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1 **Water diversion and pollution interactively shape freshwater food webs through**
2 **bottom-up mechanisms**

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27 Running head

28 Water diversion and pollution shape food webs

29

30 Abstract

31 Water diversion and pollution are two pervasive stressors in river ecosystems that often co-occur.

32 Individual effects of both stressors on basal resources available to stream communities have been

33 described, with diversion reducing detritus standing stocks and pollution increasing biomass of primary

34 producers. However, interactive effects of both stressors on the structure and trophic basis of food

35 webs remain unknown. We hypothesised that the interaction between both stressors increases the

36 contribution of the green pathway in stream food webs. Given the key role of the high-quality, but less

37 abundant, primary producers, we also hypothesised an increase of food web complexity with larger

38 trophic diversity in presence of water diversion and pollution. To test these hypotheses, we selected

39 four rivers in a range of pollution subject to similar water diversion schemes, and we compared food

40 webs upstream and downstream of the diversion. We characterised food webs by means of stable

41 isotope analysis. Both stressors directly changed the availability of basal resources, with water diversion

42 affecting the brown food web by decreasing detritus stocks, and pollution enhancing the green food

43 web by promoting biofilm production. The propagation of the effects at the base of the food web to

44 higher trophic levels differed between stressors. Water diversion had little effect on the structure of

45 food webs, but pollution increased food chain length and trophic diversity, and reduced trophic

46 redundancy. The effects at higher trophic levels were exacerbated when combining both stressors, as

47 the relative contribution of biofilm to the stock of basal resources increased even further. Overall, we

48 conclude that moderate pollution increases food web complexity and that the interaction with water

49 abstraction seems to amplify this effect. Our study shows the importance of assessing the interaction

50 between stressors to create predictive tools for a proper management of ecosystems.

51

52 Key words

53 Food web, water diversion, pollution, food web complexity, bottom-up mechanisms

54

55 Introduction

56 The rising global human population and the intensification of economic activities have increased the
57 demand for water (Crist et al., 2017; Ripple et al., 2017), which is projected to increase over 50% by
58 2050 (Leflaive, 2012). In order to satisfy water demand for agriculture, industry and domestic use
59 (Albert et al., 2021), rivers are increasingly being regulated by barriers, most of them built to control and
60 divert water flow, with weirs (30.5%) and dams (9.8%) as the most frequently built structures (Belletti et
61 al., 2020). These barriers disrupt connectivity across the fluvial network affecting dispersion of aquatic
62 organisms (Brooks et al., 2018; Jones et al., 2020) and community structure (Carpenter-Bundhoo et al.,
63 2020; Munasinghe et al., 2021). Water diversion driven by these infrastructures results in strong habitat
64 contraction (Rolls et al., 2012), or even total loss of surface water flow (Steward et al., 2012; von Schiller
65 et al., 2017). This also affects community composition (Stubbington et al., 2009), as ecosystem size is an
66 important determinant of food web structure on freshwater ecosystems (McHugh et al., 2015; McIntosh
67 et al., 2018). Moreover, water diversion can alter the availability of basal food resources in rivers (Power
68 et al., 2013). For instance, coarse detritus is reduced in the diverted sections compared to the upstream
69 reaches due to its retention in the impoundments (Schmutz and Moog, 2018) and the transport through
70 the diversion canals (Arroita et al., 2015). Alterations in the availability of basal food resources modify
71 river food webs through bottom-up mechanisms (Biggs et al., 2000; Wallace et al., 1997) and thus,
72 modify energy and matter transfer from detritus or primary producers reshaping brown or green food
73 webs, respectively.

74 Water diversion is usually accompanied by other stressors that simultaneously affect river ecosystems
75 (Ormerod et al., 2010; Sabater et al., 2018). Multiple stressors often interact in an unpredictable way
76 (Crain et al., 2008; Jackson et al., 2016; Orr et al., 2020) and generate complex effects by amplifying or
77 lessening the single effect of each stressor, which depends not only on the interaction strength but also
78 on the direction of the interaction (Piggott et al., 2015). Pollution is one of the most pervasive stressors

79 in freshwater ecosystems (Malmqvist and Rundle, 2002; Reid et al., 2019) and appears frequently in
80 conjunction with other stressors (Dolédéc et al., 2021). Depending on their effects on biota, pollutants
81 can be toxic (if they reduce biological activity at any concentration) or assimilable (if they subsidise
82 biological activity at low concentrations but become toxic at high concentrations) (Odum et al., 1979).
83 Nutrient pollution in aquatic systems, generally refers to the concentration of different forms of
84 nitrogen (N) and phosphorous (P) (Schweitzer and Noblet, 2018), which frequently limit primary
85 production (Elser et al., 2007; Tank and Dodds, 2003). Thus, enrichment of freshwaters with N and P can
86 eliminate nutrient limitation of algal communities (Marcarelli et al., 2009) and increase biofilm biomass
87 (Keck and Lepori, 2012). These changes in biofilm biomass increase initial energy flow (Canning and
88 Death, 2021) and can be propagated towards higher trophic levels (Ardón et al., 2021) altering food web
89 structure and increasing trophic diversity (García et al., 2017). In addition, as the energy loss within each
90 trophic transfer limits species population size at high trophic levels (Hutchinson, 1959; Pimm, 1982),
91 more productive ecosystems, which are not facing toxic consequences of eutrophication, should allow
92 longer food chains. The main cause for this is that energy can more easily reach higher trophic levels
93 (Pimm, 1982; Schoener, 1989) by narrowing the stoichiometric gap between consumers and their food
94 resources (Mulder and Elser, 2009). Thus, longer food chains can be a product of a greater dietary
95 generalism, which increases the trophic position of predators (O’Gorman et al., 2012).

96 There are a number of studies on the isolated effects of water diversion and water pollution on food
97 web structure (e.g. Boddy et al., 2020; Walters and Post, 2008 and García et al., 2017; Morrissey et al.,
98 2013; Price et al., 2019). There are even a few studies that have addressed the joint effects of nutrient
99 pollution and water diversion (e.g. Lange et al., 2014) or flow reduction, a consequence of water
100 diversion (e.g. Elbrecht et al., 2016; Matthaei et al., 2010) on river biota and functioning. Nevertheless,
101 there is still a lack of studies assessing the effects of both stressors on the structure of food webs. Thus,
102 the aim of this study is to assess the isolated and interactive effects of water diversion and water
103 pollution on river food webs and trophic niche distribution. We hypothesise that (Figure 1):

104 1) Water diversion will affect different dimensions of food web complexity in different ways.

105 We expect that both the stock of coarse detritus and its contribution to the diet of primary
106 consumers will decrease in diverted reaches, with a consequent increase in trophic diversity

107 and a reduction of trophic redundancy by feeding more on the less abundant biofilm.

108 However, reduced stock of basal resources will reduce food chain length (FCL).

109 2) Moderate pollution will increase food web complexity. We expect biofilm production and its
110 contribution to the diet of primary consumers to increase with nutrients from moderately
111 polluted waters, leading to an increase in FCL and trophic diversity.

112 3) The interaction between water diversion and pollution will increase even further food web
113 complexity, as the reduction of coarse detritus stock will be accompanied by a larger biofilm
114 availability. Consequently, the combination of water diversion and pollution will raise
115 trophic diversity and reduce redundancy even further.

116 With this purpose, we analysed carbon and nitrogen stable isotopes, which provide a time-
117 integrated measurement of trophic structure and interactions by elucidating the relative trophic
118 positions of species in the food web (nitrogen isotope) and the relative contribution of different
119 basal resources to the consumers (carbon isotope) (Peterson and Fry, 1987; Phillips, 2012).

120 Materials and methods

121 Sampling design and study sites

122 We selected four rivers within the temperate region of the northern Iberian Peninsula, which differed in
123 their ecological status and water quality (Aguirre et al., 2017) (Table 1). None of the selected rivers
124 showed a bad ecological status, which indicates that the pollution ranged from low to moderate. The
125 cover and maturity of the riparian forests also differed between rivers (higher in Urumea and Leitzaran
126 than in Kadagua and Deba), which was inversely related to the level of urbanisation (Table 1). The four
127 rivers had a similar water diversion scheme, consisting of a low weir (3-6.5 m high) and a canal that can
128 divert up to 90% of the river flow to hydropower. We defined two 100 m-long reaches in each river: a
129 control reach upstream from the stagnant water retained by the weir and a diverted reach in the
130 bypassed section immediately downstream from the weir.

131 Baseline data on water characteristics and basal resources

132 To set the baseline status of each river and include variability of water diversion and non-diversion
133 periods, available information on water characteristics and basal food resources of three sampling

134 campaigns (late spring of 2017, autumn of 2017 and late spring of 2018) were gathered. Water
135 characteristics differed among rivers, but they were unaffected by water diversion (Table S1). According
136 to the pollution gradient (Table 2, which comprehended a wide range of pollutants apart from nutrients
137 (see Aguirre et al. (2017), but was represented in our study by the Total Dissolved Nitrogen (TDN)
138 gradient), Urumea was the least polluted river, followed by Leitzaran, Kadagua and Deba. This gradient
139 correlated with the concentrations of most solutes, pH, conductivity, and temperature (Table S1, Figure
140 S1). Although we are aware that water nitrogen content was not the only driver shaping food webs and
141 that the other physicochemical variables (e.g. temperature, oxygen or water flow) might also play a role,
142 water TDN served as an effective surrogate when representing pollution in our systems. During these
143 sampling campaigns, mean discharge and mean wet width showed a reduction (from 39.2% to 68.9%
144 and from 4.6% to 25.9% respectively) downstream from the weirs (Table 2, Table S1). On each occasion,
145 reach discharge ($\text{m}^3 \text{s}^{-1}$) was measured with an acoustic doppler velocity meter (ADV; Flow Tracker 2,
146 SonTekHandheld-AD®, USA) through a cross-section. Wet channel mean width was obtained from
147 equidistant transects every 10 m. Water was characterised by measuring temperature ($^{\circ}\text{C}$), pH, electrical
148 conductivity ($\mu\text{S cm}^{-1}$) and dissolved oxygen saturation (% DO) using hand-held probes (WTW Multi 350i
149 and WTW 340i SET, WTW Wissenschaftlich, Weilheim, Germany; YSI ProODO handled; YSI Incorporated,
150 Yellow Springs, OH, USA). Information on chemical composition of water samples were also gathered for
151 each sampling occasion through analysis of filtered (0.7- μm pore size pre-combusted glass-fiber filters,
152 Whatman GF/F, Whatman International Ltd., Kent, UK) and frozen (-20°C) water samples. The
153 concentrations of nitrate (NO_3^- , mg L^{-1}), sulfate (SO_4^{2-} , mg L^{-1}) and chloride (Cl^- , mg L^{-1}) in water samples
154 were determined with capillary ion electrophoresis (Agilent G1600AX 3D, Agilent Technologies,
155 Wilmington, DE, USA) (Environmental Protection Agency, 2007). Spectrophotometric (Shimadzu UV-
156 1800 UVeVis, Shimadzu Corporation, Kyoto, Japan) methods were used to measure the concentration of
157 soluble reactive phosphorus (SRP, $\mu\text{g P L}^{-1}$) [molybdate method (Murphy and Riley, 1962)] and
158 ammonium (NH_4^+ , $\mu\text{g N L}^{-1}$) [salicylate method (Reardon et al., 1966)]. Dissolved organic carbon (DOC,
159 mg C L^{-1}) and total dissolved nitrogen (TDN, mg N L^{-1}) were measured by catalytic oxidation (Shimadzu
160 TOC-L analyser coupled to a TNM-L unit).

161 We compiled the available information on the main basal food resources, to characterize the accessible
162 food resources for the benthic community in each river and reach. Coarse detritus was collected by
163 means of a Surber sampler (0.09 m²), and the organic matter retained on an 8-mm sieve was processed.
164 Nine benthic samples were randomly collected in each reach on the aforementioned sampling
165 campaigns. Information on fine detritus from two sampling campaigns (late spring and autumn 2017)
166 was also gathered for each reach. Nine samples were randomly collected per reach in each sampling
167 campaign using a sediment corer (surface 81.7 cm²). Both types of organic matter samples were oven-
168 dried (70°C, 72h) and combusted (500°C, 4h) to determine their ash free dry mass (AFDM, g m⁻²).
169 Information on biofilm biomass was gathered from a single sampling campaign in late spring of 2018,
170 which was measured by means of a BenthosTorch fluorometer (Benthos Torch, bbe-Moldaenke, Germany)
171 on 18 cobbles per reach. For details regarding the collected data, see de Guzman et al. (2021).

172 Stable isotope analysis

173 A single food-web sampling campaign for stable isotope analysis (SIA) was carried out during late spring
174 of 2018, a period when the flow differences between upstream and downstream reaches from dams are
175 greatest because of low precipitations but still active diversion canals. All the available basal food
176 resources were collected from each reach: biofilm, fine detritus and leaves of alder (*Alnus glutinosa* (L.)
177 Gaertn) were present in every river and reach, while the gathering of filamentous green algae,
178 bryophytes and macrophytes varied from reach to reach. Other basal resources, such as phytoplankton,
179 were not collected due to their extremely low abundance in these river sections. Six composite samples
180 of biofilm were collected in each reach by scrapping the whole surface of nine cobbles and collecting the
181 slurry in filtered river water (0.7 µm pore size, Whatman GF/F). The remaining resources were
182 individually gathered from the riverbed. Alder leaves found on the riverbed were collected as a
183 representative of coarse detritus since they were the dominant leaf type found in these reaches. Alder
184 leaves are a nutrient poor basal food resource compared to autochthonous resources (Cross et al.,
185 2005); although, they show a relatively higher content of nutrients compared to leaf-litter of other
186 woody plants (Kang et al., 2010). Macroinvertebrates were collected with a kick sampler (0.5 mm mesh
187 aperture) in six transects along each reach. The six most common, but trophically diverse genera were

188 collected after sorting and identifying them in the field: *Baetis*, *Ecdyonurus*, *Echinogammarus*,
189 *Ephemere*, *Hydropsyche* and *Rhyacophila*. Up to nine invertebrate samples per taxon were collected
190 in each reach, each sample containing from one to 55 individuals depending on their body mass. When
191 possible, the digestive tracts of the predators were removed, since gut contents can affect the isotopic
192 signature of the sample (Mateo et al., 2008).

193 Fish sampling was conducted along the 100-m long reaches by depletion electrofishing with a backpack-
194 electrofishing unit (Hans Grassl model IG2002/D30). Stop-nets were set upstream and downstream of
195 the reaches. All caught fish were anaesthetised with MS-222, identified and up to five individuals per
196 species in each reach were euthanized (reference number of the ethics commission: M20/2016/135).
197 Samples of dorsal muscle were extracted in the field. All the samples were immediately frozen (-20°C)
198 for processing and SIA.

199 Frozen samples were freeze-dried (VirTis Benchtop 2K) (from 12 to 72h depending on their water
200 content), grounded (Resources in a ball-mill (Vibration mill MM301, Fisher Bioblock Scientific); Animal
201 samples in a homogeniser (Precellys® 24, Bertin instruments)) and weighed (approximately 1 mg for
202 invertebrates and fish, 10 mg for fine detritus and 2 mg for other basal resources) into tin capsules
203 (Lüdiwiss Sn 98, 5 x 8 mm) for SIA. The Stable Isotope Facility of the University of California – Davis
204 performed Carbon (C) and Nitrogen (N) stable isotope analyses on a PDZ Europa 20–20 isotope ratio
205 mass spectrometer (Sercon Ltd., Cheshire, UK). Results are expressed as the relative difference between
206 ratios of samples and international standards (Pee-Dee Belemnite limestone formation for $\delta^{13}\text{C}$,
207 atmospheric N for $\delta^{15}\text{N}$) and expressed in per mil delta notation [e.g. $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times$
208 1000] (Fry, 2006) (Table S2). Analytical error (mean SD from in-house standards) associated with our
209 sample runs was estimated at 0.2 ‰ for $\delta^{13}\text{C}$ and 0.3 ‰ for $\delta^{15}\text{N}$. For details regarding the collected
210 data, see (de Guzman et al., 2021).

211 Data treatment

212 *TDN as a proxy of water pollution*

213 In order to understand the correlations among the different physicochemical properties of the water
214 and to define a gradient of pollution in the studied rivers, we carried out a principal component analysis

215 (PCA) with the data of dissolved oxygen saturation, pH, temperature and solute concentrations (NO_3^- ,
216 SO_4^{2-} , Cl^- , SRP, NH_4^+ , TDN and DOC) for each sampling campaign and reach. Due to the distribution of
217 the components in the PC1 axis (Figure S1, Table S1: correlation with PC1), the correlation of the
218 variables with the TDN (Table S1: correlation with TDN), and the importance of nitrogen in determining
219 the functioning of freshwater ecosystems (Dodds et al., 1998), we used TDN as the covariate
220 representing the pollution gradient in posterior statistical analyses (log10-transformed and centred into
221 0 using the average value of the four rivers) (Table 2).

222 *Maximum FCL*

223 Maximum FCL (the linear trophic distance between basal resources and top predators) in each site was
224 estimated following the maximum trophic position convention, assessing top predators' trophic
225 positions (TP) and comparing their $\delta^{15}\text{N}$ values to the mean $\delta^{15}\text{N}$ value of the basal resources at each
226 sampling site (Cabana and Rasmussen, 1996): $TP_{top\ predator} = \frac{(\delta^{15}\text{N}_{top\ predator} - \delta^{15}\text{N}_{baseline})}{3.4} + \lambda$.
227 Where 3.4 is the trophic discrimination factor (TDF) of $\delta^{15}\text{N}$ (Post, 2002a; Vander Zanden and
228 Rasmussen, 2001) and λ the trophic level of the baseline indicator, set as 1 because primary producers
229 were used as the baseline. We obtained the maximum FCL from the mean TP values of the individuals
230 with the highest TP in each reach (Table S3).

231 *Contribution of resources to the diet of primary consumers*

232 We used Bayesian Mixing Models to estimate the contribution of the various basal resources to the
233 diets of the primary consumer invertebrates at each river and reach using the MixSIAR package
234 (Bayesian Mixing Models in R; (Stock and Semmens, 2013). Autochthonous resources, fine detritus and
235 alder leaves were treated as separate resources. Due to the very low and sparse distribution among
236 sampling reaches biofilm, filamentous green algae, bryophytes and macrophytes were merged together
237 into the autochthonous resources category. The models consider uncertainty and variation in
238 consumers and TDF to generate a distribution of possible mixing solutions based on the available
239 resources. MixSIAR also provides error terms that contemplate variation due to sampling processing and
240 due to consumers' variability itself (i.e. individual differences in digestibility, assimilation efficiency and

241 metabolic rates) (Stock and Semmens, 2016). We used TDF and uncertainties specific for aquatic
242 invertebrates ($0.1 \pm 2.2\%$ for $\delta^{13}\text{C}$ and $2.6 \pm 2.0\%$ for $\delta^{15}\text{N}$ (Brauns et al., 2018)). Concentration
243 dependence (Phillips and Koch, 2002) and a multiplicative error structure (Stock and Semmens, 2016)
244 were also considered in the models. Posterior estimates of the proportional contribution of each
245 resource to each consumer's diet were obtained for each reach. Consumer stable isotope data was
246 previously checked for outliers through simulated mixing polygons (Smith et al., 2013) with the packages
247 *sp* (Pebesma et al., 2012) and *splancs* (Bivand et al., 2017). The method uses a Monte Carlo simulation
248 to iterate Convex hulls ('mixing polygons') based on means and SD of source data and TDF. It applies the
249 point-in-polygon assumption to test if source contributions can explain consumer's isotopic signature in
250 the proposed mixing model. Following the recommendations by Smith et al. (2013), no data had to be
251 excluded.

252 *Community iso-space metrics*

253 The trophic structure of the consumer community was estimated for each river and reach using the
254 community-wide metrics described in Layman et al. (2007a) and Jackson et al. (2011). We considered
255 three functional groups: primary consumers (*Baetis*, *Ecdyonurus*, *Echinogammarus*, *Ephemere* and
256 *Hydropsyche*), predatory invertebrates (*Rhyacophila*), and fish. Some metrics consider the distribution of
257 the components of each community in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ space to inform about the trophic diversity within
258 each food web. Mean distance to centroid (CD) is one of these metrics, which provides information on
259 the trophic niche through the species distribution in the iso-space. Trophic redundancy was estimated
260 using mean nearest neighbour distance (MNND) and standard deviation of the nearest neighbour
261 distance (SDNND). MNND is the main metric representing trophic redundancy, which provides a
262 measure of density and grouping of the community members. SDNND gives a measure of evenness of
263 spatial density and packing. Smaller MNND represents food webs with taxa having more similar trophic
264 ecologies, whereas smaller SDNND indicates a more uniform spacing of taxa in the food web space
265 (Abrantes et al., 2014). Thus, smaller values of MNND and SDNND represent greater trophic
266 redundancy, as species have more similar trophic niches. In communities with similar MNND (mean
267 distance) values, smaller SDNND represent higher trophic redundancy. A Bayesian approach to these
268 metrics was performed with the SIAR package in R (Stable Isotope Analysis in R; Jackson et al., 2011;

269 Parnell and Jackson, 2008), which allows comparing communities containing different sample sizes. The
270 method also allows propagating sample error on the estimates of the means of community components
271 to provide measures of uncertainty surrounding the metrics, making possible robust statistical
272 comparisons among communities. Standard ellipse areas (SEA) were also calculated with the SIBER
273 package (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011) to quantify the isotopic niche of each
274 community. This Bayesian standard ellipse is less sensitive to low sample size and extreme values than
275 the total area proposed by Layman et al. (2007b). Therefore, it is a more robust approach for
276 comparisons between communities.

277

278 *Statistical analyses*

279 All statistical analyses were performed using R software, version 3.6.0. (R Core Team, 2019). We used
280 Linear Models in this study as four values in the covariate (pollution) seem to be not enough for reliable
281 discrimination between linear and non-linear curve fitting (Jenkins and Quintana-Ascencio, 2020). For
282 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of each resource and taxon, biofilm stock and fine detritus Linear Models were built by
283 including TDN (covariate), Reach (factor) and their interaction as sources of variation. The same sources
284 of variation were used for coarse detritus stock in Linear-Mixed Effects Models (function lme, in R
285 package nlme (Pinheiro et al., 2020)) with Sampling campaign as random factor. Variance components
286 of Mixed Effects Models were estimated by means of restricted maximum likelihood and p values
287 estimated by means of likelihood ratio tests (Pinheiro and Bates, 2006). We also divided samples of each
288 food web in four functional groups: basal resources, primary consumers, predatory invertebrates, and
289 fish. We analysed the stable isotopes of these groups by means of Linear-Mixed Effects Models with
290 Taxa as random factor (except for predatory invertebrates which only contained one taxon and were
291 analysed by means of a Linear Model). FCL was also modelled with Linear Models including TDN, Reach
292 and their interaction as sources of variation. To test for the effect of water diversion, pollution and their
293 interaction on diet contribution analyses and the iso-space metrics, we used Generalised Linear Models
294 (GLMs) on the posterior estimates of the Bayesian models, since including these variables into the
295 Bayesian models caused a lack of convergence. We included 3000 posterior estimates on diet
296 contribution analyses and 4000 posterior estimates in the iso-space metrics analyses for each variable

297 and community. Different numbers of posterior estimates were included in GLMs because settings to
298 avoid convergence problems in Bayesian models differed. Posterior estimates related to diet
299 contribution analyses were adjusted to a binomial distribution (link: logit) and estimates related to
300 community iso-space metrics followed Gaussian distribution (link: identity) (Zuur et al., 2009). Different
301 GLMs were built for each variable using TDN, Reach and their interaction as sources of variation: null
302 model, two models with a single source of variation, a model with both sources of variation and the
303 maximal model, which also included the interaction term. As the sample size was large, Bayesian
304 Information Criterion (BIC) was used to penalize size and select the best explanatory model in each case
305 (Brewer et al., 2016). Model selection was made with the 'modelsel' function of the MuMIn package
306 (Barton, 2020). Due to the large amount of posterior estimates, violin plots were used instead of
307 boxplots to show the distribution of the results whenever Bayesian modelling was applied. For all the
308 linear models we repeated the analysis considering River as a factor instead of TDN as covariate and we
309 tested for pairwise differences between reaches of the same river by means of Post Hoc analysis using
310 the t-statistic (Multcomp package, Hothorn et al., 2008).

311 Results

312 *How did water diversion affect food web complexity?*

313 Water diversion had important effects at the base of the food web that did not propagate to higher
314 trophic levels. This stressor reduced coarse detritus stock by 17.6 % on average from control to diverted
315 river sections ($F_{1,208} = 17.72$, $p < 0.001$, coefficient Reach Diverted = -0.28; Figure 2a, Table S4), although
316 no within-river differences were observed in the pairwise comparisons (Figure 2a). Fine detritus showed
317 an overall increase downstream from the weirs ($F_{1,140} = 5.23$, $p = 0.024$, coefficient Reach-Diverted =
318 0.16; Figure 2b, Table S4), which was driven by the significant difference between reaches of the most
319 polluted river (Figure 2b). Biofilm biomass, however, was unaffected by diversion ($F_{1,140} = 0.10$, $p =$
320 0.752, Figure 2c, Table S4). The contribution of different basal resources to the diet of primary
321 consumers showed different patterns. Coarse detritus (alder) contribution showed a slight decrease on
322 diverted reaches (Table 3; Figure 3a; Table S5), which was mainly driven by the pairwise difference
323 between reaches of one of the rivers (Figure 3a). Similarly, the overall contribution of autochthonous
324 resources also decreased on diverted reaches (Table 3; Figure 3c; Table S5). Contrarily, fine detritus

325 contribution increased on diverted sites (Table 3; Figure 3b; Table S5). The $\delta^{15}\text{N}$ signatures showed no
326 difference between control and diverted reaches, neither for the entire community nor for functional
327 groups (Figure 4a, Figure S2; Table S6) or most of the analysed taxa (Table S7). Consequently, we found
328 similar maximum food chain length (FCL) in diverted and control reaches ($F_{1,35} = 2.35$, $p = 0.134$, Table
329 S3, Figure 5). In addition, the same fish species were found in both reaches, except for Kadagua that
330 only shared 3 out of the 7 species present in the river (Table S3). Other aspects of trophic structure were
331 weakly affected by water diversion, with a small increase in trophic diversity (CD) and trophic
332 redundancy (lower MNND; although SDNND was higher, and represented more heterogeneous spacing
333 of taxa), and a slight decrease in community niche space (SEA) (Table 4).

334

335 *Did moderate levels of pollution increase food web complexity?*

336 Pollution modified the base of the food web and lead to important changes in food web structure.
337 Biofilm biomass increased along the pollution gradient, most clearly at the beginning of the gradient
338 (Table S4, $F_{1,140} = 28.35$, $p < 0.001$, coefficient $\log_{10}\text{TDN} = 1.26$ Figure 2c). However, the amounts of
339 coarse and fine detritus showed no significant relationship with the pollution gradient ($F_{1,208} = 1.54$, $p =$
340 0.216 and $F_{1,140} = 0.08$, $p = 0.771$ respectively, Figure 2a and b). There was an overall decrease of the
341 contribution of autochthonous resources to the diet of consumers in control reaches (Table 3; Figure 3c;
342 Table S5), with no other basal resources changing their overall contribution (Table 3; Figure 3a and b;
343 Table S5). The $\delta^{15}\text{N}$ signatures increased significantly with pollution for the entire community, each
344 functional group and most of the analysed taxa (Figure 4a, Figure S2; Table S6; Table S7). In addition, the
345 maximum FCL (Figure 5, Table S3) increased significantly with pollution ($F_{1,35} = 138.06$, $p < 0.001$).
346 Besides differences in the identity of the apex predator among rivers, trophic position of every fish
347 species increased with pollution (Table S3). This stressor also affected every dimension of trophic
348 structure, increasing trophic diversity (CD) and community niche space (SEA) and reducing redundancy
349 (higher MNND; although SDNND was lower, and represented more homogeneous spacing of taxa)
350 (Table 4).

351

352 *Did food web complexity increase even further when water pollution and diversion interacted?*

353 With the increasing pollution, fine detritus abundance in the diverted reaches surpassed the abundance
354 found in control reaches (interaction: $F_{1,140} = 16.32$, $p < 0.001$, Figure 2b, Table S4), with the largest, and
355 significant, difference observed in the most polluted river. However, the stock of coarse detritus and
356 biofilm showed no significant interaction between stressors ($F_{1,208} = 0.17$, $p = 0.684$ and $F_{1,140} = 0.47$, $p =$
357 0.493 , Figure 2a and c). Only contribution of autochthonous resources showed an interaction between
358 pollution and water diversion, which decreased in the control reaches along the pollution gradient but
359 remained constant in the diverted ones (Table 3; Figure 3c; Table S5). Neither $\delta^{15}\text{N}$ signatures (Figure 4a,
360 Figure S2; Table S6) nor maximum FCL ($F_{1,35} = 0.15$, $p = 0.702$, Table S3, Figure 5) responded interactively
361 to both stressors. However, $\delta^{13}\text{C}$ values for the entire community and for fish decreased more along the
362 pollution gradient in diverted than in control reaches (Figure 4b; Table S6). Community-wide metrics of
363 consumers were also best modelled by considering the interaction term (Table 4). Trophic diversity (CD,
364 Figure 6a; Table S8) became larger in the diverted reaches of the most polluted rivers (Table 4). These
365 rivers also showed larger community niche space (larger SEA, Figure 6b; Table S8) differences between
366 control and diverted reaches, with the smallest difference between reaches in the least polluted river
367 (Table 4). Trophic redundancy decreased with pollution (higher MNND, Figure 6c; Table S8), with larger
368 reductions (steeper positive slope) for diverted sites (Table 4). Evenness of this metric (SDNND) was
369 lower in the diverted site of the less polluted river, but higher in the diverted sites of the other three
370 rivers (Figure 6d; Table S8).

371

372 Discussion

373 Water diversion and pollution are two pervasive stressors affecting freshwater ecosystems (Dudgeon et
374 al., 2006). Our study has identified the unique and joint effects of both stressors on different dimensions
375 of the complexity of freshwater food webs. We found that water diversion modified the base of the
376 brown food web by reducing the abundance of detritus. In contrast, nutrients from polluted water
377 stimulated the base of the green food web by promoting biofilm production. How these changes at the
378 base of the food web propagated to higher trophic levels differed between stressors. Water diversion
379 had little effect on the structure of the entire food web but nutrient pollution increased its complexity.
380 Interactive, although weak, effects were very common among the response variables.

381 *The effects of water diversion at the base of the food web did not propagate to higher trophic levels*

382 The reduction of stocks of detritus in the diverted reaches agrees with previous studies (Casas et al.,
383 2000; Martínez et al., 2013). This effect is likely to be a consequence of the retention of detritus in the
384 impoundments above weirs (Schmutz and Moog, 2018), and its deviation through the diversion canals
385 (Arroita et al., 2015). These impoundments reduce the size of coarse detritus very efficiently and export
386 fine detritus downstream (Mbaka and Wanjiru Mwaniki, 2015). Concerning autotrophic basal resources,
387 biofilm can respond non-linearly to river flow and water velocity. Water velocity increases nutrient
388 exchange rates, enabling faster biofilm growth (Dewson et al., 2007), with the highest shear forces
389 limiting biofilm accrual (Hondzo and Wang, 2002). Nevertheless, water diversion did not significantly
390 change biofilm biomass in our study. The few instant velocity measures we had available, although not
391 enough to properly capture flow velocity differences among reaches, did not suggest big velocity
392 changes from control to diverted reaches, in accordance with the lack of changes in biofilm biomass.

393 Supporting our first hypothesis, the reduction of detritus by water diversion was followed by lower
394 contribution to consumers' diets. However, autochthonous resources remained the main contributors
395 to the diet of primary consumers, even in the diverted reaches, where their contribution was lower than
396 in the control reaches. Considering that water diversion did not change the stock of biofilm, the
397 reduction in autochthonous resource contribution in diverted reaches suggests that the turnover of the
398 biofilm was reduced with the diversion. However, biofilm was not the only autochthonous resource
399 sampled for SIA, and thus, we cannot determine whether turnover or a change in the stock of other

400 autochthonous resources of low abundance was responsible for this decrease. The reduced
401 contributions of coarse detritus and autochthonous resources to the diets in the diverted sites were
402 compensated by an increase in the contribution of fine detritus, which can be linked to the larger
403 abundance of this resource in the diverted sections.

404 Many studies suggest complex relationships between FCL and ecological drivers, such as ecosystem size,
405 perturbations and resource availability (e. g. Post, 2002b; Takimoto et al., 2012; Takimoto and Post,
406 2013). In our study, FCL was not reduced because of habitat contraction nor flow reduction driven by
407 water diversion. Neither was it reduced due to the decrease in the stock and contribution of detritus in
408 the diverted sites, which is poorer in nutrients than the autochthonous basal resources (Cross et al.,
409 2005). The ability to incorporate a basal resource into the biomass of consumers is given by its
410 abundance and its biochemical composition (Brett et al., 2017). Algae can support upper trophic levels
411 across many aquatic systems due to the high nutritional quality of their amino and fatty acids (Brett et
412 al., 2017) and can be more relevant than the detrital input in determining food web structure
413 (Townsend et al., 1998). Thus, longer food chains can be held in more productive ecosystems (Post,
414 2002b). We did not observe any change in the stock of biofilm due to the diversion; however, the lower
415 contribution of autochthonous resources to the diets of consumers in the diverted reaches compared to
416 control reaches (mainly in the less polluted streams) should also have been accompanied by a reduction
417 of the maximum FCL, which did not happen. Fine detritus, richer in nutrients than coarse detritus (Cross
418 et al., 2005), contributed more in the diets of consumers in the diverted sites. The shift from one
419 nutrient-rich resource to another could have maintained the consumer-resource stoichiometric
420 imbalance, and thus, FCL. Kautza and Sullivan (2016) assigned changes in FCL of a regulated river to a
421 combination of mechanisms such as addition and deletion of top predators and insertion of
422 intermediate predators, shifts in the degree of omnivory, and changes in the strength of intraguild
423 predation. Nevertheless, we found the same set of top predators when comparing control and diverted
424 reaches in three out of four rivers, explaining the lack of effects of the diversion on FCL. Similar results
425 to ours were reported by Walters and Post (2008), who did not observe a decrease in FCL as a
426 consequence of water diversion. However, they described a shift in body-size structure, suggesting that
427 the structural complexity of the food web allowed the conservation of the FCL.

428 We expected diversification of the trophic niches due to the reduction of relative abundance the low-
429 quality coarse detritus in comparison to the abundance of biofilm and fine detritus driven by water
430 diversion. In line with this, Kaymak et al. (2018) reported higher trophic diversity and a larger
431 community niche space in the regulated reach downstream from a large dam. They linked it to a higher
432 dominance of trophic generalists, who can shift among alternative resources (Layman et al., 2007b).
433 However, the shift they found was related to decreased fish diversity in the downstream reach, which
434 has not been corroborated in our study. The changes we observed in the iso-space metrics occurred
435 regardless of the lack of large taxonomic changes, at least for top predators. In addition, our models
436 indicate a larger trophic diversity and a smaller community niche space in the diverted reaches for all
437 our systems when looking at the selected consumer taxa. Thus, water diversion produced a collapse of
438 generalist species in the iso-space (i.e., the core of the iso-space). In contrast, more specialised
439 consumers and/or species at the top and bottom of the food webs expanded the overall isotopic space
440 of the community. A plausible explanation for this contrasting pattern can be found in the competition
441 exerted by the more specialised consumers at the edges of the iso-space that might have reduced
442 resource availability for the consumers at the core of the food web.

443 *Pollution promoted biofilm production and increased food web complexity*

444 A non-linear effect of nutrient pollution on biofilm production is frequently described in the literature,
445 with stimulating effects of moderate levels of nutrients (e.g. Ardón et al., 2021; Pereda et al., 2020;
446 Ribot et al., 2015), where subsidy effects of nutrients override toxic effects of other compounds.
447 Similarly, along our pollution gradient, biofilm biomass increased. In addition, previous studies that
448 assessed the effects of land use (and thus, of nutrient concentrations; Baumgartner and Robinson, 2017;
449 Pastor et al., 2014; Price et al., 2019) stated that all community compartments increased in $\delta^{15}\text{N}$ along
450 the pollution gradient; a result that was completely paralleled in our study. Both total nitrogen and $\delta^{15}\text{N}$
451 concentration can be associated with agriculture runoff (Bergfur et al., 2009; Harrington et al., 1998;
452 Pastor et al., 2014) and urbanisation (Pastor et al., 2014; Smucker et al., 2018), and thus, are often
453 correlated. Additionally, our study highlights that the $\delta^{15}\text{N}$ increase along the TDN gradient was stronger
454 for consumers than for basal resources, which points towards a reorganization of food webs, and not
455 only to a propagation of the isotopic signal of basal resources. This reorganization was also represented

456 by the longer FCL with the increase in nitrogen, which is in line with previous observations (Kaunzinger
457 and Morin, 1998) and in accordance to the productivity hypothesis (Pimm, 1982). Although other
458 variables, such as water temperature and conductivity, covaried with the pollution gradient, the good fit
459 between $\delta^{15}\text{N}$ or FCL with water TDN points to pollution, and specially nutrient concentration, as the
460 main driver shaping food webs in this study.

461 With more nutrients in the water column and higher biofilm biomass, a scarce but high-quality resource,
462 we anticipated a reorganization of the niche space of the consumers, with more separate and diverse
463 niches. Moderate nutrient pollution, and consequent biofilm availability, have been linked to a larger
464 isotopic variability (García et al., 2017; Parreira de Castro et al., 2016) as isotopic diversity of basal
465 resources increases. However, further pollution of water by nutrients can also cause a drastic reduction
466 of the diversity of resources (reducing isotopic variability among the available resources), leading to
467 narrower isotopic variation among consumers (García et al., 2017). In our study, we observed an overall
468 increase in trophic diversity and a decrease in redundancy along the pollution gradient (i.e. a
469 diversification on consumers' diet and a more uniform spacing of taxa), suggesting that our systems did
470 not suffer from the effects of severe nutrient pollution. However, we must bear in mind that the works
471 cited above are based on isotopic analyses of the entire community, whereas we have centred our study
472 on the core communities of the studied systems, i.e. the same six invertebrate taxa that appeared in all
473 sampling sites plus fishes. Thus, despite responses in our study cannot be attributed to interspecific, but
474 to intraspecific variation, the isotopic patterns are similar.

475 *Effects of water diversion and pollution on food web complexity were exacerbated in combination*

476 When dealing with multiple stressors in the same study it is of interest to rank the stressors in order of
477 ecological relevance and to describe the kind of interaction that they create in response variables. Few
478 studies have already addressed the combined effects of flow reduction and nutrient enrichment (e.g.
479 Elbrecht et al., 2016; Lange et al., 2014; Matthaei et al., 2010). In mesocosms studies, Elbrecht et al.
480 (2016) and Matthaei et al. (2010), observed pervasive and stronger effects of flow reduction than those
481 associated with nutrient enrichment on the studied variables regarding benthic macroinvertebrates and
482 algal biomass. In contrast, in a field study, Lange et al. (2014) showed that nutrient pollution had a larger
483 effect than water diversion on fish populations. The severity of both stressors can vary hugely, as

484 droughts can be created by diversion, and some local extinctions can be the outcome of nutrient
485 pollution. In our case, food webs were more sensitive to pollution than to water diversion. Moreover,
486 pollution was modulating the response of some food web properties to diversion. For instance, when
487 focusing on the iso-space metrics of the selected consumer taxa of the studied rivers, interaction was
488 the norm: trophic diversity was higher and redundancy lower in the diverted sites of the most polluted
489 rivers. Thus, the increase of the availability of biofilm along the pollution gradient led detritus-deprived
490 consumers of the diverted reaches to expand further their diet towards autotrophic resources.

491 Conclusions

492 Ecosystems face multiple stressors. It is crucial to study multiple stressors simultaneously to understand
493 interactive effects, create predictive tools and rank their relevance based on their relative ecological
494 impact. In this study based on a representative subset, both pollution and water diversion affected food
495 webs by means of bottom-up mechanisms and nutrient pollution intensified the effects of diversion on
496 the community food web structure. We expect these results to be widespread and strong across
497 freshwater ecosystems that depend mostly on low quality detrital resources, whereas we anticipate
498 these effects to be weaker in systems that mostly depend on high-quality resources, such as biofilm. In
499 addition, both pollution and water diversion can vary in their intensity, resulting in different outcomes
500 on food webs. More severe degrees of pollution and larger water removals are expected to trigger local
501 extinctions and hence food web simplification. It is uncertain to what extent non-linear responses to
502 both stressors will emerge as their intensity increase (Hillebrand et al., 2020). We believe our results will
503 foster further research on the interactive effects of multiple stressors of varying intensities to better
504 understand their effects on freshwater ecosystems globally.

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518 Conflict of interest

519 Authors declare that there is no conflict of interest regarding the material discussed in the manuscript.

520 Data availability statement

521 The original data that support the findings of this study are openly available in Figshare and GitHub
522 (<https://doi.org/10.6084/m9.figshare.17014022.v1>).

523

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823

824 Tables

825 **Table 1.** Main characteristics of the studied rivers. The total annual precipitation and mean annual air
 826 temperature are the average values for 2017 and 2018 (www.euskalmet.euskadi.eus). Ecological status
 827 and the Referenced Physicochemistry Index (RPI) for the period 2012-2016 are shown (Aguirre et al.,
 828 2017); the asterisk (*) indicates rivers with a heavily altered hydromorphology. Rivers are ordered
 829 following $\log_{10}(\text{TDN})$ values from left to right.

		Urumea	Leitzaran	Kadagua	Deba
Basin		Urumea	Oria	Kadagua	Deba
Coordinates of the dam	Latitude	43°12'53.5"N	43°07'57.6"N	43°13'37.9"N	43°09'37.6"N
	Longitude	1°54'16.7"W	1°56'13.4"W	3°00'58.8"W	2°24'08.6"W
Elevation (m asl)		69	354	37	122
Total annual precipitation (mm)		1838.6	2268.4	1288	1316.2
Mean annual air temp. (°C)		13.5	13.6	13.3	12.7
Upstream catchment area (km ²)		186.1	62.8	449	355.1
Land use (%) in upstream catchment area	Urban	0.1	1.1	2.5	4.6
	Agriculture	0.8	10.7	25.8	17.4
	Forestry	98.3	88.2	71.5	77.8
	Water	0.8	0.0	0.3	0.2
Ecological status		Good	Good	Good*	Moderate*
RPI		0.80 ± 0.01	0.79 ± 0.01	0.78 ± 0.01	0.68 ± 0.02
Maximum concession volume (m ³ s ⁻¹)		5.8	3.0	4.0	5.0

830

831 **Table 2.** Compiled mean and standard error of physicochemical descriptors in each reach of the studied rivers. TDN gradient score for each river is also indicated in the
 832 table. Rivers are ordered following $\log_{10}(\text{TDN})$ values from left to right.

	Urumea		Leitzaran		Kadagua		Deba	
	Control	Diverted	Control	Diverted	Control	Diverted	Control	Diverted
pH	7.65 ± 0.09	7.54 ± 0.08	8.13 ± 0.05	8.14 ± 0.02	8.16 ± 0.13	8.27 ± 0.10	8.14 ± 0.19	8.15 ± 0.04
Conductivity ($\mu\text{S cm}^{-1}$)	75.13 ± 5.89	74.97 ± 6.32	243.00 ± 19.14	242.33 ± 19.64	586.00 ± 38.32	590.00 ± 45.51	505.00 ± 78.23	508.67 ± 61.48
Temperature ($^{\circ}\text{C}$)	14.80 ± 1.21	15.00 ± 1.10	15.13 ± 2.14	15.73 ± 2.21	16.70 ± 2.39	17.00 ± 2.30	18.30 ± 0.38	17.90 ± 0.38
Dissolved oxygen (%)	108.90 ± 5.77	108.60 ± 6.82	103.30 ± 6.58	102.3 ± 0.88	97.00 ± 0.05	103.9 ± 1.93	115.40 ± 0.91	105.80 ± 4.68
Cl^{-} (mg L^{-1})	4.16 ± 1.50	3.00 ± 0.38	6.06 ± 0.28	6.98 ± 2.73	14.28 ± 5.37	8.03 ± 1.06	12.22 ± 1.97	12.37 ± 1.70
SO_4^{-2} (mg L^{-1})	2.55 ± 0.91	2.1 ± 0.46	7.07 ± 0.95	7.18 ± 3.17	35.83 ± 10.93	20.32 ± 1.06	19.85 ± 5.99	20.02 ± 5.70
NO_3^{-} (mg L^{-1})	1.58 ± 0.67	1.04 ± 0.22	2.53 ± 0.11	2.81 ± 0.94	3.56 ± 2.70	0.98 ± 0.17	2.13 ± 0.38	2.22 ± 0.17
NH_4^{+} ($\mu\text{g N L}^{-1}$)	15.65 ± 2.69	16.68 ± 5.61	14.32 ± 4.70	13.90 ± 5.38	56.72 ± 8.61	51.53 ± 9.82	27.02 ± 7.07	24.50 ± 6.75
DOC (mg C L^{-1})	1.91 ± 0.14	1.91 ± 0.48	3.39 ± 0.15	3.97 ± 0.39	6.40 ± 0.52	7.89 ± 0.83	5.67 ± 0.96	6.14 ± 0.26
TDN (mg N L^{-1})	0.85 ± 0.06	0.85 ± 0.04	1.11 ± 0.10	1.26 ± 0.17	1.54 ± 0.10	1.47 ± 0.11	1.94 ± 0.28	1.94 ± 0.35
SRP ($\mu\text{g P L}^{-1}$)	6.78 ± 1.12	9.92 ± 1.73	32.18 ± 11.42	29.04 ± 9.58	31.59 ± 11.10	28.10 ± 9.90	54.11 ± 9.90	49.25 ± 16.45
Wet width (m)	21.57 ± 0.57	15.98 ± 0.75	10.12 ± 0.42	9.66 ± 0.40	20.88 ± 0.79	16.89 ± 0.74	20.61 ± 0.79	16.58 ± 0.44
Discharge ($\text{m}^3 \text{s}^{-1}$)	4.60 ± 1.43	1.71 ± 0.23	1.67 ± 0.62	0.9 ± 0.68	2.57 ± 1.22	0.80 ± 0.10	1.55 ± 0.63	0.94 ± 0.13
TDN gradient ($\text{Log}_{10}\text{TDN}$)	-0.064 ± 0.017		0.073 ± 0.035		0.177 ± 0.021		0.288 ± 0.043	

833

834

835 **Table 3.** Model-selection for the drivers (pollution -Log₁₀TDN-, water diversion -Reach-, both -Log₁₀TDN
 836 + Reach- and their interaction -Log₁₀TDN *Reach-) affecting basal resource (alder, fine detritus and
 837 autochthonous resources) contribution to primary consumers. Degrees of freedom (df), log-likelihood
 838 ratios (logLik), Bayesian Information Criterion (BIC), and the difference with the model with lowest value
 839 (ΔBIC) are given. Models with the lowest BIC are shown in bold. Coefficients for the best model are
 840 shown.

841

Resource consumption	Model	df	logLik	BIC	ΔBIC	Coefficients		
						Log ₁₀ TDN	Reach (D)	Log ₁₀ TDN : Reach (D)
Alder	Reach	2	-2739.7	5499.6	0		-0.245	
	Null	1	-2746.6	5503.3	3.68			
	Log ₁₀ TDN + Reach	3	-2742.1	5514.5	14.85			
	Log ₁₀ TDN	2	-2749.0	5518.1	18.51			
	Log ₁₀ TDN * Reach	4	-2768.8	5577.9	78.30			
Fine detritus	Reach	2	-6067.3	12154.8	0		1.107	
	Log ₁₀ TDN * Reach	4	-6228.3	12497.0	342.12			
	Log ₁₀ TDN + Reach	3	-6241.3	12512.8	357.99			
	Null	1	-6527.1	13064.3	909.50			
	Log ₁₀ TDN	2	-6693.5	13407.2	1252.33			
Autochthonous resources	Log₁₀TDN * Reach	4	-10473.3	20987	0	-3.692	-0.716	3.624
	Null	1	-10584.3	21178.6	191.66			
	Log ₁₀ TDN	2	-10587.4	21195.0	208.02			
	Reach	2	-10598.7	21217.5	230.57			
	Log ₁₀ TDN + Reach	3	-10604.0	21238.2	251.28			

842

843 **Table 4.** Model-selection for the drivers (pollution -Log₁₀TDN -, water diversion -Reach-, both -Log₁₀TDN
844 + Reach- and their interaction -Log₁₀TDN : Reach-) affecting community iso-space metrics of the
845 consumers (invertebrates and fish). Degrees of freedom (df), logarithmic transformation of the
846 likelihood function used to fit models (logLik), Bayesian information criterion (BIC), and difference
847 between a given model and the model with the lowest BIC value (Δ BIC) are given. The most
848 parsimonious model for each community metric is shown in bold. Described community metrics are: CD
849 (distance to centroid representing trophic diversity), SEA (standard ellipse area regarding the niche
850 space), MNND (mean nearest neighbor distance, related to trophic redundancy), and SDNND (standard
851 deviation of the nearest neighbor distance also related to trophic redundancy).

852

Community metrics	Model	df	logLik	BIC	Δ BIC	Coefficients		
						Log ₁₀ TDN	Reach (D)	Log ₁₀ TDN : Reach (D)
CD	Log₁₀TDN * Reach	5	-4064.04	8180.0	0	0.270	0.034	1.167
	Log ₁₀ TDN + Reach	4	-5241.88	10525.3	2345.30			
	Log ₁₀ TDN	3	-5298.68	10628.5	2448.52			
	Reach	3	-7503.20	15037.5	6857.56			
	Null	2	-7552.52	15125.8	6945.84			
SEA	Log₁₀TDN * Reach	5	-76361.37	152774.6	0	13.423	-2.075	-4.480
	Log ₁₀ TDN + Reach	4	-76556.47	153154.4	379.83			
	Log ₁₀ TDN	3	-78842.71	157716.5	4941.95			
	Reach	3	-80779.97	161591.1	8816.46			
	Null	2	-82564.15	165149.1	12374.46			
MNND	Log₁₀TDN * Reach	5	-7159.00	14369.9	0	2.124	-0.015	0.620
	Log ₁₀ TDN + Reach	4	-7440.63	14922.8	552.89			
	Log ₁₀ TDN	3	-7450.10	14931.3	561.44			
	Null	2	-19126.94	38274.6	23904.75			
	Reach	3	-19122.37	38275.9	23906.00			
SDNND	Log₁₀TDN * Reach	5	-29462.16	58976.2	0	-3.293	0.129	2.039
	Log ₁₀ TDN + Reach	4	-30207.15	60455.8	1479.60			
	Log ₁₀ TDN	3	-30378.40	60787.9	1811.73			
	Reach	3	-33470.14	66971.4	7995.21			
	Null	2	-33609.93	67240.6	8264.43			

853

854 Figure captions

855 **Figure 1.** Conceptual figure of the proposed hypotheses: H1 refers to the hypothesis regarding water
856 diversion, H2 refers to the one related to the increase in pollution and H3 refers to the interaction
857 between the two stressors. Control reach and diverted reach refer to the sampling sites above and
858 below the weirs. Low pollution and moderate pollution is a simplification of the pollution gradient.
859 CPOM and FPOM are coarse and fine detritus. FCL refer to food chain length. Basal food resources,
860 coarse detritus, fine detritus and biofilm, are represented in dark brown, light brown and light green
861 respectively in the figure, and consumers are represented in dark red. The food web arrangement of the
862 C-N biplot from Control-Low pollution site is redrawn in lighter colours in the other biplots as reference.
863 $\delta^{15}\text{N}$ indicates the trophic position of each element of the biplot, whereas $\delta^{13}\text{C}$ informs about the
864 relative proximity to the basal resources. (+) and (-) symbols indicate an increase or a decrease
865 respectively.

866

867 **Figure 2.** Resource abundance in the studied reaches (white for control; grey for diverted): (a) coarse
868 detritus (CPOM), (b) fine detritus (FPOM) and (c) biofilm represented along the total dissolved nitrogen
869 (TDN) gradient. The box plots show the median, the interquartile range and the tails of the distribution.
870 Black regression lines (solid line for control; dashed line for diverted) are drawn with the significant
871 coefficients from linear (biofilm) and linear mixed effect models (coarse and fine detritus). A single grey
872 line is shown when only the TDN was significant in the model, and black regression lines (solid line for
873 control; dashed line for diverted) are drawn when the effect of the diversion differed. Bands around the
874 line represent the 95% confidence interval. Significant differences between the control and diverted
875 reaches within each river are marked with an asterisk.

876

877 **Figure 3.** Bayesian posterior estimates showing the contribution of (a) Alder, (b) fine detritus (FPOM)
878 and (c) autochthonous resources (biofilm, filamentous green algae, bryophytes and macrophytes) to the
879 diets of consumers (white for control; grey for diverted) along the total dissolved nitrogen (TDN)
880 gradient. Black regression lines (solid line for control; dashed line for diverted) are drawn according to

881 the preferred model. Significant differences between the control and diverted reaches within each river
882 are marked with an asterisk.

883

884 **Figure 4.** (a) Nitrogen stable isotope ratios ($\delta^{15}\text{N}$, ‰) and (b) Carbon stable isotope ratios ($\delta^{13}\text{C}$, ‰) of
885 the entire community in the studied reaches (white for control; grey for diverted) represented along the
886 total dissolved nitrogen (TDN) gradient. The box plots show the median, the interquartile range, and the
887 tails of the distribution. A single grey regression line is represented when only the TDN gradient was
888 significant and black regression lines (solid line for control; dashed line for diverted) are drawn when the
889 effect of the diversion differed. Bands around the line represent the 95 % confidence interval.

890

891 **Figure 5.** Maximum food chain length (FCL) in the studied reaches (white for control; grey for diverted)
892 represented along the total dissolved nitrogen (TDN) gradient. The box plots show the median, the
893 interquartile range and the tails of the distribution. A single grey regression line was represented as only
894 the TDN gradient was significant. Bands around the line represent the 95 % confidence interval.

895

896 **Figure 6.** Bayesian posterior estimates of community wide metrics of the iso-space for consumers: (a)
897 distance to centroid (CD), (b) standard ellipses area (SEA), (c) mean nearest neighbour distance (MNND)
898 and (d) standard deviation of nearest neighbour distance (SDNND). These metrics provide information
899 about trophic diversity, community niche space and redundancy of the eight consumer communities
900 (white for control; grey for diverted) along the total dissolved nitrogen (TDN) gradient, respectively.
901 Black regression lines (solid line for control; dashed line for diverted) are drawn according to the
902 preferred model. Significant differences between the control and diverted reaches within each river are
903 marked with an asterisk.