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1 **Disentangling dam impacts in river networks**

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12 **Abstract**

13 Damming is one of the most widespread impairments of river systems around the world. The
14 formulation of scientifically justified guidelines for restoration and remediation of impairments
15 requires better understanding of the relationships between alteration and stream condition. The present
16 study examines relationships between the presence and density of dams and biological metrics of river
17 health in the context of a variety of environmental drivers over the Loire river basin. We hypothesized
18 that dam density measured at supra-reach level would show more significant influence on river health
19 than the local level density, and further that the impact of dams is best estimated with measures for the
20 functional traits of biotic assemblages. An extensive dataset of fish (169 sites) and invertebrate (211
21 sites) communities in the Loire river basin, described with metrics of density of ecological guilds,
22 taxonomic richness and life history traits, and coupled with reach hydromorphology and catchment
23 characteristics was constructed. Generalized linear modelling was performed in order to quantify dam
24 impact and investigate the importance of regional- and local-scale measures of dam density to the
25 structure of biotic communities. The analysis showed that community structure at the basin scale
26 responded significant to dam presence and confirmed that the strongest relationships were observed
27 for specific functional trait-based metrics. For the macroinvertebrates the observed impact counts up to
28 25% of the variance in the trait-based quality indices, whereas for fish communities the dam density
29 only explains up to 12%. Macroinvertebrate responses were stronger at higher scale level, and
30 especially the upstream context explained on its own 70% of the observed impairment. For fish
31 communities, the local context prevails and explained up to 70% of the dam impact. These results can
32 be explained by the biotic processes ruling community assembly in the specific groups, passive
33 dispersal for the invertebrates and migrations between habitats for fish. The geographic context
34 furthermore explains the differentiation in these responses, reflecting the metacommunity structure of
35 invertebrate assembly over the river basin. We conclude that for upstream parts of the river basin,
36 locally based management actions can be successful in restoring biotic integrity, whereas more
37 downstream, dam removal actions require more integrated measures at regional rather than local scale.

39 **Highlights**

- 40 ► Dam density is proposed as a multi-scale indicator distinguishing local and network scale impact.
- 41 ► Responses in macroinvertebrate and fish communities are strongest for functional trait metrics
- 42 ► Macroinvertebrate communities respond strongest to upstream dam density whereas for fish the
- 43 local context prevails. ► Invertebrate assembly and responses reflect metacommunity structure. ►
- 44 Upstream-downstream contexts and responses differ and demand for different restoration strategies.

45
46 **Keywords:** dam density indicators; biotic integrity; macroinvertebrates; fish; trait metrics.

52 **1. Introduction**

53 Large-scale and even globally programs are launched targeting the rehabilitation of river systems and
54 water allocation for a sustainable provision of services of freshwater ecosystems (Vörösmarty, 2010).
55 The great majority of river systems of the world are subjected to flow regulation and impoundment;
56 over half of the world's large river systems are affected by dams (Nilsson et al., 2005), and, for
57 example, Graf (2001) estimates that only 2% of rivers in the United States remain unaffected by dams.
58 Reported impacts of dams concern a degradation of habitat and a fragmentation of populations, with
59 losses of productivity, reduced distribution ranges and changes documented for fish community
60 composition (Santucci et al., 2005 ; Catalano et al., 2007 ; Slawski et al., 2008), as well as for aquatic
61 invertebrate communities (Brittain and Saltveit, 1989; Watters, 1996; Cortes et al., 1998; Benstead et
62 al., 1999; Conception & Nelson, 1999; Marchant and Hehir, 2002; Stanley et al., 2002; Blakely et al.,
63 2006).

64
65 Recently, questions on the opportunity of dam removal and the ecological benefits of such restoration
66 measures arise, but for specific contexts, the general rationale for restoring natural features often
67 seems to get lost, and not only due to uses conflicts (Donnelly et al., 2002; Lejon et al., 2009). Often
68 there is a local attachment to existing landscape features and scenery, but more importantly river
69 managers encounter resistance of conservationist and fisheries stakeholders that question the potential
70 gains and stress the risks of species loss. Nevertheless there is general agreement to the injurious
71 character of human alterations and to the application of a reference approach (Hansen and Hayes,
72 2012). But especially the strong emphasis on the river's corridor functioning and the impact of
73 obstacles to ecological networks, demands for dam removal. As a result, there's need for advanced
74 assessments of the role and effects of dams within river networks to support strategies for mitigating
75 ecohydrological and socioeconomic costs, and recently important efforts are made globally to the
76 inventory of reservoirs and dams (Lehner et al., 2011), or to evaluate their impact on river ecology
77 (Petts, 1984; Acreman and Ferguson, 2010). In France and Western Europe in general, the high degree
78 of flow regulation and the governmental initiatives to address environmental problems under the
79 Water Framework Directive provide the need and impetus for environmental water allocations and the
80 need to monitor and assess the ecological effects.

81
82 In literature, impact of dams is generally examined on the local context, and very often, no significant
83 negative effect to local biotic communities can be attributed (Pohlon *et al.*, 2007). From a long year
84 study to the effects of an impoundment (Maynard and Lane, 2012) observed even an increase in
85 species richness, which they attributed to the buffering effects to peak velocity and low flows. Recent
86 studies, dealing with the question at a more comprehensive level, include the entire drainage basin
87 because of the importance of tributary-main stem and upstream-downstream connections in a drainage
88 basin (Wohl, 2012). The basin context of dam impacts has been elucidated for sediment provision,
89 water allocation, fish diversity and food security (Fitzhugh, 2011). Of course this impact is most clear
90 for diadromous species. But, for example, Ziv et al. (2012) demonstrate the damaging impact on
91 resident fish populations at river basin scale revealing strong impacts of upstream tributary dams on
92 overall sustainability of fish populations. With the individual dam's geographic setting, aspects of the
93 position and accumulation of dam impacts in the river network are a key issue in assessment (Poff and
94 Hart, 2002). Therefore the entire drainage must be included in such studies in paying a particular
95 attention on the geographical context because the response to damming may also be expected to differ
96 between small upstream streams and large alluvial rivers (Nilsson *et al.*, 2005).

97
98 From a metacommunity perspective, a loss of connectivity can cause local extirpations due to changes
99 in environmental conditions (Chase and Leibold, 2002) or to a lack of re-colonization sources
100 (Mouquet and Loreau, 2002). Knowledge on the metacommunity structure and the nature of the
101 impairments, whether the disconnection or habitat degradation impact dominates, can generate
102 important information to determine conservation and restoration actions. Trait-based bio-assessment
103 may in this respect have several advantages to enhance causal diagnosis over taxonomically based
104 methods (Archambault *et al.*, 2010). These include providing mechanistic linkages of biotic responses
105 to environmental conditions, and consistent descriptors or metrics across broad spatial scales (Culp *et*
106 *al.*, 2011).

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In this paper, two hypotheses are put forward for these questions to biotic community changes caused by dams with regard to geography and network constellation. Firstly, the impact of dams on the biotic communities in the river network is supposed to count more at the regional than just the local scale. And if so, does this mean that the disconnection impact is stronger than the habitat degradation impact? The second hypothesis deals with the specificity of biotic groups; different responses are expected for different groups. Based on the higher mobility of fish compared to invertebrates, impact on fish is most expected for connectivity and at a larger scale, whereas for invertebrate communities local habitat degradation should prevail. So, in addition to this second hypothesis questions arise for the geographic aspect. Does a general highland-lowland distinction control the impacts; in highlands mostly measurable in habitat degradation, whereas for lowland regions more connectivity aspects are involved?

To deal with the hypotheses, an analysis is presented on a representative part of the French river network, for the largest river basin of the Loire River that is governed and surveyed by a single authority, offering a homogeneous set of data for both dams and biotic surveys in the network. Moreover, as dams and weirs on the French rivers are present for a long-time, the consequences of disconnection can be assessed without risk of delayed response; if it takes time for the consequences of damming to impact on communities (Ormerod *et al.*, 2010), by now these consequences should be in place.

2. Material and methods

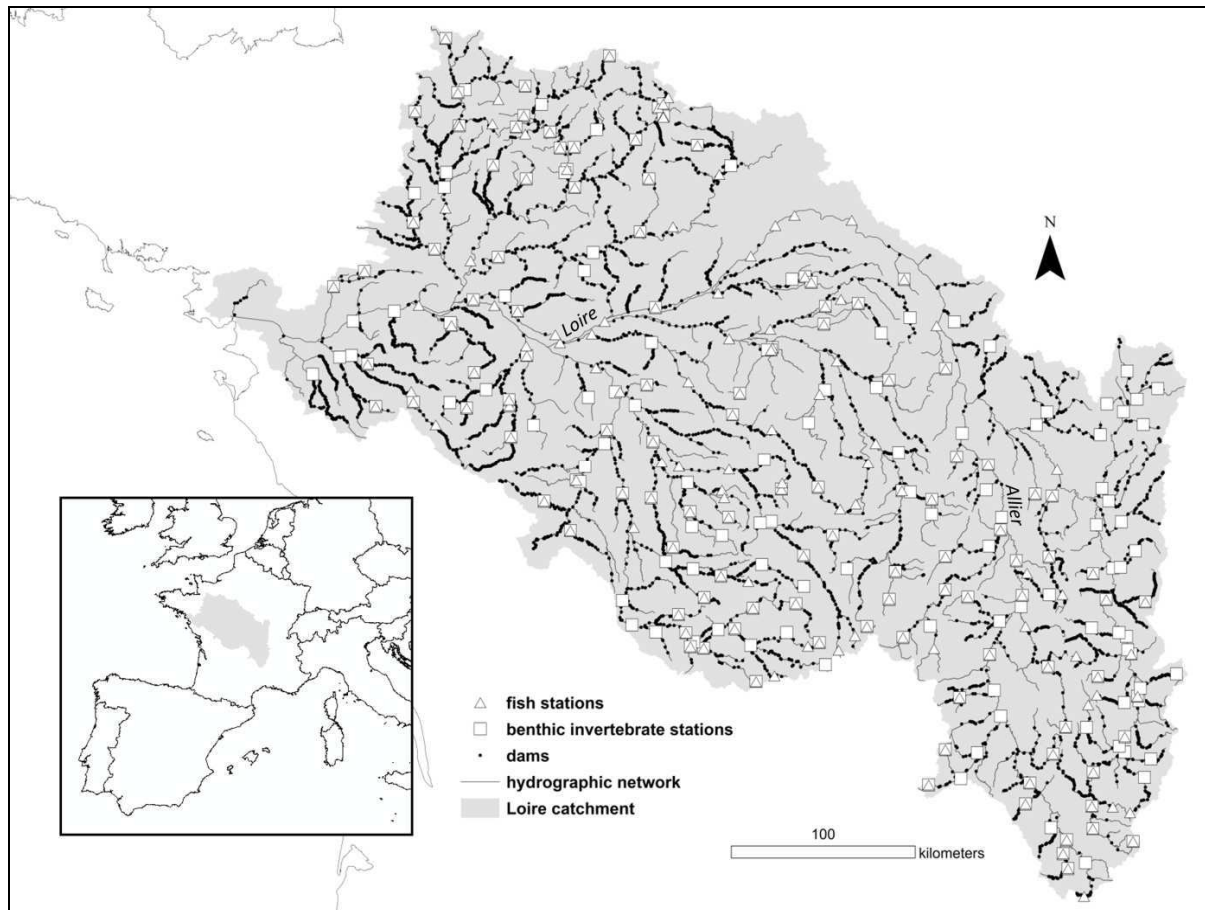
2.1 Study area and datasets

The Loire river basin covers a total area of 155,000 km² or 22% of French territory, which makes it one of the largest in Western Europe (see Figure 1). The Loire is more than 1,000 km in length and has its source at 1,048 m altitude. With its preserved free-flowing character the main river has an exceptional conservation value. The basin offers a stronghold for anadromous migratory fish species for the European mainland, with a unique relic Atlantic salmon population. The surveyed river network consists of 17000km river length, divided in 4930 river segments homogeneous in geomorphological characteristics. The splitting into these geo-morphological units is based on a semi-automatic sectioning that distinguishes changes in geological entities, channel form, sinuosity and valley floor width (Chandesris *et al.*, 2008). Resulting river segments range from 1km on average for small streams, up to 20km on average for large rivers. The gradation in length conforms to the increase in size of rivers and of their functional mesohabitat entities. This spatial framework allows studying dam impacts (disconnection and impoundments) over the entire basin independently of geomorphological gradients and variation.

This hierarchical spatial framework was constructed for the entire French river network and is a product of the national hydromorphology audit system, SYRAH (Chandesris *et al.*, 2008). This database also provides, for each of these river segments, information on both natural and anthropogenic hydromorphological pressure variables at two spatial scales (the upstream catchment and the local river segment), using suitable spatial data available over the national territory. At the upstream catchment scale land cover information was derived from the CORINE land cover database (drawn from satellite imagery at a scale of 1: 100 000, with a minimum polygon size of 25 ha, <http://www.eea.europa.eu/publications/COR0-landcover>). At local river segment scale, hydromorphological pressures were derived from the French geo-database with metric precision (IGN, RGE® database, <http://www.ign.fr/institut/activites/referentiel-a-grande-echelle>). Moreover, it informs on the risk alterations of hydromorphological processes. The hydro-morphological variables and alteration risk information collected in this study are summarized in Table 1.

Then, information on dams was gathered over the Loire basin from the French obstacles inventory (ROE® database, finalized version November 2011, <http://www.onema.fr/REFERENTIEL-DES-OBSTACLES-A-L>), that is produced by the national agency for water and aquatic environments (Onema) and gives reliable information on the localization of dams. More than 5500 dams are present in the surveyed network according to the ROE® database, with a relative absence of dams on the downstream part of the Loire and its main tributary the Allier (see Figure 1)

160 And finally, biological data was retrieved from the French national monitoring network which gives
 161 information on of the water quality on a stabilised set of 1649 stations. The spatial distribution of the
 162 monitoring stations tries to achieve a type-selective and spatial coverage for a general quality
 163 assessment. The local sampling site selection is intended to be representative for the overall biotic
 164 quality of the specific river reach. We selected a set of stations that correspond to a spatial and type-
 165 specific distribution at the scale of theLoire River basin, and we applied a neighbourhood criterion to
 166 reduce spatial autocorrelation (nearest station in the network were eliminated).. This resulted in a
 167 network consisting of 211 invertebrate and 169 fish stations evenly distributed over the hydro-
 168 ecoregions and river types in the river basin.
 169
 170



171
 172 Figure 1. Localization of the Loire Basin with dams of national obstacle inventory (ROE®) and fish
 173 and benthic invertebrate sampling stations of the national monitoring network.
 174

175 Table 1: hydro-morphological variables and alteration risk information from SYRAH database
 176

Scale	hydro-morphological variable type	Name	Description
upstream catchment	pressure	urbanisation	percentage cover of urban land use class in CORINE land cover data of the upstream catchment
		intensive agriculture	percentage cover of intensive agricultural CORINE land cover classes of the upstream catchment
		natural	percentage cover of near-natural CORINE land cover classes data of the upstream catchment
local river segment	geography	altitude	elevation at downstream point of river segments
		river slope	slope of the river bed over the segment
		valleyslope	valley slope perpendicular to the river
		Discharge	mean annual discharge for gauging station or model prediction at river segment level

	Sinuosity	sinuosity of the river bed over the segment
pressure	channelstraightening	percentage of straight reaches over the segment, weighed by river type
	riparian infrastructure	percentage cover of infrastructure over riparian buffer of three river widths of the segment
	riparian urbanisation	percentage cover of urbanisation for the 100m riparian buffer of the river segment
	riparianforestcover	percentage cover of forest patches for the 30m riparian buffer of the river segment
alteration risk	bed structure	bedsubstrate alteration risk based on local re-dimensioning and upstream sediment blocking
	hydrodynamics	alteration risk to hydrological regime, based on upstream abstractions and reservoirs

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179 2.2 Construction of dam impact indicators

180 Indicators for dam impact in the river network at three distinct scale levels were developed for the
 181 appraisal of the distinct effects of dam presence to biota and computed for each biological station.
 182 At the local level, four indicators were designed. First, the elementary number of dams ($dam\#$) per
 183 river segment, it is defined as follows:

184

$$185 (1) \quad dam\# = Nb_{dams}$$

186

187 where Nb_{dams} is the number of dams geo-localized by the ROE® database on the river segment.

188

189 Second, the normalized density of dams which corresponds to the number of dams per km and ranges
 190 between 0 and 1. It is given by:

191

$$(2) \quad Ddam\#_L = \frac{dam\#_L - \max dam\#_L}{\max dam\#_L}$$

192 with:

$$193 \quad dam\#_L = \frac{\sqrt{dam\#}}{L_{rs}}$$

194 where L_{rs} is the length of the river segment in km and $\max dam\#_L$ the maximum dam density observed
 195 over the entire surveyed network.

196

197 Third a slope-weighted measure for the normalized dam density:

198

$$(3) \quad Ddam\#_{LS} = \frac{Ddam\#_L}{\sqrt{S_{rs}}}$$

199 where S_{rs} the river segment's slope in percentage. This measure diminishes the influence of the
 200 geographic setting to the dam impact: under lower slopes the dam creates larger impounded sections.
 201 This slope weighing gives a reliable estimate to the impounded fraction in the absence of complete
 202 data on the height of dams. For the analysis, it offers the opportunity to distinguish between
 203 predominance of habitat degradation impact by impoundment and the disconnection impact measured
 204 by the obstacle density.

205

206 Fourth the network distance to the nearest downstream dam, a measure that is commonly described in
 207 literature (Cumming, 2004; Musil *et al.*, 2012), is defined as follows:

208

$$209 (4) \quad nearD_{dam} = d_{curv}$$

210
 211 whered_{curv} is the network (curvilinear) distance between the biological station and the nearest
 212 downstream dam. This distance is measured using dynamic segmentation techniques available in ESRI
 213 software.

214
 215 At the regional scale, a series of true network indicators for dam density are constructed with a river-
 216 adapted version of the Integral Index of Connectivity (IIC) concept designed in (Pascual-Hortal and
 217 Saura, 2006, Pascual-Hortal and Saura, 2008), using the *dIIC* metric. This metric addresses the
 218 contribution of an individual node to connectivity in the network according to a given descriptive
 219 variable.

220 In our river network adaptation, network nodes correspond to river segments. For the connected
 221 dendritic structure of the river network, a constrained connectivity analysis can be proposed, for which
 222 each segment is regarded in relation to its surrounding segments with a restriction in distance. In such
 223 network, d_{netij} corresponds to the topological distance between any i and j river segment. With
 224 $i \in [1; N]$ where N is the total number of river segments in the river network; and $j \in [1; N_{(i)}]$
 225 where $N_{(i)}$ is the total number of neighbouring river segments to segment i within a specified
 226 topological distance inferior to $d_{net}x$. This maximum topological distance, defined by the operator, is
 227 introduced in order to build *dIIC* metrics across different neighbour networks. When $i = j$ then
 228 $d_{netij} = 0$, see Figure 2A for an illustration of spatial configuration of the river segment network and
 229 topological distance.

230 From this spatial configuration *dIIC* for a X river segment is given by:

231 (5)
$$dIIC_{(X)} = 100 \frac{IIC_{(1 \leq i \leq N)} - IIC_{(1 \leq i \leq N, i \neq X)}}{IIC_{(1 \leq i \leq N)}}$$

232 with

233
$$IIC_{(x_1 \leq i \leq x_2)} = \sum_{i=x_1}^{x_2} \frac{\sum_{j=1}^{N_{(i)}} \frac{a_i \cdot a_j}{1 + d_{netij}}}{L_{N_{(i)}}}$$

234 where x_1 and $x_2 \in [1; N]$, a is the descriptive variable – a segment-scale dam density measure here –
 235 for the river segment, $L_{N_{(i)}}$ the length of the considered neighbouring network. *IIC* ponders the
 236 descriptive variable according to the topological distance: the higher the topological distance, the
 237 lower the weight attributed to the descriptive variable in its calculation. It ranges from 0 to 1 and
 238 increases with higher connectivity, which depends on both the quality (according to the descriptive
 239 variable) and the density (branchiness) of the river network.

240 *dIIC* is the percentage of index value loss when the river segment is removed from the overall index
 241 calculation. The *dIIC* measures the contribution of the individual segment to the overall network
 242 connectivity (Pascual-Hortal and Saura 2008). As the *dIIC* is a quality measure, the inverse dam
 243 density of the segments was used in its calculation (and thus shows an opposite sign in the analyses
 244 compared to the other measures). Separate *dIIC* values were calculated for the inverse dam density
 245 $D_{dam\#_L}$ and the slope weighed dam density $D_{dam\#_Ls}$ in order to evaluate the dominance of
 246 impoundment impact (if weighed measure prevails) over disconnection impact (measured with dam
 247 density). Furthermore, the *dIIC* was calculated for different distances of network neighbours: with 5
 248 neighbouring segments ($d_{net}x = 5$, *dIIC*₅) and with a more regional network, 10 neighbouring segments
 249 ($d_{net}x = 10$, *dIIC*₁₀). The *dIIC* values range from 0 to 100 (*dIIC* = 0 in the hypothetical case that the

250 given river segment does not contribute to the network). An illustration of $dIIC$ values for $Ddam\#_L$ is
 251 presented in Figure 3 for each river segment of the Loire Basin.

252 The neighbourhood matrix for the upstream-downstream connections between river segments in the
 253 network is constructed with python using the network topology format provided by ESRI software. The
 254 ConforSensinode 2.2 software (Saura and Torné, 2009) was used to calculate the $dIIC$ values.

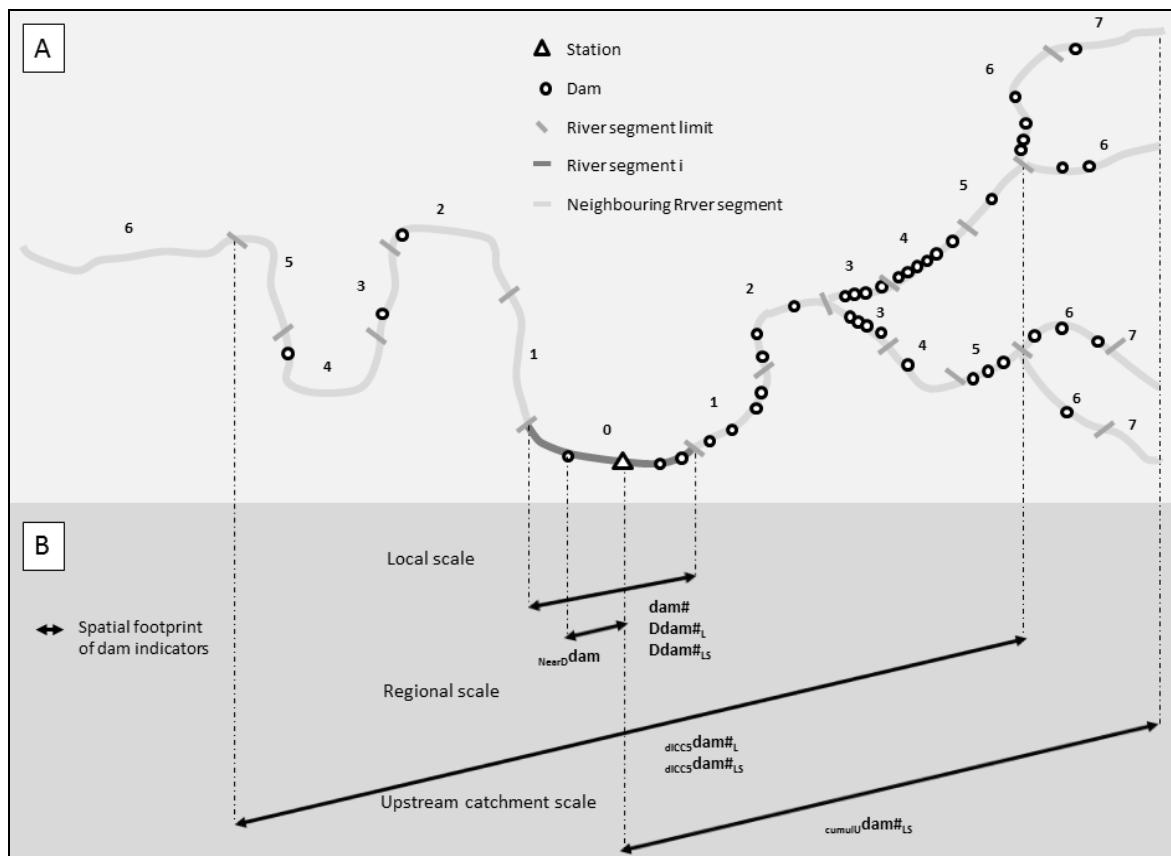
255 Finally, at the highest scale level, an indicator for the accumulation of dams in the upstream river
 256 network is calculated as the averaged segment dam density for the entire upstream catchment. For this
 257 measure, all the segment's dam densities have the same weight (in contrast to the $dIIC$ measure), and
 258 the measure gives a relative measure of dam density for the entire upstream basin to the local site. At
 259 this scale, only the slope weighed dam density ($Ddam\#_{LS}$) was aggregated as follows:

260 (6)
$$cumulu\ dam\#_{LS} = \frac{\sum_{i=1}^{N_u} dam\#_{LS(i)}}{N_u}$$

261 where $dam\#_{LS(i)}$ is the $dam\#_{LS}$ for the river segment i and N_u the number of upstream river
 262 segment. This measure corresponds to the average of $dam\#_{LS}$ over the upstream catchment. Upstream
 263 river segment are selected using the network topology format provided by ESRI software.

264

265 Table 2 summarizes the description of each dam impact indicator and Figure 2B presents the spatial
 266 footprint of dam density indicators on the river network at the different scales.



267

268

269 Figure 2. Spatial configuration of river network for building dam indicators based on the geo-
 270 morphological river segments and schematisation of dam indicators spatial footprint for the different
 271 scales (local, regional and upstream catchment scale). Numbers are relative to the topological distance
 272 to the river segment i . See Table 2 for the labels of indicators.

273
 274

275 Table 2: Dam impact indicators computed for each biological station
 276

Scale	Label	Description
local river segment	dam#	number of weirs/dams per segment
	NearDdam	Nearest network distance to a downstream dam
	Ddams# _L	number of weirs/dams per segment, divided by river length
	Ddams# _{LP}	weighed dam density for slope of river segment more related to impoundment impact (under lower slopes the dam creates larger impounded sections)
regional network	dIIC ₅ dams# _L	Individual segment's contribution to the overall network connectivity according to dam density for 5 neighboring river segments
	dIIC ₅ dams# _{LP}	Individual segment's contribution to the overall network connectivity according to slope weighed dam density for 5 neighboring river segments
	dIIC ₁₀ dams# _L	Individual segment's contribution to the overall network connectivity according to dam density for 10 neighboring river segments
	dIIC ₁₀ dams# _{LP}	Individual segment's contribution to the overall network connectivity according to weighed dam density for 5 neighboring river segments
upstream catchment	cumulUdam# _{LP}	Averaged slope weighed dam density of upstream river segments

277 **2.3 Assessing biotic integrity**

278

279 To evaluate the general ecological quality, aspects of taxonomic richness and abundance for the biotic
 280 communities are investigated. For our analysis we consider both the multi-metric general biotic
 281 integrity indicators and the underlying metrics (see Table 3). All the used metrics are constructed in
 282 the same way for a type-specific evaluation of community composition. Both the overall multi-metric
 283 biotic integrity indices as the constituting taxonomic or life history trait-based metrics are conceived as
 284 distance to a type-specific reference condition (for construction, see Mondy et al., 2012). This
 285 application of reference-based metrics allows removing the principal problems of spatial structuring
 286 and autocorrelation of the data, as with these integrity metrics the natural community richness and
 287 composition gradients are eliminated. With the construction of the site-specific and hierarchic spatial
 288 indicators for dam density, and the type-specific distribution of the biological monitoring sites, the
 289 problem of spatial autocorrelation is largely omitted. This was further tested with correlation testing
 290 for geographic context of altitude and bed slope.

291

292 For fish, a standardised protocol of biannual sampling has been in place for the last 8 years. A standard
 293 electrofishing protocol is carried out during low-flow periods (May-October) to collect information
 294 about fish assemblages in the monitoring network. The biotic index used in the evaluation of the
 295 ecological quality is the French fish-based index for the assessment of river health (IPR) (Oberdorff *et*
 296 *al.*, 2002). The national fish-based multi-metric index IPR is composed of a set of seven metrics of
 297 taxonomic richness, abundance, habitat and trophic guilds and pollution sensitivity (see Table 3).
 298 Macro-invertebrate data is collected following the national protocol in summer with a Surber net
 299 sampler (Archambault et al., 2005). Taxa are identified at the genus level (except for Diptera and
 300 Oligochaeta for which the family level is used) and based on biological traits and abundances of taxa,
 301 the biological metrics are calculated for the sites. The French multi-metric index (I2M2) is composed
 302 of five metrics calculated at the reach level (Mondy *et al.*, 2012) (see Table 3). Metrics both for fish as
 303 invertebrates are calculated based on the traits of the species for each site,
 304 based either on richness or abundance of taxons, measuring the deviation between the observed and
 305 the type-specific expected values. This reference-based approach gives for each trait-based metric a
 306 distance to reference condition for a site. Both for invertebrates and for fish the data of 2009 were
 307 selected from the database for each site.

308

309 Table 3: Multi-metric indices for both macroinvertebrate and fish communities
 310

Community	Multi-metric Index	Metrics	metrics label
Macro invertebrate	I2M2	the relative abundance of multivoltine species in the assemblage	Polyv.
		the relative abundance of ovoviviparous species	Ovov.
		Shannon diversity index	Shan.
		species tolerance in original ASPT	ASPT
		score a measure of taxonomic richness	TAX
Fish	IPR	Taxonomic richness	NTE
		number of rheophilic species	NER
		number of lithophilic species	NEL
		Abundance of tolerant species	DIT
		Abundance of invertivorous species	DII
		Abundance of omnivorous species	DIO
		total fish abundance	DTI

311
 312

313 2.4 Statistical analysis

314

315 Three successive statistical analyses were designed in order to distinguish upon the elements under
 316 question: whether the local or network impact of dam density prevails, whether functional metrics of
 317 the structure of the biotic communities explain more accurately the potential dam effects of
 318 community degradation, differentiate between impoundment habitat degradation and disconnection.
 319 First, a straightforward correlative analysis is performed where the biotic metrics (see Table 2) are
 320 confronted with the dam indicators (see Table 3) and hydromorphological stressor measures (see Table
 321 1) using Spearman correlation testing.

322 Secondly, a multiple linear regression modeling (GLM) to determine the strength of the response
 323 between biotic indices and dam density measures at the local, regional and upstream catchment scale
 324 is performed. The first indications in the correlation analysis are used to select the metrics and
 325 predictors that we integrate in the GLM. Moreover, the GLM multiple regression enables to
 326 distinguish the variance explained by the different predictors at the different scale levels.

327 Thirdly, as both the stressor and natural geographic context can influence the response, a residual
 328 analysis to show the interference of both environmental and community compositional factors to the
 329 dam response is performed. From the GLM multiple regression for the detected strongest explaining
 330 variables we will look in detail what factors of geography and hydromorphology are influencing this
 331 response, with a correlation analysis of the residuals for this regression.

332
 333

334 3. Results

335 3.1 Local and network dam impact

336 Both for fish as for invertebrates significant relationships with local dam density are only present for
 337 specific trait-based metrics and not for the global biotic integrity indices (see Table 4). The integrated
 338 network measure of dam density shows stronger correlations than the local dam density also both for
 339 fish as invertebrate metrics, indicating the accumulation of dam impact in the river network. For the
 340 network measures some significant responses are observed for the global indexes IPR and I2M2 as
 341 well. The dam density showed no specific spatial structure and so no spatial autocorrelation confounds

342 these results. With correlation testing we found no relationship with altitude for dam density (R -0.04)
 343 and only a minor correlation of density with bed slope (R 0.18).

344
 345 For fish the strongest correlations are observed for the rheophilic species metric NER and the
 346 lithophilic species NEL. Both metrics correspond to the groups of (often migratory) species of free
 347 flowing river reaches. For the NER and NEL metrics the network impact shows the strongest
 348 responses. These responses are the same for slope weighed and non-weighed measures, and in the
 349 same order for network and local measures. For the density of omnivorous species DIO we observe a
 350 local dam density impact. The insectivorous species DII respond significantly to the non-weighed dam
 351 density in the local network. The species richness NTE on the contrary responds positive to network
 352 dam density.

353 For macro-invertebrates response is only present for slope weighed measures and gradually increasing
 354 from local to larger network measures of dam density, a strong response of the trait-based metrics of
 355 multivoltinism and ovoviviparity is observed. Shannon diversity shows a same response but less
 356 pronounced for the network, whereas the ASPT sensitive taxa only show a response to the network
 357 dam density.

359 Table 4: Spearman correlation values for the fish and invertebrate metrics and multi-metric index with
 360 the dam stressor indicators (N=179 for fish, N=211 for macro-invertebrates). See Table 2 and 3 for
 361 variable labels.* Significant correlations $p < 0.05$.

Community	Metrics	Local				Regional network			Upstream
		<i>dam#</i>	<i>dam#_L</i>	<i>dam#_{LS}</i>	<i>NearDdam</i>	<i>IIC_dam#_L</i> <i>vois5</i>	<i>IIC_dam#_{LS}</i> <i>vois5</i>	<i>IIC_dam#_{LS}</i> <i>vois10</i>	<i>CumulDdam</i>
Fish	IPR	-0,08	-0,12	-0,14	0,10	-0,19*	-0,21*	-0,15*	-0,11
	NTE	0,03	0	0,05	0,07	0,05	0,15*	0,15*	0,19*
	NER	-0,12	-0,16*	-0,21*	0,04	-0,26*	-0,26*	-0,24*	-0,22*
	NEL	-0,11	-0,15*	-0,2*	0,17	-0,24*	-0,29*	-0,27*	-0,27*
	DIT	0,01	0	0,04	0,04	0,01	0,00	0,05	0,01
	DII	-0,13	-0,14	-0,07	-0,01	-0,17*	0,10	-0,01	0,07
	DIO	-0,18*	-0,19*	-0,15*	0,03	-0,16*	-0,02	0,07	0,05
Macro invertebrate	I2M2	0,02	-0,01	-0,09	0,03	-0,01	-0,28*	-0,37*	-0,38*
	Polyv.	0,01	0,01	-0,15*	0,01	0,01	-0,40*	-0,43*	-0,45*
	Ovov.	-0,02	-0,02	-0,19*	0,06	-0,02	-0,37*	-0,50*	-0,60*
	Shan.	-0,08	-0,09	-0,17*	0,07	-0,09	-0,20*	-0,24*	-0,13
	ASPT	0,07	0,06	-0,04	0,01	0,06	-0,25*	-0,38*	-0,38*
	TAX	0,08	0,03	0,08	-0,02	0,03	0,09	0,02	0,04

362

363 3.2 Disentangling disconnection and habitat degradation effect

364

365 The respective weight of effects of disconnection and impoundment to overall dam impact can be
 366 discerned from the measured biological responses for the different predictor variables.

367

368 First, the difference in response to the slope weighed and non-weighed dam density measures
 369 (*Ddam#_{LS}* and *Ddam#_L* respectively) can reveal impoundment impact. For fish the aspect of
 370 disconnection plays a major role, as both for the local and network context the non-weighed and

371 weighed measures showed the same response. For macro-invertebrates the absence of a response to the
372 non-weighted dam density indicates the prevailing impoundment habitat degradation effect.

373

374 Second from specific indicators for habitat alteration: the alteration risk of bed substrate and structure
375 and alteration risk to flow regime (hydrodynamics). Especially the trait-based metrics for fish showed
376 different responses to the specific indicators for habitat alteration. The density of invertivorous (DII)
377 and tolerant (DIT) species at the local scale only respond to hydrodynamics (Spearman R 0.29 and
378 0.19 respectively), whereas the density of omnivorous species (DIO) only responds to disconnection
379 impact (same response to both dam density indicators). For the bed structure the rheophilic and
380 lithophilic species metric responded the most significantly (NER: R 0.27 and NEL: R 0.31). NER and
381 NEL respond strongly to both disconnection and habitat degradation.

382

383 For the macro-invertebrates the trait-based metrics of ovoviviparity and multivoltinism also show
384 significant responses both to disconnection as local habitat degradation: for bed structure R -0.31 and -
385 0.23 respectively, for hydrodynamics only the ovoviviparity correlates R -0.23. At the local scale,
386 habitat degradation effect dominates, whereas in general the contact with the upstream network is
387 crucial and dominates strongly the community structure and diversity.

388

389 **3.3 Fish versus macro-invertebrate response**

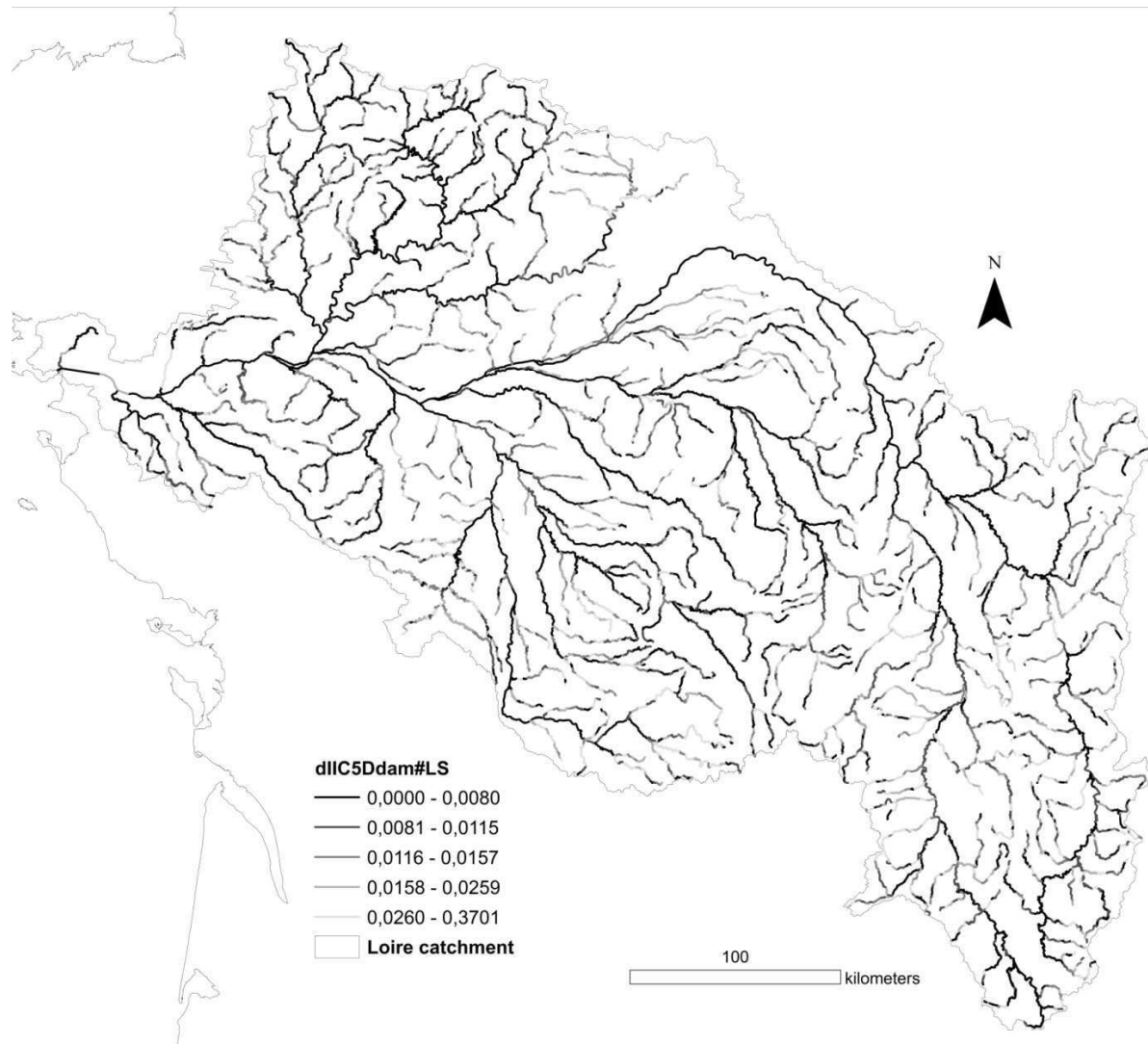
390

391 The regression for the strongest explaining fish metrics of NER and NEL with the slope weighed dam
392 density ($D_{dam\#_{LS}}$) at the three scale levels showed explained variances in the communities of 12 and
393 9%. The integrated local network indicator (IIC, Fig. 3) was the strongest significant overall descriptor
394 for this regression (Wilk's lambda 0.92, F 6.72, p 0.0015).

395 Yet, the partitioning of the explained variance showed that for the fish response, the explained fraction
396 is much larger for local $D_{dam\#_{LS}}$ (68% for NER and 61% for NEL), whereas the local network
397 $D_{dam\#_{LS}}$ explained respectively 25 and 33% for NER and NEL, and the upstream network
398 $D_{dam\#_{LS}}$ only accounts for less than 5% of the response (Fig. 4).

399

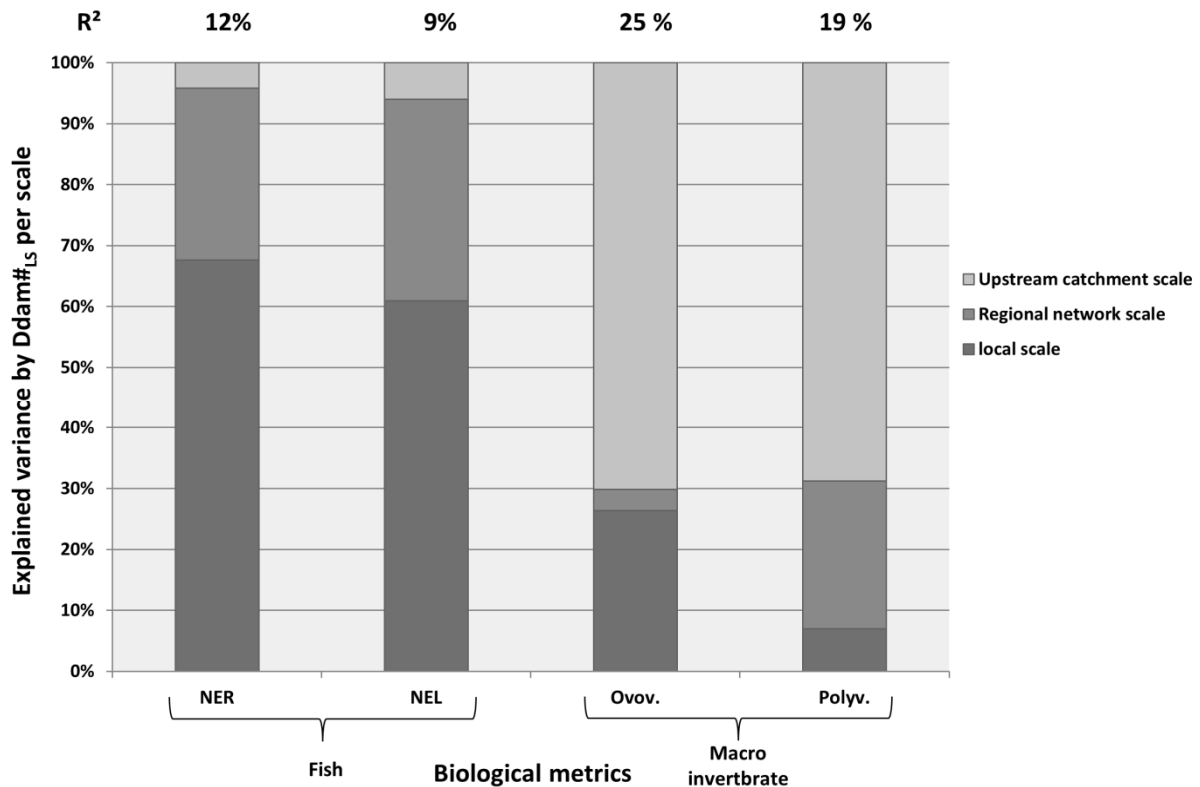
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Figure 3. The diIC values of each Loire Basin river segment, calculated with topological distance 5 and slope weighed dam density ($Ddam\#_{LS}$), show the best connected local networks, least impacted by damming. Higher index values occur when local networks show low dam densities and high connectivity (river network branch density).

Stronger results are observed for invertebrate metrics, with a higher explained variance for the trait-based metrics of multivoltinism (19%) and ovoviviparity (25%) and here the upstream dam density ($\text{cumulu}Ddam\#_{LS}$) is by far the strongest significant descriptor (Wilk's lambda 0.99, $F 47.29$, $p < 0.0001$). The $\text{cumulu}Ddam\#_{LS}$ measure on its own explained 70% of the response to dam density and nearly 18% of the total variance observed for the macroinvertebrate trait-based metrics.



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Figure 4. R² and explained variance by the slope weighed dam density (Ddam#_{LS}) per scale for NER and NEL fish metrics and ovoviviparity and multivoltinismmacroinvertebrate metrics from linear regression analyses. See Table 3 for metric labels.

422 3.4 Upstream-downstream responses

423

424 First observation for the correlations between the residuals and the geographic and geomorphic factors
 425 in Table 5 is that most of the fish residual responses are opposite to those for macro-invertebrates.

426 For the fish-based metrics the only significant correlation between geographical variables and the
 427 residuals is present with the altitude (R -0.18). This negative relationship with altitude reveals that the
 428 fish community response is the clearest in higher parts of the river basin. Or put the other way: in the
 429 plains the fish communities respond less clearly to damming and impoundment, most probably due to
 430 confounding presence of many other stressors. The NEL metric shows high values for bed structure,
 431 indicating its strong response to local bed substrate and profile.

432 The residuals for the invertebrate response to dam density show a significant correlation to altitude,
 433 slope and naturalness of the catchment; but this time a positive correlation. The response of the
 434 invertebrate communities is less clear upstream than downstream. Multivoltinism and ovoviviparity
 435 only respond downstream. The response of multivoltinism and ovoviviparity is different with respect
 436 to river strahler order; negatively correlated for multivoltinism and positively for ovoviviparity. So, the
 437 response of the multivoltinism metric is more pronounced in the larger rivers. Ovoviviparity in
 438 contrast, shows a clearer response for the small lowland streams.

439

440

441 Table 5: Spearman correlation ranking between the geographical and geomorphological variables and
 442 the residuals of the regressions of the trait-based metrics with the the slope weighed dam density
 443 measure (Ddam#_{LS}). See Table 1 and 3 for variable labels.

444

	Fish		Macro invertebrate	
	Residuals NER	Residuals NEL	Residuals Ovov.	Residuals Polyv.
Altitude	-0,18*	-0.16*	0,55*	0,42*
Strahlerorder	0,10	0.11	0,19*	-0,13*
River slope	-0,09	-0.10	0,30*	0,36*
Natural	-0,12	-0.08	0,40*	0,36*
Channel straightening	0,09	0.05	-0,03	0,01
Bed structure	-0.27*	-0.31*	0.31*	0.22*
Riparianforestcover	0.07	0.01	-0.01	0.07
Hydrodynamics	0.10	0.07	0.24*	0.16*

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449 4. Discussion

450

451 4.1 Strength of responses

452 Where we observe significant relationships between the biological metrics and dam density,
 453 nevertheless the presence of dams only explains a minor fraction of the variance observed for these
 454 metrics in our dataset. Reasons for this weak explicative power are in the first place the large scale
 455 data used in this analysis, with many sources of variance of both natural and human origin and a
 456 sampling that mostly avoided immediate dam influences, which hampers the investigation of direct
 457 causal relationships. Moreover, stations are retrieved from the national monitoring network which is
 458 not designed to evaluate dam presence. For that purpose a specific set of sampling sites should be
 459 established, with the distinction of dam functionalities and characteristics of dam height and
 460 impounded section. Second confusing element to the detection of dam impact is the presence of
 461 multiple stressors in the river basin, with water pollution undoubtedly as main cause of injury.

462

463 Nevertheless these low values of explained variance (R^2 max ~ 12% for fish and 25% for macro-
 464 invertebrates) for the stress response correspond to documented values for responses to alterations and
 465 human stressors in literature. In a similar analysis of Australian rivers based on macro-invertebrate
 466 data (Bush *et al.*, 2012), a stronger response was detected downstream (with 5.3% of the variance
 467 explained by human pressure) than upstream (with only 1.1% explained variance). The same values
 468 and conformity of macroinvertebrate response to human stressors restricted to the lower reaches was
 469 observed by Yuan (2010). Wang *et al.* (2011) show significant responses for both general biological
 470 integrity measures and for specific habitat indicators, with dam impact explaining 20% of the variance
 471 for the indicators in their data, as other co-varying aspects were detected both linked to size, hydro-
 472 regime and water quality stressors.

473

474 As in other studies of damming impact, no significant effect is evidenced in species diversity measures
 475 (Maynard and Lane, 2012). Yet, a significant decrease is observed for trait-based metrics that prove
 476 more relevant to identify specific stressors to aquatic communities (Brooks *et al.*, 2011; Wooster *et al.*,
 477 2012; Vaughn 2012). Conform to the hypotheses, specific responses of the functional metrics to the
 478 spatially explicit dam density measures allow distinguishing impact scales and effects (habitat
 479 degradation and disconnection). Both the hypotheses find partly positive answers in these observed
 480 relationships: network impact proves more important than local habitat impacts for the invertebrate

481 community, but not for the fish metrics. On the other hand disconnection impact prevails in fish
482 response whereas habitat degradation dominates the macroinvertebrate response. The hypothesis of the
483 scale-effect in disconnection impact with respect to mobility for respectively fish and invertebrates
484 does not appear as straightforward in the observations.
485

486 **4.2 Impact in the network**

487 The overall community response is more significant to dam density measured at the regional scale
488 level than for the individual reach. Our observations are for this aspect in agreement with the conclusion
489 of Musil and colleagues for fish communities (Musil *et al.*, 2012). In their analysis of 54 sites, fish
490 biotic indices responded strongest to an integrated measure for dam density with respect to the
491 distance to the site. In a similar study, Eros and colleagues showed that the larger the connected
492 network without obstacles, the higher the conservation value for fish populations (Eros *et al.*, 2011).
493 Wang *et al.* (2011) concluded for fish population integrity to be influenced by the dam density
494 downstream and upstream of a site. Here we observed this cumulative network impact for both fish
495 and invertebrate communities and we go a step further even in explaining this network aspect by
496 disentangling habitat degradation from connectivity aspects in the responses, and by linking specific
497 responses to the geographic context of upstream-downstream and mountainous-lowland setting.
498

499 Where for fish no differentiation of the effect is observed between upstream and downstream
500 accumulation (same response for IIC and upstream accumulation), for macroinvertebrates the
501 strongest response was clearly for upstream dam density. Where Cumming (2004) observed the
502 strongest impact on fish communities of downstream dam density and distance; here we observed
503 neither for fish nor for macroinvertebrates a significant effect for distance to the nearest downstream
504 dam. Yet, the absence of a fish response to the upstream basin context conforms to the statement of
505 Cumming, that for fish connections are either locally in both directions, or for migratory species the
506 downstream context is most relevant. As we did not distinguish the migratory species in our metrics,
507 no specific response to downstream connectivity is observed.
508

509 **4.3 Specific responses of biotic communities**

510 First observation is that general taxonomic richness and diversity indices do not respond to dam
511 density measures, neither for fish (NTE taxonomic richness and DTI taxonomic diversity), nor for
512 invertebrates (Shannon diversity and taxonomic richness). Same counts for multi-metric biotic
513 integrity indices, which are constructed to detect general degradations, yet are unable to identify
514 specific stressors or pressure gradients. As significant relationships are only present for specific trait-
515 based metrics and not for the global biotic integrity indices, this pleads for the application of specific
516 metrics, more than the generalized multi-metric indices. As dam alterations can both result in
517 increased metric values (f.i. for overall species number mostly) as degraded notes (for rheophilic
518 species), the multi-metric indices do not respond consistently to the impairments associated with
519 damming.
520

521 Based on these observed specific responses, selections of metric groups can be identified among the
522 trait-based metrics for specific questions (detecting alterations, follow-up of restoration,...). For the
523 expression of the local environment and habitat quality the trait-based metrics of NEL, DIT and DII
524 can be considered, whereas for connectivity aspects the metrics DIO and NER are most susceptible to
525 respond. The number of rheophilic species (NER) responds both to disconnection and local habitat
526 degradation, and the number of lithophilic species (NEL) shows a response to disconnection as well.
527 For macroinvertebrates the two trait-based metrics responded both to habitat degradation and
528 disconnection.
529

530 Where all above discussed responses are general, the observed specific relationships to the geographic
531 context are probably specific to the chosen dataset, and thus to the Loire River basin. A geographic
532 differentiation was present in both groups. For the fish community the response is the clearest in the
533 upstream parts of the basin. This geographic distinction is also observed in other fish studies and

534 accredited to a trade-off between contact and diversity and furthermore to the absence of interference
535 with others stressors upstream (Hitt and Angermeier, 2008).

536

537 The macroinvertebrate communities reflect more clearly the dam impacts in the lower parts of the
538 basin. For the downstream invertebrate communities more mass effects are at play, and the
539 relationship with the perturbations is clearest for the abundances and especially for the dominance
540 of eurytopic, multivoltine and ovoviviparous species. The response of the multivoltinism metric is more
541 pronounced in the larger rivers as this trait of multivoltinism detects best the mass effects. Whereas the
542 ovoviviparity in contrast shows a clearer response for the little lowland streams, as it is a metric that is
543 most sensible to habitat degradation. This differentiation shows the conformity for these responses to
544 findings for riverine ecosystem structuring (Brown and Swan, 2010) referring to the metacommunity
545 mechanisms (Leibold *et al.*, 2004), with downstream more mass effect relationships and regional
546 forces dominating, whereas in more upstream parts community assemblage is more driven by species
547 sorting mechanisms due to varying environmental conditions.

548

549 **4.4 Conclusions and recommendations**

550 Our analysis over the Loire Basin confirms that the impact of dams on the biotic communities is
551 stronger at the regional than just at the local scale. With the functional trait metrics and the spatially
552 explicit dam density measures the impact scales and effects of habitat degradation and disconnection
553 could be discerned.

554 To management strategies and restoration options we can conclude that for upstream reaches the local
555 habitat quality prevails and local restoration measures or dam removal can be successful. For
556 downstream sections on the other hand, the presence of multiple stressors and the dominance of mass
557 effects in biotic communities, imposes to look to the broader context and spatial scale. Restoration
558 efforts will fail if we do not evaluate the need for contact between restoration site and regional pools,
559 particularly for the restoration of communities that rely on the continual flux of individuals to and
560 from regional dispersal pools like the invertebrates (Palmer *et al.*, 1997, Spaenhoff and Arle, 2007).
561 Local restoration efforts have moreover proven insufficient in lowland rivers with multiple stressors
562 (Jaehnig *et al.*, 2010; Stranko *et al.*, 2012). So, for downstream sections focus must be on connectivity
563 and more comprehensive approaches to restoration on larger watershed scales are needed.

564

565

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