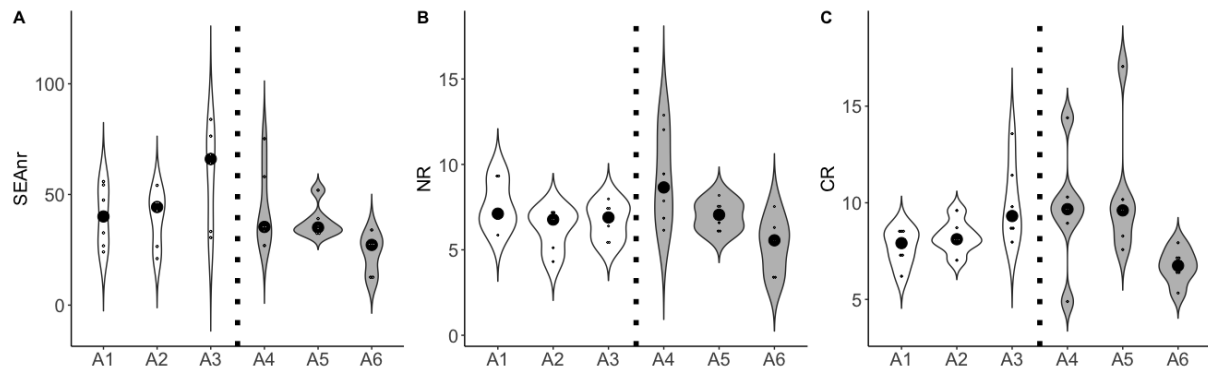
**Figure 4.**



**Figure 5.**



**Figure 6.**



**Figure 7.**

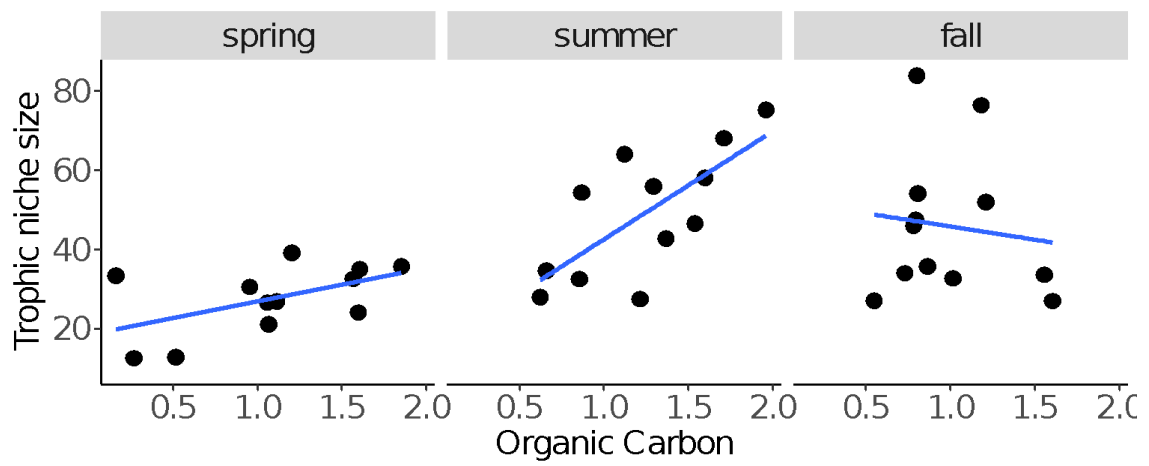


Figure 8.