1

2

River impoundments cause little change in fish boreal diversity, but clear species assemblage shifts

5

6

7 Katrine Turgeon*[1], Christian Turpin[2] & Irene Gregory-Eaves[1]

8

9 [1]Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, QC,

10 CANADA, H3A 1B1

11 [2]Hydro-Québec, Environment and Corporate Affairs, 75 René-Lévesque, Montréal, QC,

12 CANADA, H2Z 1A4

13

14 **Corresponding author**: katrine.turgeon@mail.mcgill.ca

Abstract

16   Hydroelectricity is often presented as a clean and renewable energy source, but river

17   impoundment, regulation and fragmentation caused by dams have been reported to have varying

18   effects on aquatic biodiversity and ecosystem functions. The effects of river impoundment on

19   fish are often difficult to isolate because of the presence of confounding factors such as stocking,

20   fishing, species introduction and other human activities. In our study, we examined changes in

21   littoral fish communities over 20 years, using a network of sites located in remote boreal

22   ecosystems (northern Québec, Canada) with minimal confounding pressures. We found little

23   evidence of divergent temporal trends in contemporary diversity metrics in reservoirs relative to

24   reference sites across three spatial scales (*i.e.,* sampling station, reservoir and hydroelectric

25   complex). Using β-diversity analyses, we detected a high degree of stability in fish composition

26   over time and space at the complex and reservoir scales. However, at the scale of the sampling

27   station, we observed higher rates of species turnover coincident with the time of reservoir filling

28   and shortly after. Likewise, species assemblage shifts that correlated with time since

29   impoundment were detectable only at the sampling station scale. Our work shows that examining

30   community data at different scales is key when trying to understand the anthropogenic impacts

31   on fish biodiversity, and in designing impact assessment studies. Overall, the isolated effect of

32   hydroelectricity production in these remote boreal ecosystems caused little change in fish

33   diversity but resulted in species assemblage shifts.

36

Introduction

One of the most important challenge we face as a society is the increased demand for energy worldwide (SEforALL 2016). In response to this demand, many large dams are currently in operation, or are being constructed in developing economies to provide hydroelectricity (Grill et al. 2015, Winemiller et al. 2016). Even though hydroelectricity is often presented as a relatively clean, and renewable energy source (Teodoru et al. 2012), the regulation of river flow and fragmentation caused by dams can impact ecosystem functions and biodiversity (Rosenberg et al. 2000, Renöfalt et al. 2010).

Dams constructed for hydroelectricity production usually transform large rivers and surrounding lakes into a large reservoir, or a series of reservoirs. This transformation shifts the ecosystem regime from a lotic to a lentic one, and can change the direction of some important physical, chemical and biological processes (Friedl and Wüest 2002, Haxton and Findlay 2009). Upstream of the dam, reservoirs can experience variation in water levels and in flow outside of their natural amplitudes (Kroger 1973; Zohary and Ostrovsky 2011). Downstream of the dam, seasonal and interannual streamflow magnitude and variability are generally reduced (Friedman et al. 1998, Graf 2006) but can also be increased (Cushman 1985). These alterations can influence the biodiversity, abundance, distribution and community structure of many taxa of the aquatic food web (*e.g.*, Nilsson and Berggren 2000, Furey et al. 2006, Vörösmarty et al. 2010).

The effects of dams and their management on fish species richness and diversity have been extensively studied, but divergent effects have been described. At regional and global scales, links between river fragmentation or regulation and the homogenization of fish communities have been reported (Poff et al. 2007, Villéger et al. 2011, Liermann et al. 2012). In

59 smaller scale studies, some authors found a decrease in richness/diversity in reservoirs and

60 regulated streams when compared to reference sites (examples from cross-sectional studies;

61 Reyes-Gavilán *et al.* 1996; Sá-Oliveira *et al.* 2015), some found lower richness/diversity after

62 impoundment when compared to before impoundment conditions (examples from longitudinal

63 studies; Pyron *et al.* 1998; Gehrke, Gilligan & Barwick 2002; Mérona, Vigouroux & Tejerina-

64 Garro 2005; Lima *et al.* 2016), and many have found no difference (see meta-analysis from Liew

65 et al. 2016, see Guenther and Spacie 2006 and Irz et al. 2006 for cross-sectional examples, and

66 Martinez et al. 1994 for a longitudinal example).

67   Although the presence and direction of change in fish richness/diversity across smaller

68 scale studies are divergent, a shift in fish assemblages was observed in the majority of the

69 studies. The direction and magnitude of the change in fish assemblages depend on a series of

70 mechanisms. The main suggested mechanisms are: 1) barriers to movement caused by dams,

71 which detrimentally affect migratory fish (Martinez et al. 1994, Gehrke et al. 2002, Guenther and

72 Spacie 2006), 2) drastic changes in habitat, from lotic to lentic conditions, favoring facultative

73 riverine and opportunistic species in reservoirs (Nelson and Walburg 1977, Rodriguez Ruiz

74 1998, Penczak and Kruk 2005, Affonso et al. 2015), 3) alterations in flow and water levels (*e.g.,*

75 drawdown) that can affect temperature regimes and water quality (Ward and Stanford 1983,

76 1995, Kruk and Penczak 2003, Sutela and Vehanen 2008), and finally 4) introductions of

77 invasive and exotic species in reservoirs that can modify trophic interactions in the food web

78 (Johnson et al. 2008, Pelicice and Agostinho 2008, Clavero and Hermoso 2010).

79   Clearly, earlier works have provided valuable information about the effects of

80 hydroelectricity production on fish communities, but the lack of consensus across studies

81 impedes the development of strong conclusions regarding the effects of hydroelectrical facilities

82   on fish communities. Furthermore, very few studies have adequate information on fish

83   communities as many do not span both before and after impoundment, nor extend over a long

84   period (*i.e.*, after the trophic surge, Grimard and Jones 1982, Turgeon et al. 2016). Likewise,

85   comparable data from reference sites are often lacking. Isolating the effects of hydroelectricity

86   production from other confounding factors such as land use changes, stocking and the

87   introduction of invasive species is also often hard, if not impossible in some systems (Cumming

88   2004). Finally, the ecoregion, and associated physico-chemical and biological conditions of

89   impounded rivers and reservoirs can strongly affect the response in fish communities (Rosenberg

90   et al. 1997, Vörösmarty et al. 2010).

91   In this study, we examined changes in fish diversity and species assemblages in a long-

92   term dataset collected by Hydro-Québec for the La Grande hydroelectric complex and for the

93   Sainte-Marguerite complex. The time series for each complex span from before the construction

94   to 10 or 20 years after the start of its operation. This dataset provides us with a rare opportunity

95   to isolate the effect of impoundment on fish communities because confounding factors were

96   minimal. Moreover, no fish stocking program was implemented and there are no known invasive

97   species. A second strength of the dataset is that the large network of sampling stations ranging

98   from upstream to downstream stations of different habitats as well as reference sites allows for a

99   thorough evaluation of the impact associated with an hydroelectricity project. We analysed data

100   from a total of 27 sampling stations distributed across 4 reservoirs from two complexes. Finally,

101   the extensive temporal nature of the dataset allows us to quantify long-term changes in fish

102   communities in large boreal reservoirs.

Methods

Study sites

La Grande complex - The La Grande Rivière mega-hydroelectric complex (hereafter called the LG complex) is located on the eastern side of James Bay (Québec, Canada), and the whole region is situated on the Canadian Shield. The LG complex resulted in the creation of several large reservoirs (Table 1, Fig. 1) and in the diversion of three main rivers, the Caniapiscau (water flow at its mouth reduced by 45%), the Eastmain (water flow at its mouth reduced by 90%) and the Opinaca. Through these substantial hydrological inputs, the average annual flow in La Grande Rivière has increased from approximately 1700 $m^3 \cdot s^{-1}$ to 3400 $m^3 \cdot s^{-1}$, and its mean winter flow is 8 to 10 times higher than before. At the onset of the hydroelectricity project, the territory was free of any industrial activity and sparsely occupied by native Cree so confounding factors were minimal.

The construction of the complex was carried out in two phases. In Phase I (1973-1985), three power stations were built along La Grande Rivière and each has a reservoir (Robert-Bourassa, La Grande 3 and La Grande 4; Fig. 1). The oldest reservoir is Robert-Bourassa (formerly known as La Grande 2) and was impounded in November 1978. To increase flows in the La Grande Rivière for hydroelectricity production, three rivers were partially diverted. The Eastmain and Opinaca rivers were cut off in 1980 to create the Opinaca reservoir. The reservoir Opinaca was impounded in April 1980 and flows into Robert-Bourassa reservoir via the Boyd-Sakami diversion. To the east, the northward-flowing Caniapiscau River was cut off in October 1981 to create Caniapiscau reservoir. Caniapiscau reservoir is the largest in the complex, which drains into LG4 reservoir via the Laforge diversion and regulate the inter-annual flow in the La

125   Grande Rivière. In Phase II (1987-1996), one new reservoir was created (Laforge I; Fig. 1), and

126   five additional power stations were constructed along the river (La Grande 1, La Grande 2A,

127   Laforge I, Laforge II and Brisay), increasing the average annual flow to 4400 $m^3 \cdot s^{-1}$.

128   In the LG complex, water in reservoirs is naturally highly transparent, well oxygenated,

129   slightly acidic (pH 5.9 to 6.9), with low mineral content (specific conductivity 8 to 30 µS/cm)

130   and poor in nutrients (0.004 to 0.01 $mg \cdot L^{-1}$ total P). In this study, we focused on three reservoirs

131   in the LG complex: the Robert-Bourassa, the Opinaca and the Caniapiscau reservoirs (Table 1,

132   Fig. 1). Each of the three reservoirs of the LG complex was paired with a reference site (*i.e.*, a

133   natural lake in proximity to the reservoir; represented by stations starting with "REF" in the

134   figures; Fig. 1). In Robert-Bourassa reservoir, fish community data were collected in one station

135   downstream of the dam ("DO"; Fig. 1) and in six stations upstream of the dam (three were rivers

136   or streams before being a reservoir ("UR") and three were lakes ("UL"; Fig. 1). This distinction

137   is important because we expected that UR stations would demonstrate a more pronounced

138   change in diversity and fish assemblages than UL stations because of the distinct change in

139   habitat. For the Opinaca reservoir, data were collected from two downstream stations and four

140   upstream stations (two UR and two UL). For Caniapiscau, data were collected from one

141   downstream station and six upstream stations (six UL; Table 1, Fig. 1).

142   *Sainte-Marguerite complex* - The Sainte-Marguerite complex (SM) is located on the

143   Moyenne-Côte Nord portion of the Canadian Shield (Eastern Québec, Canada), on the north

144   shore of the Saint Lawrence estuary in Quebec (Fig. 1). The Sainte-Marguerite 3 dam (SM3) and

145   reservoir were under construction from 1994 to 2001. SM3 was impounded in April 1998 and

146   took 4 years to fill (1998 to 2002). The reservoir SM2 was created in 1954 and is not managed

147   by Hydro-Québec. The Sainte-Marguerite watershed is relatively free of anthropogenic

7

148   perturbation. Fish community data were collected in two stations upstream of the SM3 dam (two

149   UR), in one station in SM2 reservoir that is downstream of SM3 (one UR), and one reference site

150   station (Table 1, Fig. 1).

151   **Field sampling**

152   In Robert-Bourassa and Opinaca reservoirs, littoral fish communities were sampled

153   annually from 1978 to 1984, and then in the years 1988, 1992, 1996 and 2000. In Robert-

154   Bourassa, the pre-impoundment period corresponds to data collected in 1978 whereas in Opinaca

155   this period corresponds to the years 1978 and 1979. In Caniapiscau reservoir, fish communities

156   were sampled annually from 1980 to 1982, and in the years 1987, 1991, 1993, 1997 and 1999. In

157   Caniapiscau, pre-impoundment data correspond to the years 1980-1981. For the three reservoirs,

158   sampling occurred monthly from June to September-October, with a total of five sampling times

159   per season in the Robert-Bourassa and Opinaca reservoirs, and four times per season in

160   Caniapiscau until 1995. After 1995, the fishing protocol was optimized to concentrate the

161   sampling effort in July and August (Deslandes and Fortin 1994). To obtain comparable data from

162   1978 to 2000, only data available for the months of July and August were used in this study.

163   Sampling was performed using four multifilament gill nets 45.7 m in length x 2.4 m in depth, set

164   in pairs. Each net pair consisted of a piece of 7.6 cm stretched mesh attached to an experimental

165   gill net (where mesh sizes ranged between 2.5 to 10.2 cm). One pair of nets was set

166   perpendicular to the shore and the other pair was set near the shore (within 5 m from the shore).

167   Each sampling period lasted 48 h until 1982 and 24 h from 1983 and on. When the effort lasted

168   48 h, the nets were nevertheless visited every 24 h. The fish caught were counted, measured and

169   weighed. In SM3 and SM2, the fish community was sampled in 1992, 1996, 2005 and 2011. In

170   SM complex, pre-impoundment data correspond to the years 1992 and 1996.Sampling was

8

171 performed using the same nets as in LG complex. No seine net or minnow traps were used in this

172 sampling program. Thus, the dataset likely underestimates the presence and abundance of small

173 species from the littoral area. Likewise, there is the potential that abundance and prevalence of

174 pelagic species were underestimated because no gill nets were set in the pelagic zone. Despite

175 these caveats, a long-term and consistent sampling program was established.

176 Starting in 1978, changes in water quality in the photic zone (0 - 10 m) were monitored at

177 the same sampling stations in LG complex. Water quality variables measured were water

178 temperature, water transparency (measured as secchi depth), dissolved oxygen concentration, pH

179 and specific conductivity (all measured with an Hydrolab multiprobe). Details of the

180 methodology used in the collection and analysis of these data were presented by Fréchette

181 (1980).

182 **Statistical analyses**

183 *Contemporary diversity metrics*

184 Diversity was assessed with extrapolated species richness, Pielou's J Evenness index, and

185 Shannon's H′ diversity index to describe different aspects of community diversity (Purvis and

186 Hector 2000). The extrapolated species richness represents the number of species for a given

187 standardized number of net lifts per sampling station in July and August. This metric can be

188 based on either the chao, jackknife, second-order jackknife (Jack2) or bootstrap richness

189 estimators and computed with the function specpool in the vegan R package v. 2.4-1 (Oksanen et

190 al. 2016). We found that richness estimators were strongly correlated (mean $\pm$ SD r^2 = 0.89 $\pm$

191 0.07; range = 0.77 to 0.98) and thus decided to focus on the Jack2 metric because this method is

192 amongst the most recommended nonparametric resampling measures (Brose et al. 2003).

9

193   Shannon's H′ diversity index ($H' = -\sum_{i=1}^{R} p_i \ln p_i$) takes evenness and species richness into

194   account and quantifies the uncertainty in predicting the species identity of an individual that is

195   taken at random from the dataset and where p_i is the proportion of individuals belonging to the ith

196   species in the dataset. Pielou's J′ Evenness index ($J' = \frac{H'}{\ln S}$) ranges from near 0 (indicating

197   pronounced dominance) to near 1 (indicating an almost equal abundance of all species) and H′ is

198   the Shannon's H′ diversity index where S is the total number of species.

199   To assess if river impoundment influences contemporary diversity metrics, we used

200   General Linear Mixed Effects Models (glmm; applying the lme function in nlme package v. 3.1-

201   128) to examine changes in diversity metrics over time in impacted stations in relation to

202   reference sites. Here, we were interested in the slope of the relationship (testing if it was

203   significantly different from zero) and whether the regression slope of impacted stations differed

204   from that of reference sites (*i.e.,* focusing on the interaction term between time since

205   impoundment [TSI] and impacted vs. reference sites [RI] denoted as [TSI*RI], Table 2). We

206   examined the effect of river impoundment on contemporary diversity metrics at three spatial

207   scales: at the hydroelectric complex scale (pooling data from impacted sampling stations across

208   the three La Grande reservoirs and comparing it to the data pooled from three reference sites), at

209   the reservoir scale (pooling data from all impacted sampling stations for a given reservoir and

210   comparing these results with the reservoir's reference site) and at the sampling station scale

211   (considering each sampling station of a given reservoir and comparing it with the reservoir's

212   reference site). To control for spatio-temporal dependence, we used a random factor where

213   sampling stations were nested within reservoirs: ~1 + TSI |STATION/RES (where RES stands

214   for reservoir identity). We also used an autoregressive correlation structure (corAR1) to control

215   for temporal autocorrelation in our glmms. We determined the autoregressive process in each

216   time series by plotting each time series and by observing the autocorrelation function (ACF) and

217   the partial autocorrelation function (PACF) on detrended data using an ARIMA (autoregressive

218   integrated moving average model) diagnostic (astsa package v. 1.3 in R; Stoffer 2014). For each

219   time series, errors were specified to follow an autoregressive process of degree 1 (*i.e.,* the

220   autocorrelation is highest between sequential years). Our glmms models with autocorrelated

221   structure did not perform better than those without based on AICc scores (Burnham and

222   Anderson 2002) and so we present below only the glmms without the autocorrelated structure.

223   ***Beta-diversity analysis***

224   To test the extent to which fish assemblages for a given "station-time" combination was

225   unique compared to the other ones (*i.e.*, species turnover rate), we computed LCBD indices

226   (Local Contributions to Beta Diversity; Legendre and De Cáceres 2013). LCBD values indicate

227   how unique is any fish composition observation relative to other comparable data by assessing its

228   contribution to the total variation in fish composition in space and/or time (Legendre and De

229   Cáceres 2013, Legendre and Gauthier 2014). To assess the total variation in fish composition, we

230   first computed the total sum of squares (SStotal) of the matrix of square-rooted dissimilarities by

231   summing the dissimilarities in the lower triangular matrix and dividing by the number of

232   observations, N. We then computed total beta diversity (BDTotal) by dividing SStotal by N–1

233   (Legendre and De Cáceres 2013, Legendre and Gauthier 2014). We measured LCBDs directly

234   from the dissimilarity matrix of all observations as the diagonal elements of the matrix

235   containing the centered dissimilarities, divided by SStotal (Legendre and De Cáceres 2013,

236   Legendre and Gauthier 2014). We computer LCBD at the complex level, evaluating the

237   uniqueness of all possible combinations station-time (including and excluding reference sites), at

238   the reservoir level (including and excluding reference sites) and at the sampling station level. At

239   the sampling station level, each station was evaluated separately, so the turnover rate was in

240   relation to time only.

241   To assess individual species' influences on beta diversity, we computed 'Species

242   Contributions to Beta Diversity' (SCBD indices) using a Hellinger distance measure (Legendre

243   and De Cáceres, 2013). SCBD allowed us to identify species that were important contributors to

244   spatial or/and temporal beta diversity. LCBD and SCBD indices were calculated using the

245   *beta.div* function (available at http://adn.biol.umontreal.ca/~numericalecology/FonctionsR/).

246   SCBD were also computed for each scale (complex, reservoir and sampling station).

247   ***RDA and variation partitioning***

248   The role of temporal, spatial, environmental and sampling variability as possible

249   predictors of fish species assemblages was investigated with redundancy analysis (RDA; vegan

250   R package v. 2.4-1; Oksanen *et al.* 2016). Specifically, time since impoundment [TSI], was

251   measured as years before or after impoundment, whereas spatial heterogeneity [SH] among

252   sampling stations or reservoirs was measured using the latitude and longitude of each sampling

253   station. Environmental variability among sites was measured using the following water quality

254   variables [WQV]: transparency, dissolved oxygen, pH, conductivity, temperature. Finally,

255   differences in fishing gear [G] among sampling stations or between years were also considered.

256   RDA is an extension of multiple regression for the analysis of multivariate response data and is

257   used to quantify the degree to which different predictors explain variation in the community data

258   (Borcard et al. 2011). We used the Hellinger-transformed abundance values of species as

259   response variables. To produce the most parsimonious model, we performed forward selection

260   using the double stopping criteria (ordiR2step function in the vegan R package v. 2.4-1), in

261   which new variables added to the model had to achieve a 0.05 α level and the cumulative

262   adjusted R^2 of the variable set could not exceed the adjusted R^2 of the full model (Blanchet et al.

263   2008). Because of a small sample size, these analyses were not possible in the SM complex.

264   We examined fish assemblages in LG complex using RDA at the three scales. Because of

265   multicollinearity among variables when using TSI and WQV simultaneously in the RDA, we ran

266   two separate sets of RDAs to understand the patterns and variation explained by both TSI and

267   WQV. Two RDAs were produced at the LG complex level (one including time since

268   impoundment and one including water quality variables), six RDAs at the reservoir level, and 46

269   at the sampling stations level.

270   We also conducted unbiased variation partitioning based on RDAs and adjusted R^2

271   (Peres-Neto et al. 2006) using the varpart function in the vegan package v. 2.4-1. We used the

272   forward selection procedure of Blanchet et al. (2008). The overall variation in species

273   assemblages can be divided into "fractions" attributable to different data matrices as well as

274   combinations of these explanatory matrices (*i.e.*, shared variation). Here, we use our four

275   matrices: time since impoundment [TSI], spatial heterogeneity [SH], water quality variables

276   [WQV] and fishing gear [G]. The total variation of species assemblages was decomposed into 15

277   fractions at the complex and reservoir levels and eight at the sampling station levels because the

278   [SH] matrix is irrelevant at the sampling station level.

279   **Results**

280   **Little change in fish diversity in response to impoundment over 20 years**

281   Overall, directional trends in extrapolated richness, diversity, or evenness during the first

282   20 years (in LG) or 10 years (in SM) following impoundment were weak, as in most cases the

283   95% confidence intervals for slope estimates overlapped with zero (Fig. 2, Table 2). Across all

284   scales (*i.e.*, complex, reservoir and sampling stations), and categories of impacted stations (U, D,

285   UR and UL), we did not detect significant differences in the diversity trends from impacted

286   stations compared to those observed from reference sites (Fig. 2, Tables 2-3, and Appendix S1:

287   Tables S1-S4). Likewise, temporal trends in extrapolated richness, diversity and evenness did not

288   differ across reservoirs (Table 3, Appendix S1: Tables S1-S4). Opinaca reservoir had an overall

289   higher richness and Saint-Marguerite 3 had an overall lower richness than Robert-Bourassa and

290   Caniapiscau reservoirs (Table 1).

291   For completeness, we also examined the temporal trends among the categories of

292   impacted stations to probe for variability. To do this, we excluded reference sites from the

293   analysis and examined the additive effects of TSI and categories of impacted stations instead of

294   their interaction. At the complex level, we did not detect a difference in trends for extrapolated

295   richness, diversity and evenness when impacted stations categories were combined (*i.e.*, only the

296   effect of TSI in the model; Appendix S1: Table S5). When station categories were added in the

297   model (categorized according to their position relative to the dam and original habitat type; D vs.

298   U or D, vs UR and UL), richness decreased significantly over time (Appendix S1: Table S5).

299   This trend was strongly driven by the unusually low richness values observed in 2000 in Robert-

300   Bourassa (which had lower fishing effort in this one year). When this data point was excluded

301   from the analysis, the trend in richness was not significant anymore. No significant temporal

302   trends were detected for diversity and evenness (Appendix S1: Table S5). Downstream stations

303   had consistently higher extrapolated richness than upstream stations, but did not differ in

304   diversity and evenness (Appendix S1: Table S5). At the reservoir level, we detected a significant

305   decreasing trend in diversity for the Robert-Bourassa reservoir across all categories of impacted

306   stations (Appendix S1: Table S6), but no significant trend in extrapolated richness, diversity and

307   evenness in Opinaca, Caniapiscau and Sainte-Marguerite (Appendix S1: Table S6). At the

308   reservoir level, we did not detect a consistent difference between downstream and upstream

309   stations for the three metrics, and across reservoirs (Appendix S1: Table S6).

310   The absence of a clear directional trend in contemporary diversity metrics was also

311   mirrored in the β-diversity results, which did not show clear patterns across space and time at

312   either the complexes (Fig. 3a, Appendix S2: Fig. S1) or reservoirs levels (Appendix S2: Fig. S2).

313   At these two levels, very few Local Contribution to Beta-Diversity (LCBD) values were

314   significant, and the highest LCBD values did not seem to relate to impoundment. Overall,

315   reference sites had LCBD values comparable to impacted stations (Fig. 3a and Appendix S2).

316   When β-diversity analyses were conducted at the sampling station level (*i.e.,* only comparing any

317   one site to itself through time), we found that some of the highest LCBD values were apparent in

318   upstream stations (and significant in some cases) during and shortly after filling, (Fig. 3b) which

319   shows a higher species turnover rate during this period at this scale.

Change in species assemblages following impoundment

321   At the complex and reservoirs scales, the spatial heterogeneity associated with the

322   sampling stations was the main driver structuring fish assemblages, and masked the effect of

323   impoundment (Fig. 4 a-b, Appendix S3: Figs. S1-S2). The effect of impoundment (measured as

324   time since impoundment; TSI) only became a dominant predictor at the scale of the sampling

325   station (Fig. 4c, Appendix S3: Figs. S3, Appendix S4: Tables S1-S2). Fishing gear explained

326   only a small independent fraction of the variation at all scales (Fig. 4).

327   At the scale of the LG complex, fish assemblages were structured spatially (SH), and to a

328   lesser extent by water quality variables (WQV) and time since impoundment (Fig. 4a and

329   Appendix S3: Fig. S1). Spatial heterogeneity explained 45% of the variation across all shared

330   fractions (25% explained by SH alone). Most of the variation shared with SH overlapped with

331   WQV (a total of 15%; Fig. 4a). This was corroborated by the RDAs, where SH explained 44% of

332   the variation (Appendix S3: Fig. S1a; 42% if we excluded reference sites) and TSI explained an

333   additional 4% (Appendix S3: Fig. S1a; 6% if we excluded reference sites). When we used WQV

334   instead of TSI in the RDA, SH still explained 45% of the variation (43% excluding reference

335   sites), and WQV explained less than 3% of additional variation (Appendix S3: Fig. S1b).

336   A similar pattern was observed at the scale of reservoirs (Fig. 4b and Appendix S3: Fig.

337   S2). From the variation partitioning analyses, SH explained the highest proportion of the

338   variation across reservoirs (mean total variation of 37%; Appendix S4: Table S1). From this, 2%

339   was shared with TSI and 21% with WQV (Fig. 4b and Appendix S4: Table S1). In RDAs, SH

340   also explained most of the variation in species assemblages with an average value of 30%

341   including or excluding reference sites (RB = 30%; OP = 36%; CA = 23%; Appendix S3: Fig. S2

342   a, c, e). TSI explained on average an additional 6% of the variation (RB = 7%, OP = 3%, CA =

343   7%; Appendix S3: Fig. S2 a, c, e), and this value increased to 11% if we excluded reference sites

344   (RB = 13%, OP = 76%, CA = 14%). When using WQV in the RDAs, variables explained less

345   than 5% of the variation, including or excluding reference sites (Appendix S3: Fig. S2 b, d, f).

346   At the scale of the sampling stations, most of the variation in fish assemblages was

347   explained by the shared effect of TSI and WQV (variation partitioning; Fig. 4c and Appendix S4:

348   Table S2). This suggests that fish responded in a large extent to changes in water quality

349   experienced during and after impoundment. In RDAs, TSI was also the main driver structuring

350 fish community (Fig. 4c, Appendix S4: Table S2), and the assemblages followed a consistent

351 trajectory over time in most impacted stations (see examples in Appendix S3: Fig. S3). In RDAs,

352 when using WQV, variables explained a similar, but always a lower proportion of the variation

353 than TSI (average for all impacted stations; TSI = 22%, WQ = 15%).

Species affected by impoundment

355   The effect of impoundment on species differed between upstream and downstream

356 stations, and among reservoirs (Fig. 5 and Appendix S5). In several upstream stations, we

357 observed a predominant pattern where the assemblage went from a catastomids-dominated

358 community (longnose sucker, *Catostomus catostomus* and white sucker, *C. commersonii*) toward

359 a pike-coregonid (northern pike, *Esox lucius*, whitefish *Coregonus clupeaformis* and cisco, *C.

360 artedi*) dominated community after impoundment (Appendix S3: Fig. S3). This pattern was not

361 observed in reference sites nor in downstream stations (Appendix S3: Fig. S3). Changes in

362 species assemblages in upstream stations seems to have occurred within the first 5-6 years of

363 impoundment (Appendix S3: Fig. S3).

364   Species contribution to beta-diversity (SCBD) calculated at the sampling station level

365 (which is the turnover rate of individual species across time; Fig. 5) corroborated RDAs at the

366 sampling station level (Appendix S3: Fig. S3). Robert-Bourassa and Opinaca reservoirs

367 experienced very similar assemblage changes in upstream stations but differed for downstream

368 and reference sites. In upstream stations of those two reservoirs, the white sucker (decrease), the

369 walleye (*Sander vitreus*, decrease), the whitefish (increase) and the northern pike (increase) were

370 the species with the higher turnover rate (Fig. 5a, b). In Robert-Bourassa, the turnover rate was

371 subtler in the downstream station (Fig. 5b), and the walleye (decreased) and the burbot (*Lota*

17

372   *lota,* increased) demonstrated high turnover rate in the reference site (Fig. 5a). In Opinaca, the

373   lake sturgeon (*Acipenser fulvescens*) generally decreased in downstream stations and there was

374   no clear change in species turnover rate in the reference site (Fig. 5b). In Caniapiscau, we

375   observed an increase in whitefish in most upstream stations, an increase in lake trout (*Salvelinus*

376   *namaycush*) in upstream and downstream stations and a decrease in suckers and northern pike in

377   upstream stations and downstream stations (Fig. 5c). In Sainte-Marguerite, the two suckers

378   species experienced high turnover rates in upstream stations (Fig. 5d). Whitefish increased in

379   abundance in both upstream and reference sites whereas pike declined in downstream sites (Fig.

380   5d).

381   **Discussion**

382   Equipped with fish assemblage data that were collected over a long period and across a

383   large spatial network from a boreal remote area, this study is unique in its ability to isolate the

384   effect of impoundment and flow regulation from other factors that often co-occur with

385   hydroelectricity projects. Using contemporary diversity metrics, our analyses showed that there

386   were few clear directional patterns in fish richness and diversity following impoundment.

387   However, we did detect changes in fish assemblages that are associated with impoundment at the

388   sampling stations scale. Fish assemblage shifts were largely masked when analyses were

389   conducted at the larger scales, highlighting the importance of a multi-scale approach to evaluate

390   the anthropogenic impacts on ecosystems. Interestingly, published studies on the impact of

391   hydroelectricity on boreal fishes are rare compared to temperate and tropical ones. Thus, this

392   study adds to the global evaluation of the effects of hydroelectricity production on fish.

393   **Heterogeneity in fish community responses to impoundment**

394   Given that there has been a range of fish community responses to impoundment described in

395   the literature – as highlighted in the introduction – we are at a point where we need to explore

396   why there is heterogeneity, and where the heterogeneity lies within and among studies. The use

397   of ecological filters could help to think about this mechanistically and critically. To succeed in

398   the presence of the different ecological filters brought about by hydroelectricity production, fish

399   species must possess appropriate life history traits, evolutionary strategies or adaptations.

400   The first filter is associated with river fragmentation and barrier to movement. Dams can

401   block migratory route of diadromous species (*i.e.*, fish that spend part of their lives in freshwater

402   and part in saltwater; Limburg and Waldman 2009), can alter seasonal instream migration of

403   potamodromous ones (*i.e.,* fish that migrates within freshwater bodies), and can limit ontogenetic

404   movements of some species. Many studies attributed local fish species losses to river

405   fragmentation and damming in tropical settings (Okada et al. 2005, Sá-Oliveira et al. 2015,

406   Pelicice et al. 2015, Lima et al. 2016), in temperate regions dominated by large rivers system

407   (Reyes-Gavilán et al. 1996, Gehrke et al. 2002) and in prairie streams (Galat et al. 1998).

408   However, the presence of dams in our systems were likely not a dominant filter as in other areas

409   because here native fishes are not diadromous (Appendix S6) and because many of the focal

410   dams were built on obstacles that were already impassable for fish (*i.e.,* high waterfall).

411   The second filter is related to the effects of river regulation and modification of the

412   hydrological regime on fish habitat quality. The newly-created lentic ecosystem upstream of the

413   dam represents a radical transformation to fish habitats, and can exert a suite of selective

414   pressures not experienced by fish during their evolutionary history. In tropical regions, fish

415   community have evolved predominantly in flowing waters and linear systems (Gomes and

416   Miranda 2001). Not surprisingly, many studies in tropical regions found a significant lost in

417   richness or diversity following impoundment (Martinez et al. 1994, de Mérona 2002, de Mérona

418   et al. 2005, Sá-Oliveira et al. 2015 p., Lima et al. 2016). Many fish species are extirpated from

419   tropical reservoirs because they lack morphological, behavioral characteristics, reproductive

420   strategy and plasticity to successfully occupy these new habitats (Gomes and Miranda 2001,

421   Agostinho et al. 2008, Lima et al. 2016). In non-tropical regions, different effects have been

422   reported and appear to depend in part of the focal habitat under consideration (upstream or

423   downstream of the dam) and the water management of the site. For example, the slow increase in

424   water levels and new lentic conditions favored opportunistic and detritivore species in a Spanish

425   reservoir (Rodriguez Ruiz 1998). However, high drawdown reservoirs in Finland have less

426   benthivorous fish species (Sutela and Vehanen 2008). Downstream of dams in the U.S., Mims

427   and Olden (2013) found that equilibrium species (*i.e.,* a group of fish that do well in a more

428   stable, predictable environments) were favored at the detriment of opportunistic species. Species

429   responses downstream of a dam may also be dependent of flow regimes. For example, a decline

430   in discharge strongly affected changes in fish assemblages in the Canadian River (USA),

431   especially during the spawning season (Bonner and Wilde 2000). Relative to tropical systems,

432   boreal fish assemblages have a larger breadth of life-history trait strategies (Erős et al. 2012) and

433   are well adapted to both river and lake environments. This may partly explain why we did not

434   observe significant losses in richness or diversity in our system relative to reference ecosystems,

435   but rather a change in species assemblages. Walleye relative abundance decreased in some

436   stations but this species is at the limits of its northern distribution in LG and the general decrease

437   in summer water temperatures following impoundment might have affected its abundance

438   (Therrien et al. 2002). The rapid decrease in white suckers might also be the result of a

439   redistribution of the population to seek warmer temperatures (Doyon and Belzile 1998). Overall,

20

440   an average of 72% of the variation was unexplained regarding species assemblage from RDAs

441   and variation partitioning analyses at the sampling station level (see Fig. 4). This unexplained

442   variation may be related to rapid loss or gain of adequate spawning ground and preferred habitat

443   for some species resulting from a lotic to a lentic regime and to the strength of trophic

444   interactions among species that were building over time.

445   The third filter is related to the replacement of extirpated native species by non-native species

446   and changes in trophic interactions in the food web (Taylor et al. 2001, Clavero and Hermoso

447   2010, Liew et al. 2016). This filter can explain the absence of a directional trend in richness or

448   diversity, and even an increase in richness in some studies. The introduction of non-native and

449   invasive species in reservoirs (*i.e.*, high propagule pressure in reservoirs; Havel et al. 2005) can

450   promote a shift from native-dominated fish communities to invasive-dominated ones because the

451   establishment of non-native fishes has been facilitated by the new lentic habitats created

452   upstream of the dam, by the damped variability in streamflow downstream of the dam and, in

453   certain regions, by the low biotic resistance of the evolving fish community (Rodriguez Ruiz

454   1998, Johnson et al. 2008, Clavero and Hermoso 2010). Ichthyological regions and river basins

455   where endemic species are abundant might be particularly vulnerable (Dudgeon et al. 2006,

456   Lévêque et al. 2008). In some extreme cases, the introduction of a voracious non-native predator

457   (peacock-bass; *Cichla kelberi*) in Rosana reservoir (Paraná river basin), decreased fish richness

458   by 80% after three years, and caused the elimination of small-sized species (Pelicice and

459   Agostinho 2008). The creation of lentic habitats often increases the densities of piscivorous

460   fishes (Taylor et al. 2001, Gido et al. 2009, Franssen and Tobler 2013) which can be detrimental

461   for prey populations. In our system, no invasive or non-native species has been observed, and no

462   endemic species are present in the LG and SM complexes. However, the increase in northern

463   pike in many stations might be the result of predation on suckers.

464   The time needed to detect a significant change in fish assemblages will depend on the

465   dominant mechanisms affecting the stability of the food web in reservoirs, and on the temporal

466   resolution of the dataset. If the dominant mechanisms responsible for changes in fish

467   assemblages are related to reproduction and recruitment through the strength of year classes, the

468   effect may take many years to be detectable. Species with some specific life history traits (*e.g.*,

469   late age at first reproduction), or positioned at higher trophic levels may have delayed response

470   to impoundment. If the dominant mechanisms affecting fish community are through adult fish

471   movement and redistribution due to river fragmentation and change in habitat quality, the change

472   can be detectable quickly. Time needed to detect a change in fish community is highly variable

473   among studies, as it has been reported to be either quick (*i.e.,* within 5 years after impoundment

474   (Martinez et al. 1994)) or more subtle and thus requiring data that span 30 years after

475   impoundment (Quinn and Kwak 2003). In our study, the assemblages changed quickly and seem

476   to have reach an equilibrium after 5-6 years. This suggest that movement and habitat selection

477   might be driving some processes responsible for change fish assemblages in boreal reservoirs.

478   Some community states or phases (*i.e.*, dominant species in the community) can also be

479   transient. For instance, Kubečka (1993) and Říha et al. (2009) documented a five-phase

480   succession in fish species with European reservoirs aging. Fish assemblage changed successively

481   from a riverine species phase (before impoundment and shortly after), to a pike phase (*Esox*

482   *lucius*), followed by a perch phase (*Perca fluviatilis*), and then a rapid and transient perch-

483   cyprinid phase, to a final and highly stable cyprinid dominated phase. Our ability to detect

484   change in assemblages will also depend on the sampling strategy and resolution (ever year vs.

22

485   every 5 years), where some subtle changes can be missed or not captured if the time between

486   sampling events is long.

Importance of using a multi-scale approach

488   In long-term studies, it may be difficult to separate the effects of impoundment from

489   effects due to change in land use and climate change on fish community. However, with careful

490   planning and financial investment into a sound sampling design (considering what to measure

491   and where, at which scale and for how long) one can elucidate underlying biological processes

492   and mechanisms. Earlier ecological works have shown that great insights are achieved when

493   multiple spatial and temporal scales are considered because patterns observed in communities at

494   a given scale are often the consequence of a complex interplay between various processes

495   occurring at multiple scales (Wiens 1989, Whittaker et al. 2001, Mander et al. 2005, Dray et al.

496   2012). Accordingly, changes in species assemblages can result from richness difference or

497   "nestedness" (one community may include a larger number of species than another) or from

498   species replacement or species turnover (species tend to replace each other along ecological

499   gradients; Baselga 2010, Carvalho et al. 2012). In this study, change in fish assemblages in

500   response to impoundment (*i.e.,* species replacement) were only detectable at the sampling station

501   scale. At the complex and reservoirs scales, we captured richness difference where the variation

502   in species assemblages was likely due to species thinning and other large scale ecological

503   processes.

504   Certainly scale matters, but having different types of stations (upstream and downstream),

505   reference sites, and time series covering before and after impoundment periods are equally

506   important considerations. The impacts of impoundment and river regulation on fish were

23

507 different in upstream (from a lotic to lentic habitat, barrier to migration) and downstream stations

508 (reduced flow and water level fluctuations). We found an overall higher species richness in

509 downstream stations, a tendency (but not a significant trend) for a stronger impact in upstream

510 stations that were rivers before being reservoir sites, and a relatively consistent pattern in

511 upstream stations over time whereby the community shifted from one dominated by catastomids

512 to a pike and coregonids dominated systems. For this reason, data must be collected on both

513 types of stations to get a complete story. Because the impacts of river impoundment and

514 regulation on upstream and downstream stations are different, "space for time substitution"

515 designs (where downstream stations are used as an index of the fish community that were found

516 before impoundment) are not ideal and should be avoided. Furthermore, seasonal and punctual

517 climatic events (*e.g.,* strong summer storm, cold or very dry year) that are unrelated to the

518 hydroelectricity project can misrepresent the long-term average. As such, fish assemblage data

519 collected over a long period (> 5 years) need to be collected in reference sites as well.

520 Comparing reservoirs to only reference lakes or only rivers might be inadequate to evaluate how

521 fish communities differ across sites because reservoirs are neither a lake nor a river. Irz et al.

522 (2006) compared reservoir fish communities with those in rivers and lakes and found that

523 reservoir communities are more similar to lake communities than river communities, but this is

524 only one study. Finally, time series should cover the period before and after impoundment,

525 preferably lasting long enough to cover the non-equilibrium trophic surge and reach the new

526 ecosystem equilibrium (Grimard and Jones 1982, Turgeon et al. 2016).

527 **General conclusions and recommendations**

528   In this study, using a network of sites located in a remote boreal ecosystem with minimal

529 confounding pressures, we provided strong empirical evidence that the creation of large

24

530   hydroelectric complexes did not resulted in a loss of fish species nor change in diversity, but

531   resulted in a shift in fish assemblages. Both large lakes and large rivers are common in Canadian

532   boreal regions (Messager et al. 2016), and might explain why the evolutionary young fish species

533   found in this region are especially well adapted and resilient to river impoundment. Reservoirs

534   created for hydroelectricity production are now dominant features of the landscape, and they will

535   become even more dominant in the coming years, especially in tropical regions (Zarfl et al. 2014,

536   Grill et al. 2015, Winemiller et al. 2016). Identifying which ecological filters related to

537   impoundment and river flow regulation affect species, evaluating the strength of their effects,

538   and how they vary across regions might help us to assist in implementing mitigation measures to

539   minimize biodiversity loss and even revert the loss of some species, if species are only locally

540   lost. Our work also highlights that contemporary diversity and richness indices are not sensitive

541   enough to detect species replacement, which was common in the impounded rivers considered.

542   Instead, metrics that consider changes in fish community assemblages at a fine scale (like our

543   study), as well as those that evaluate the status of native populations, particularly for rare and

544   endemic species are more appropriate. Given the strength of our multi-scale approach in

545   providing a complete perspective on the scale at which river impoundment affect fish

546   community, we caution against large scale extrapolations and correlation studies that may

547   underestimate or mask the anthropogenic effects on aquatic ecosystems.

548   **Acknowledgments**

552   (Hydro-Québec) and Chris Solomon (Cary Institute, NY) for helpful suggestions and comments

553   on this manuscript.

554   **Literature Cited**

555   Affonso, I. de P., L. C. Gomes, A. A. Agostinho, H. J. Message, J. D. Latini, and E. García-

556   Berthou. 2015. Interacting effects of spatial gradients and fishing gears on characterization of

557   fish assemblages in large reservoirs. Reviews in Fish Biology and Fisheries:1–11.

558   Agostinho, A. A., F. M. Pelicice, and L. C. Gomes. 2008. Dams and the fish fauna of the

559   Neotropical region: impacts and management related to diversity and fisheries. Brazilian

560   Journal of Biology 68:1119–1132.

561   Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global

562   Ecology and Biogeography 19:134–143.

563   Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Forward selection of explanatory variables.

564   Ecology 89:2623–2632.

565   Bonner, T. H., and G. R. Wilde. 2000. Changes in the Canadian River Fish Assemblage

566   Associated with Reservoir Construction. Journal of Freshwater Ecology 15:189–198.

567   Borcard, D., F. Gillet, and P. Legendre. 2011. Canonical Ordination. Pages 153–225 Numerical

568   Ecology with R. Springer New York.

569   Brose, U., N. D. Martinez, and R. J. Williams. 2003. Estimating Species Richness: Sensitivity to

570   Sample Coverage and Insensitivity to Spatial Patterns. Ecology 84:2364–2377.

571   Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A

572   practical information-theoretic approach. Second edition. Springer-Verlag, New York.

573   Carvalho, J. C., P. Cardoso, and P. Gomes. 2012. Determining the relative roles of species

574   replacement and species richness differences in generating beta-diversity patterns. Global

575   Ecology and Biogeography 21:760–771.

576   Clavero, M., and V. Hermoso. 2010. Reservoirs promote the taxonomic homogenization of fish

577   communities within river basins. Biodiversity and Conservation 20:41–57.

578   Cumming, G. S. 2004. The impact of low-head dams on fish species richness in wisconsin, usa.

579   Ecological Applications 14:1495–1506.

580   Cushman, R. M. 1985. Review of Ecological Effects of Rapidly Varying Flows Downstream

581   from Hydroelectric Facilities. North American Journal of Fisheries Management 5:330–339.

582   Deslandes, J.-C., and R. Fortin. 1994. Optimisation du réseau de suivi environnemental des

583   populations de poissons des milieux affectés par l'aménagement du complexe La Grande

584   (Phase I).

585   Doyon, J.-F., and L. Belzile. 1998. Réseau de suivi environnemental du complexe La Grande

586   (1977-1996). Suivi des communautés de poissons et étude spéciale sur le doré (secteur ouest

587   du territoire). Page 145 p. + annexes.

588   Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, R.

589   Bivand, F. G. Blanchet, M. De Cáceres, A.-B. Dufour, E. Heegaard, T. Jombart, F. Munoz, J.

590   Oksanen, J. Thioulouse, and H. H. Wagner. 2012. Community ecology in the age of

591   multivariate multiscale spatial analysis. Ecological Monographs 82:257–275.

592   Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J.

593   Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006.

594   Freshwater biodiversity: importance, threats, status and conservation challenges. Biological

595   Reviews 81:163–182.

596   Erős, T., J. D. Olden, R. S. Schick, D. Schmera, and M.-J. Fortin. 2012. Characterizing

597   connectivity relationships in freshwaters using patch-based graphs. Landscape Ecology

598   27:303–317.

599   Franssen, N. R., and M. Tobler. 2013. Upstream effects of a reservoir on fish assemblages

600   45 years following impoundment. Journal of Fish Biology 82:1659–1670.

601   Fréchette, J.-L. 1980. Réseau surveillance écologique. Vol. 1. Société d'énergie de la Baie

602   James. Environnement.

603   Friedl, G., and A. Wüest. 2002. Disrupting biogeochemical cycles - Consequences of damming.

604   Aquatic Sciences 64:55–65.

605   Friedman, W. R. Osterkamp, M. L. Scott, and G. T. Auble. 1998. Downstream effects of dams

606   on channel geometry and bottomland vegetation: Regional patterns in the great plains.

607   Wetlands 18:619–633.

608   Furey, P. C., R. N. Nordin, and A. Mazumder. 2006. Littoral benthic macroinvertebrates under

609   contrasting drawdown in a reservoir and a natural lake. Journal of the North American

610   Benthological Society 25:19–31.

611   Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, G. T.

612   Gelwicks, J. E. Havel, D. L. Helmers, J. B. Hooker, J. R. Jones, M. F. Knowlton, J. Kubisiak,

613   J. Mazourek, A. C. McColpin, R. B. Renken, and R. D. Semlitsch. 1998. Flooding to Restore

614   Connectivity of Regulated, Large-River Wetlands. BioScience 48:721–733.

615   Gehrke, P. C., D. M. Gilligan, and M. Barwick. 2002. Changes in fish communities of the

616   Shoalhaven River 20 years after construction of Tallowa Dam, Australia. River Research and

617   Applications 18:265–286.

618   Gido, K. B., J. F. Schaefer, and J. A. Falke. 2009. Convergence of fish communities from the

619   littoral zone of reservoirs. Freshwater Biology 54:1163–1177.

620   Gomes, L. c., and L. e. Miranda. 2001. Riverine characteristics dictate composition of fish

621   assemblages and limit fisheries in reservoirs of the upper Paraná River basin. Regulated

622   Rivers: Research & Management 17:67–76.

623   Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American

624   rivers. Geomorphology 79:336–360.

625   Grill, G., B. Lehner, A. E. Lumsdon, G. K. MacDonald, C. Zarfl, and C. R. Liermann. 2015. An

626   index-based framework for assessing patterns and trends in river fragmentation and flow

627   regulation by global dams at multiple scales. Environmental Research Letters 10:015001.

628   Grimard, Y., and H. G. Jones. 1982. Trophic Upsurge in New Reservoirs: A Model for Total

629   Phosphorus Concentrations. Canadian Journal of Fisheries and Aquatic Sciences 39:1473–

630   1483.

631   Guenther, C. B., and A. Spacie. 2006. Changes in Fish Assemblage Structure Upstream of

632   Impoundments within the Upper Wabash River Basin, Indiana. Transactions of the American

633   Fisheries Society 135:570–583.

634   Havel, J. E., C. E. Lee, and J. M. V. Zanden. 2005. Do Reservoirs Facilitate Invasions into

635   Landscapes? BioScience 55:518–525.

636   Haxton, T. J., and C. S. Findlay. 2009. Variation in large-bodied fish-community structure and

637   abundance in relation to water-management regime in a large regulated river. Journal of Fish

638   Biology 74:2216–2238.

639   Irz, P., M. Odion, C. Argillier, and D. Pont. 2006. Comparison between the fish communities of

640   lakes, reservoirs and rivers: can natural systems help define the ecological potential of

641   reservoirs? Aquatic Sciences 68:109–116.

642   Johnson, P. T., J. D. Olden, and M. J. Vander Zanden. 2008. Dam invaders: impoundments

643   facilitate biological invasions into freshwaters. Frontiers in Ecology and the Environment

644   6:357–363.

645   Kroger, R. L. 1973. Biological Effects of Fluctuating Water Levels in the Snake River, Grand

646   Teton National Park, Wyoming. American Midland Naturalist 89:478–481.

647   Kruk, A., and T. Penczak. 2003. Impoundment impact on populations of facultative riverine fish.

648   Annales de Limnologie - International Journal of Limnology 39:197–210.

649   Kubečka, J. 1993. Succession of fish communities in reservoirs of Central and Eastern Europe.

650   Pages 153–168 *in* M. Straškraba, J. G. Tundisi, and A. Duncan, editors. Comparative

651   Reservoir Limnology and Water Quality Management. Springer Netherlands.

652   Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data:

653   dissimilarity coefficients and partitioning. Ecology Letters 16:951–963.

654   Legendre, P., and O. Gauthier. 2014. Statistical methods for temporal and space–time analysis of

655   community composition data. Proceedings of the Royal Society of London B: Biological

656   Sciences 281:20132728.

657   Lévêque, C., T. Oberdorff, D. Paugy, M. L. J. Stiassny, and P. A. Tedesco. 2008. Global

658   diversity of fish (Pisces) in freshwater. Hydrobiologia 595:545–567.

659   Liermann, C. R., C. Nilsson, J. Robertson, and R. Y. Ng. 2012. Implications of Dam Obstruction

660   for Global Freshwater Fish Diversity. BioScience 62:539–548.

661 Liew, J. H., H. H. Tan, and D. C. J. Yeo. 2016. Dammed rivers: impoundments facilitate fish

662   invasions. Freshwater Biology 61:1421–1429.

663 Lima, A. C., C. S. Agostinho, D. Sayanda, F. M. Pelicice, A. M. V. M. Soares, and K. A.

664   Monaghan. 2016. The rise and fall of fish diversity in a neotropical river after impoundment.

665   Hydrobiologia 763:207–221.

666 Limburg, K. E., and J. R. Waldman. 2009. Dramatic Declines in North Atlantic Diadromous

667   Fishes. BioScience 59:955–965.

668 Mander, Ü., F. Müller, and T. Wrbka. 2005. Functional and structural landscape indicators:

669   Upscaling and downscaling problems. Ecological Indicators 5:267–272.

670 Martinez, P. J., T. E. Chart, M. A. Trammell, J. G. Wullschleger, and E. P. Bergersen. 1994. Fish

671   species composition before and after construction of a main stem reservoir on the White

672   River, Colorado. Environmental Biology of Fishes 40:227–239.

673 de Mérona, B. 2002. Dynamique des peuplements de poissons dans le réservoir de Petit-Saut

674   (Fleuve Sinnamary, Guyane Française). Bulletin Français de la Pêche et de la Pisciculture:5–

675   22.

676 de Mérona, B. de, R. Vigouroux, and F. L. Tejerina-Garro. 2005. Alteration of Fish Diversity

677   Downstream from Petit-Saut Dam in French Guiana. Implication of Ecological Strategies of

678   Fish Species. Hydrobiologia 551:33–47.

679 Messager, M. L., B. Lehner, G. Grill, I. Nedeva, and O. Schmitt. 2016. Estimating the volume

680   and age of water stored in global lakes using a geo-statistical approach. Nature

681   Communications 7:13603.

682 Mims, M. C., and J. D. Olden. 2013. Fish assemblages respond to altered flow regimes via

683   ecological filtering of life history strategies. Freshwater Biology 58:50–62.

684   Nelson, W. R., and C. H. Walburg. 1977. Population Dynamics of Yellow Perch (*Perca*

685   *flavescens*), Sauger (*Stizostedion canadense*), and Walleye (*S. vitreum vitreum*) in Four Main

686   Stem Missouri River Reservoirs. Journal of the Fisheries Research Board of Canada

687   34:1748–1763.

688   Nilsson, C., and K. Berggren. 2000. Alterations of Riparian Ecosystems Caused by River

689   Regulation Dam operations have caused global-scale ecological changes in riparian

690   ecosystems. How to protect river environments and human needs of rivers remains one of the

691   most important questions of our time. BioScience 50:783–792.

692   Okada, E. K., A. A. Agostinho, and L. C. Gomes. 2005. Spatial and temporal gradients in

693   artisanal fisheries of a large Neotropical reservoir, the Itaipu Reservoir, Brazil. Canadian

694   Journal of Fisheries and Aquatic Sciences 62:714–724.

695   Oksanen, J., G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B.

696   O'Hara, G. L. Simpson, P. Solymos, H. H. Stevens, E. Szoecs, and H. Wagner. 2016. vegan:

697   Community Ecology Package. R package version 2.4-1.

698   Pelicice, F. M., and A. A. Agostinho. 2008. Fish fauna destruction after the introduction of a

699   non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biological Invasions

700   11:1789–1801.

701   Pelicice, F. M., P. S. Pompeu, and A. A. Agostinho. 2015. Large reservoirs as ecological barriers

702   to downstream movements of Neotropical migratory fish. Fish and Fisheries 16:697–715.

703   Penczak, T., and A. Kruk. 2005. Patternizing of impoundment impact (1985–2002) on fish

704   assemblages in a lowland river using the Kohonen algorithm. Journal of Applied Ichthyology

705   21:169–177.

706 Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation Partitioning of Species

707   Data Matrices: Estimation and Comparison of Fractions. Ecology 87:2614–2625.

708 Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river

709   dynamics by dams and global biodiversity implications. Proceedings of the National

710   Academy of Sciences 104:5732–5737.

711 Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. Nature 405:212–219.

712 Pyron, M., C. C. Vaughn, M. R. Winston, and J. Pigg. 1998. Fish Assemblage Structure from 20

713   Years of Collections in the Kiamichi River, Oklahoma. The Southwestern Naturalist 43:336–

714   343.

715 Quinn, J. W., and T. J. Kwak. 2003. Fish Assemblage Changes in an Ozark River after

716   Impoundment: A Long-Term Perspective. Transactions of the American Fisheries Society

717   132:110–119.

718 Renöfalt, B. M., R. Jansson, and C. Nilsson. 2010. Effects of hydropower generation and

719   opportunities for environmental flow management in Swedish riverine ecosystems:

720   Hydropower and environmental flow management. Freshwater Biology 55:49–67.

721 Reyes-Gavilán, F. G., R. Garrido, A. G. Nicieza, M. M. Toledo, and F. Braña. 1996. Fish

722   community variation along physical gradients in short streams of northern Spain and the

723   disruptive effect of dams. Hydrobiologia 321:155–163.

724 Říha, M., J. Kubečka, M. Vašek, J. Seda, T. Mrkvička, M. Prchalová, J. Matēna, M. Hladík, M.

725   Čech, V. Draštík, J. Frouzová, E. Hohausová, O. Jarolím, T. Jůza, M. Kratochvíl, J. Peterka,

726   and M. Tušer. 2009. Long-term development of fish populations in the Římov Reservoir.

727   Fisheries Management and Ecology 16:121–129.

728   Rodriguez Ruiz, A. 1998. Fish species composition before and after construction of a reservoir

729   on the Guadalete River (SW Spain). Archiv für Hydrobiologie 142:353–369.

730   Rosenberg, D. M., F. Berkes, R. A. Bodaly, R. E. Hecky, C. A. Kelly, and J. W. Rudd. 1997.

731   Large-scale impacts of hydroelectric development. Environmental Reviews 5:27–54.

732   Rosenberg, D. M., P. McCully, and C. M. Pringle. 2000. Global-Scale Environmental Effects of

733   Hydrological Alterations: Introduction. BioScience 50:746–751.

734   Sá-Oliveira, J. C., J. E. Hawes, V. J. Isaac-Nahum, and C. A. Peres. 2015. Upstream and

735   downstream responses of fish assemblages to an eastern Amazonian hydroelectric dam.

736   Freshwater Biology 60:2037–2050.

737   SEforALL. 2016. Sustainable energy for all. Strategic framework for results 2016-2021. Going

738   further, faster - Together.

739   Stoffer, D. 2014. astsa: Applied Statistical Time Series Analysis. R package version 1.3.

740   Sutela, T., and T. Vehanen. 2008. Effects of water-level regulation on the nearshore fish

741   community in boreal lakes. Hydrobiologia 613:13–20.

742   Taylor, C. A., J. H. Knouft, and T. M. Hiland. 2001. Consequences of stream impoundment on

743   fish communities in a small North American drainage. Regulated Rivers: Research &

744   Management 17:687–698.

745   Teodoru, C. R., J. Bastien, M.-C. Bonneville, P. A. del Giorgio, M. Demarty, M. Garneau, J.-F.

746   Hélie, L. Pelletier, Y. T. Prairie, N. T. Roulet, I. B. Strachan, and A. Tremblay. 2012. The net

747   carbon footprint of a newly created boreal hydroelectric reservoir. Global Biogeochemical

748   Cycles 26:GB2016.

749   Therrien, J., R. Verdon, and R. Lalumière. 2002. Suivi environnemental du complexe La Grande.

750   Évolution des communautés de poissons. Rapport synthèse 1977-2000. Page 131 p. et

751   annexes. Groupe conseil GENIVAR inc. et direction Barrages et Environnement, Hydro-

752   Québec Production.

753   Turgeon, K., C. T. Solomon, C. Nozais, and I. Gregory-Eaves. 2016. Do novel ecosystems

754   follow predictable trajectories? Testing the trophic surge hypothesis in reservoirs using fish.

755   Ecosphere 7: ecs2.1617.

756   Villéger, S., S. Blanchet, O. Beauchard, T. Oberdorff, and S. Brosse. 2011. Homogenization

757   patterns of the world's freshwater fish faunas. Proceedings of the National Academy of

758   Sciences 108:18003–18008.

759   Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S.

760   Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann, and P. M. Davies. 2010. Global threats

761   to human water security and river biodiversity. Nature 467:555–561.

762   Ward, J. V., and J. A. Stanford. 1983. The Serial Discontinuity Concept of River Ecosystems.

763   Page Dynamics of lotic ecosystems. In T.D. Fontaine, S. M. Bartell. Ann Arbor Science.

764   Ward, J. V., and J. A. Stanford. 1995. The serial discontinuity concept: Extending the model to

765   floodplain rivers. Regulated Rivers: Research & Management 10:159–168.

766   Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general,

767   hierarchical theory of species diversity. Journal of Biogeography 28:453–470.

768   Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology 3:385–397.

769   Winemiller, K. O., P. B. McIntyre, L. Castello, E. Fluet-Chouinard, T. Giarrizzo, S. Nam, I. G.

770   Baird, W. Darwall, N. K. Lujan, I. Harrison, M. L. J. Stiassny, R. a. M. Silvano, D. B.

771   Fitzgerald, F. M. Pelicice, A. A. Agostinho, L. C. Gomes, J. S. Albert, E. Baran, M. Petrere,

772   C. Zarfl, M. Mulligan, J. P. Sullivan, C. C. Arantes, L. M. Sousa, A. A. Koning, D. J.

773   Hoeinghaus, M. Sabaj, J. G. Lundberg, J. Armbruster, M. L. Thieme, P. Petry, J. Zuanon, G.

774   T. Vilara, J. Snoeks, C. Ou, W. Rainboth, C. S. Pavanelli, A. Akama, A. van Soesbergen, and

775   L. Sáenz. 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong.

776   Science 351:128–129.

777 Zarfl, C., A. E. Lumsdon, J. Berlekamp, L. Tydecks, and K. Tockner. 2014. A global boom in

778   hydropower dam construction. Aquatic Sciences 77:161–170.

779 Zohary, T., and I. Ostrovsky. 2011. Ecological impacts of excessive water level fluctuations in

780   stratified freshwater lakes. Inland Waters 1:47–59.

781

782   **Table 1.** Reservoirs characteristics in the La Grande hydroelectricity complex (Opinaca,

783   Robert-Bourassa and Caniapiscau) and in Sainte-Marguerite 3 reservoir. Reservoir area

784   represents the surface covered with water at maximum pool. The area flooded represents the

785   surface of terrestrial land flooded following impoundment and, in brackets, the percentage of

786   the reservoir that was terrestrial land before impoundment.

Variables	Reservoirs			
	Opinaca	Robert-Bourassa	Caniapiscau	Ste. Marguerite 3
Latitude	52°38′58″N	53°45′00″N	54°31′46″N	50°42′52″N
Longitude	76°19′54″W	77°00′00″W	69°51′18″W	66°46′54″W
Trophic status	Oligotrophic	Oligotrophic	Oligotrophic	Oligotrophic
Area (km^2)	1040	2835	4275	262
Area flooded (km^2)	740 (71%)	2630 (92%)	3430 (80%)	230.5 (88%)
Volume (km^3)	8.4	61.7	53.8	12.5
Year of impoundment	1980	1979	1982	1998
Filling time (y)	0.5	1	2	4
Residency time (days)	124	183	803	366
Mean depth (m)	8	22	12	22.4
Max depth (m)	51	137	49	145
Annual drawdown (m)	3.6	3.3	2.1	14
Watershed area (km^2)	30 000	97 643	36 800	9 000
Extrapolated richness	11.1 ± 3.7	9.9 ± 3.1	9.3 ± 2.7	7.5 ± 3.1
Diversity (H' Shannon)	1.53 ± 0.28	1.48 ± 0.27	1.40 ± 0.28	1.23 ± 0.38
Evenness (J' Pielou)	0.76 ± 0.13	0.78 ± 0.12	0.72 ± 0.13	0.87 ± 0.11

787

37

788 **Table 2**. Estimate ± Standard error (SE), 95% Confidence intervals (95% CI), t-values and Degrees of Freedom (DF) of model

789 parameters used to predict change in extrapolated richness (Double jackknife estimation method), diversity (Shannon's H') and

790 evenness (Pielou's J') in La Grande mega-hydroelectricity complex (3 reservoirs, 23 stations). General linear mixed effects models

791 were used to evaluate the effect of time since impoundment (TSI), stations types (Impacted stations vs. reference sites) and their

792 interaction on diversity metrics. Predictors that did not include 0 within their 95% CI (*i.e.*, statistically "significant") are in bold.

793 Reference sites are used as contrasts in the models.

Model parameter	Extrapolated richness		Diversity (Shannon's H')		Evenness (Pielou's J')	
	Estimate ± SE (95% CI)	t-value (DF)	Estimate ± SE (95% CI)	t-value (DF)	Estimate ± SE (95% CI)	t-value (DF)
All impacted stations combined						
Intercept	-0.073 ± 0.309 (-0.678 to 0.532)	-0.236 (171)	0.485 ± 0.248 (-0.001 to 0.972)	1.954 (171)	0.421 ± 0.292 (-0.151 to 0.993)	1.443 (171)
Time since impoundment (TSI)	0.042 ± 0.179 (-0.309 to 0.393)	0.233 (171)	-0.184 ± 0.218 (-0.610 to 0.243)	-0.844 (171)	-0.145 ± 0.191 (-0.520 to 0.231)	-0.755 (171)
Ref vs. Impacted (RI)	0.052 ± 0.331 (-0.596 to 0.701)	0.159 (21)	**-0.562 ± 0.266 (-1.085 to -0.040)**	**-2.111 (21)**	-0.505 ± 0.312 (-1.117 to 0.107)	-1.616 (21)
TSI*RI	-0.186 ± 0.194 (-0.566 to 0.193)	-0.962 (171)	0.108 ± 0.235 (-0.352 to 0.569)	0.461 (171)	0.206 ± 0.206 (-0.199 to 0.611)	0.998 (171)
Upstream (Up) and downstream (D) stations separately						
Intercept	-0.069 ± 0.270 (-0.598 to 0.461)	-0.254 (170)	0.480 ± 0.250 (-0.010 to 0.969)	1.920 (170)	0.424 ± 0.286 (-0.136 to 0.984)	1.483 (170)
TSI	0.036 ± 0.175 (-0.308 to 0.380)	0.207 (170)	-0.176 ± 0.227 (-0.620 to 0.269)	-0.776 (170)	-0.147 ± 0.190 (-0.518 to 0.225)	-0.775 (170)
Ref vs. D	0.592 ± 0.350 (-0.094 to 1.277)	1.692 (20)	-0.388 ± 0.323 (-1.020 to 0.244)	-1.203 (20)	**-0.778 ± 0.370 (-1.502 to -0.053)**	**-2.104 (20)**
Ref vs. Up	-0.098 ± 0.295 (-0.676 to 0.480)	-0.333 (20)	**-0.609 ± 0.273 (-1.144 to -0.074)**	**-2.233 (20)**	-0.432 ± 0.311 (-1.043 to 0.178)	-1.388 (20)
TSI*Ref. vs D	-0.309 ± 0.226 (-0.752 to 0.134)	-1.366 (170)	0.239 ± 0.295 (-0.339 to 0.817)	0.811 (170)	0.316 ± 0.244 (-0.163 to 0.794)	1.294 (170)

TSI*Ref. vs Up	-0.149 ± 0.194 (-0.530 to 0.232)	-0.767 (170)	0.055 ± 0.250 (-0.435 to 0.545)	0.220 (170)	0.177 ± 0.209 (-0.233 to 0.588)	0.848 (170)
Upstream river (UR), upstream lake (UL) and downstream (D) stations separately						
Intercept	-0.071 ± 0.271 (-0.603 to 0.461)	-0.261 (169)	0.488 ± 0.248 (0.003 to 0.974)	1.971 (169)	0.441 ± 0.247 (-0.044 to 0.926)	1.783 (169)
TSI	0.035 ± 0.178 (-0.312 to 0.383)	0.200 (169)	-0.192 ± 0.206 (-0.595 to 0.211)	-0.934 (169)	-0.164 ± 0.175 (-0.508 to 0.180)	-0.936 (169)
Ref vs. D	0.593 ± 0.351 (-0.095 to 1.282)	1.690 (19)	-0.401 ± 0.320 (-1.029 to 0.226)	-1.254 (19)	**-0.792 ± 0.319 (-1.418 to -0.167)**	**-2.484 (19)**
Ref vs. UL	-0.024 ± 0.308 (-0.628 to 0.580)	-0.078 (19)	**-0.654 ± 0.282 (-1.208 to -0.101)**	**-2.316 (19)**	**-0.655 ± 0.281 (-1.206 to -0.104)**	**-2.329 (19)**
Ref vs. UR	-0.233 ± 0.338 (-0.895 to 0.429)	-0.689 (19)	-0.544 ± 0.309 (-1.149 to 0.061)	-1.762 (19)	-0.044 ± 0.307 (-0.646 to 0.559)	-0.142 (19)
TSI*Ref. vs D	-0.309 ± 0.229 (-0.757 to 0.139)	-1.351 (169)	0.249 ± 0.267 (-0.274 to 0.773)	0.934 (169)	0.336 ± 0.226 (-0.108 to 0.779)	1.483 (169)
TSI*Ref. vs UL	-0.120 ± 0.206 (-0.524 to 0.284)	-0.581 (169)	0.233 ± 0.237 (-0.232 to 0.698)	0.981 (169)	0.311 ± 0.204 (-0.089 to 0.711)	1.524 (169)
TSI*Ref. vs UR	-0.202 ± 0.228 (-0.650 to 0.246)	-0.884 (169)	-0.244 ± 0.265 (-0.764 to 0.276)	-0.918 (169)	-0.030 ± 0.226 (-0.473 to 0.413)	-0.133 (169)

794 **Table 3**. Estimate ± Standard error (SE), 95% Confidence intervals (95% CI) and t-values of model parameters used to predict change

795 in extrapolated richness (Double jackknife estimation), diversity (Shannon-Weaver H') and evenness (Pielou J') in La Grande

796 complex reservoirs and Ste-Marguerite 3 reservoir. Generalized mixed effects models were used to evaluate the effect of time since

797 impoundment (Year), stations and their interaction on diversity metrics. Reference sites are used as contrasts.

Model parameter	Extrapolated richness		Diversity (H')		Evenness (J')	
	Estimate ± SE (95% CI)	t-value (DF)	Estimate ± SE (95% CI)	t-value (DF)	Estimate ± SE (95% CI)	t-value (DF)
Robert-Bourassa						
Intercept	-0.325 ± 0.500 (-1.305 to 0.655)	-0.650 (70)	0.380 ± 0.357 (-0.301 to 1.061)	1.066 (70)	0.609 ± 0.375 (-0.111 to 1.328)	1.622 (70)
TSI	-0.003 ± 0.270 (-0.531 to 0.526)	-0.011 (70)	-0.450 ± 0.245 (-0.929 to 0.032)	-1.835 (70)	-0.457 ± 0.254 (-0.955 to 0.041)	-1.798 (70)
Ref vs. Impacted (RI)	0.361 ± 0.535 (-0.689 to 1.410)	0.674 (6)	-0.430 ± 0.383 (-1.022 to 0.144)	-1.122 (6)	-0.683 ± 0.403 (-1.450 to 0.094)	-1.696 (6)
TSI*RI	-0.232 ± 0.296 (-0.812 to 0.348)	-0.784 (70)	0.099 ± 0.270 (-0.451 to 0.615)	0.365 (70)	0.351 ± 0.281 (-0.211 to 0.890)	1.250 (70)
Opinaca						
Intercept	0.058 ± 0.604 (-1.125 to 1.241)	0.096 (62)	0.539 ± 0.527 (-0.468 to 1.545)	1.023 (62)	0.362 ± 0.587 (-0.761 to 1.484)	0.616 (62)
TSI	0.011 ± 0.299 (-0.576 to 0.598)	0.037 (62)	-0.143 ± 0.293 (-0.716 to 0.430)	-0.490 (62)	0.022 ± 0.282 (-0.531 to 0.574)	0.076 (62)
Ref vs. Impacted (RI)	-0.061 ± 0.652 (-1.339 to 1.217)	-0.094 (5)	-0.628 ± 0.569 (-1.715 to 0.459)	-1.104 (5)	-0.431 ± 0.634 (-1.645 to 0.780)	-0.681 (5)
TSI*RI	-0.118 ± 0.323 (-0.751 to 0.515)	-0.366 (62)	0.200 ± 0.316 (-0.419 to 0.818)	0.632 (62)	0.156 ± 0.305 (-0.439 to 0.753)	0.511 (62)
Caniapiscau						
Intercept	-0.061 ± 0.514 (-1.068 to 0.945)	-0.120 (35)	0.346 ± 0.501 (-0.612 to 1.303)	0.690 (35)	0.214 ± 0.579 (-0.612 to 1.303)	0.369 (35)
TSI	0.559 ± 0.528 (-0.475 to 1.593)	1.060 (35)	0.532 ± 0.514 (-0.451 to 1.515)	1.034 (35)	0.347 ± 0.505 (-0.451 to 1.515)	0.688 (35)
Ref vs. Impacted (RI)	0.031 ± 0.538 (-1.024 to 1.086)	0.057 (6)	-0.410 ± 0.525 (-1.413 to 0.593)	-0.782 (6)	-0.244 ± 0.612 (-1.413 to 0.593)	-0.400 (6)

40

TSI*RI	-0.672 ± 0.552	-1.217	-0.376 ± 0.538	-0.700	-0.194 ± 0.529	-0.366
	(-1.753 to 0.410)	(35)	(-1.405 to 0.652)	(35)	(-1.405 to 0.652)	(35)
Ste-Marguerite 3						
Intercept	0.162 ± 0.659	0.876	-0.627 ± 0.585	-1.072	**-1.457 ± 0.398**	-3.660
	(-1.130 to 1.454)	(7)	(-1.676 to 0.422)	(7)	**(-2.164 to -0.751)**	(7)
TSI	-0.297 ± 0.569	0.117	0.063 ± 0.504	0.125	0.056 ± 0.343	0.164
	(-1.412 to 0.817)	(7)	(-0.840 to 0.967)	(7)	(-0.553 to 0.666)	(7)
Ref vs. Impacted (RI)	-0.199 ± 0.751	-0.979	0.785 ± 0.654	1.199	**1.863 ± 0.450**	4.144
	(-1.670 to 1.273)	(2)	(-0.388 to 1.957)	(2)	**(1.062 to 2.661)**	(2)
TSI*RI	0.302 ± 0.697	0.488	0.286 ± 0.598	0.478	-0.174 ± 0.411	-0.423
	(-1.063 to 1.667)	(7)	(-0.786 to 1.357)	(7)	(-0.905 to 0.557)	(7)
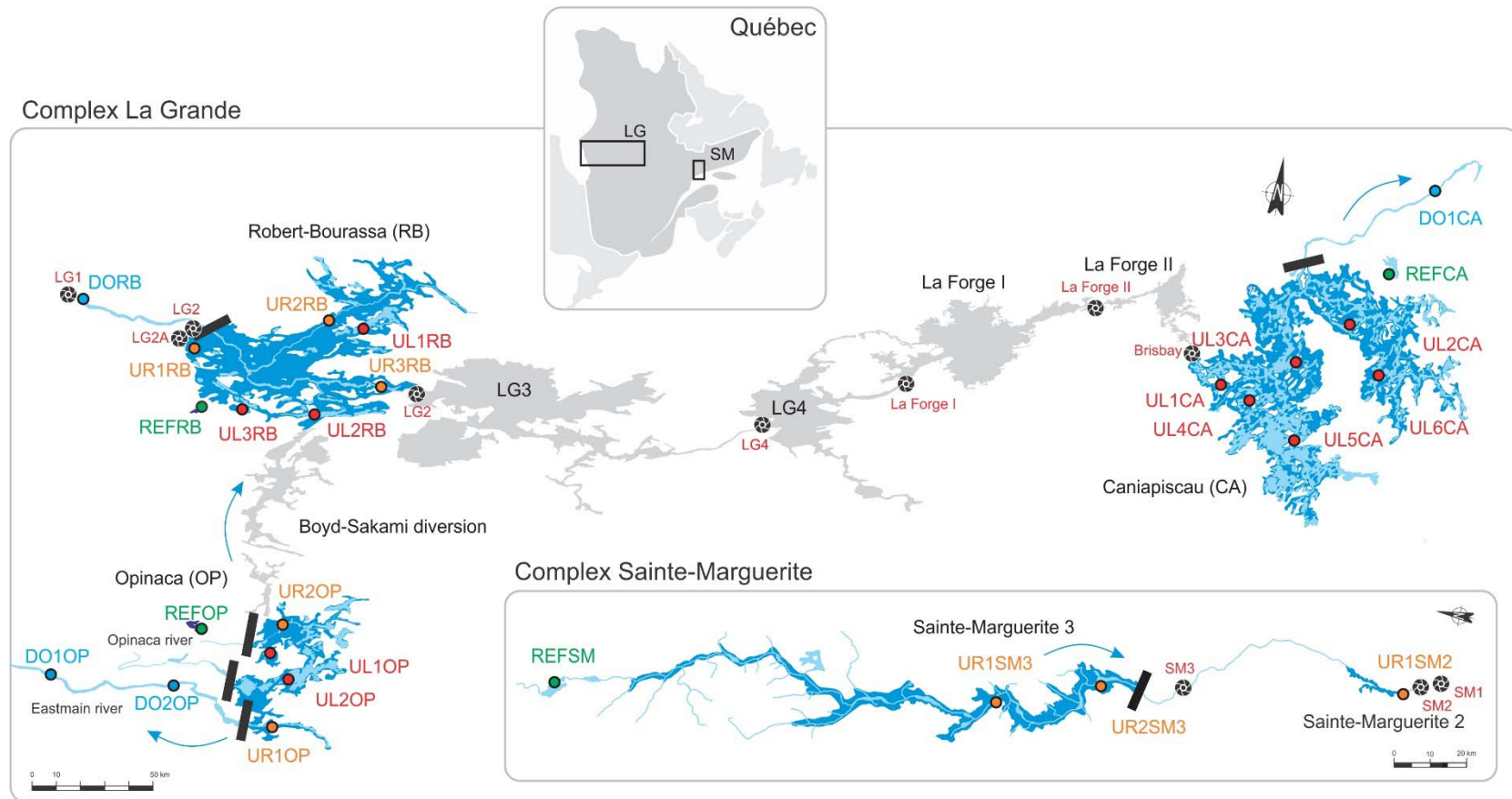
Figure 1. Map representing the before and after impoundment hydrology conditions and the location of the 23 sampling stations in the La Grande hydroelectricity complex (three reservoirs; Robert-Bourassa, Opinaca and Caniapiscau) and 4 sampling stations in Sainte-Marguerite complex, Northern Québec. Before impoundment hydrology conditions are in light blue and after impoundment conditions (reservoirs) are in dark blue. Stations located upstream of the dams that were in a river before impoundment are in orange, and the ones that were in lakes before impoundment are in red. Sampling stations that were located downstream of the dams are in blue, and reference sites paired with each reservoir are in green. Dams are represented by a black line and power station by a turbine symbol.
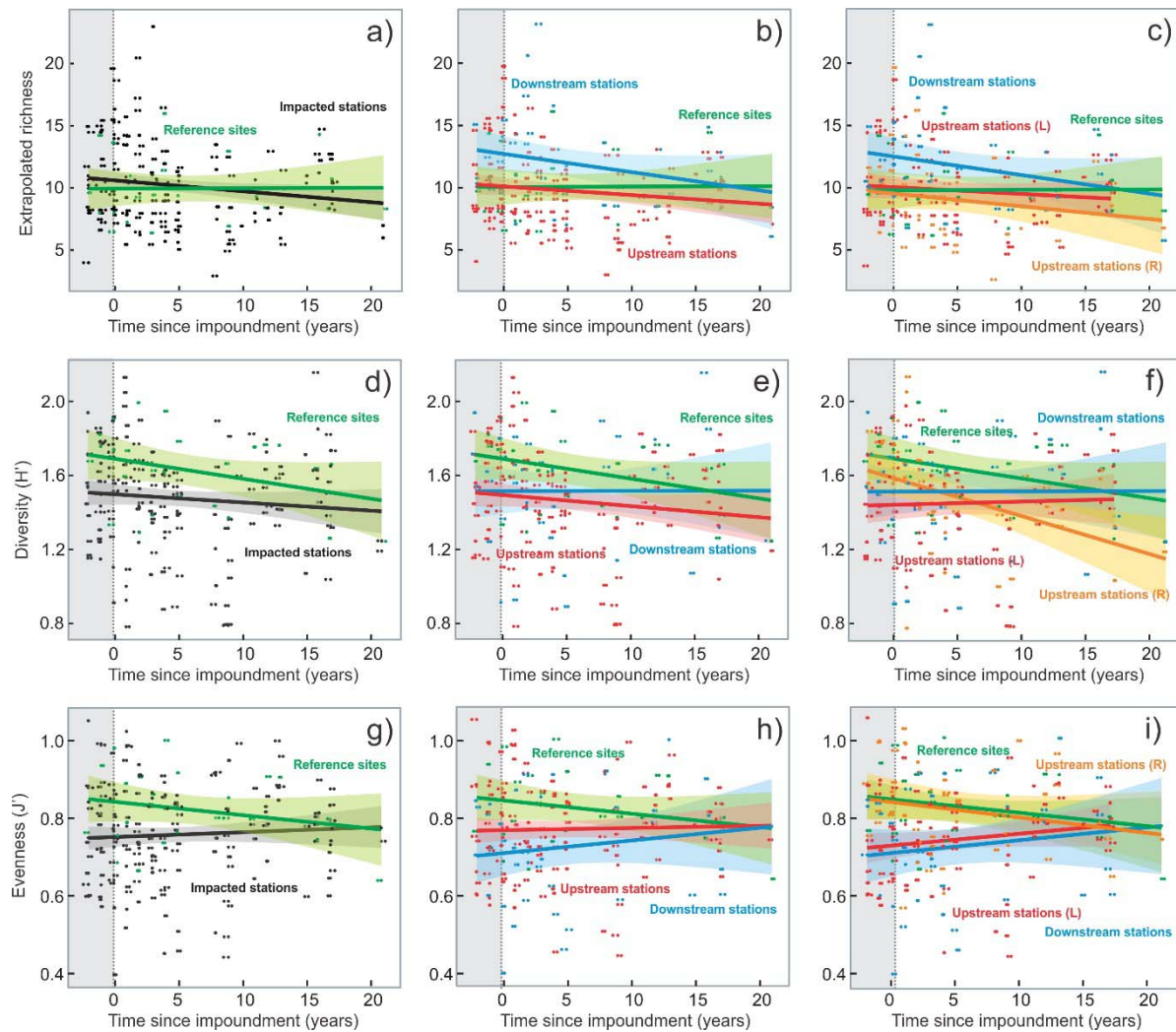
Figure 2. Variation in extrapolated richness, diversity (H' Shannon-Weiver index) and evenness (J' Pielou index) over time in impacted and reference stations at the LG complex level. Change in richness, diversity and evenness over time in references sites (green dots and lines) where compared with impacted stations (all impacted station types combined from the three reservoirs in a, d, g panels, with impacted stations upstream and downstream of the dams in b, e, h panels, and compared with upstream stations that were lakes before being a reservoir (UL) with upstream stations that were a river or a stream before being a reservoir (UR) in c, f, i panels.
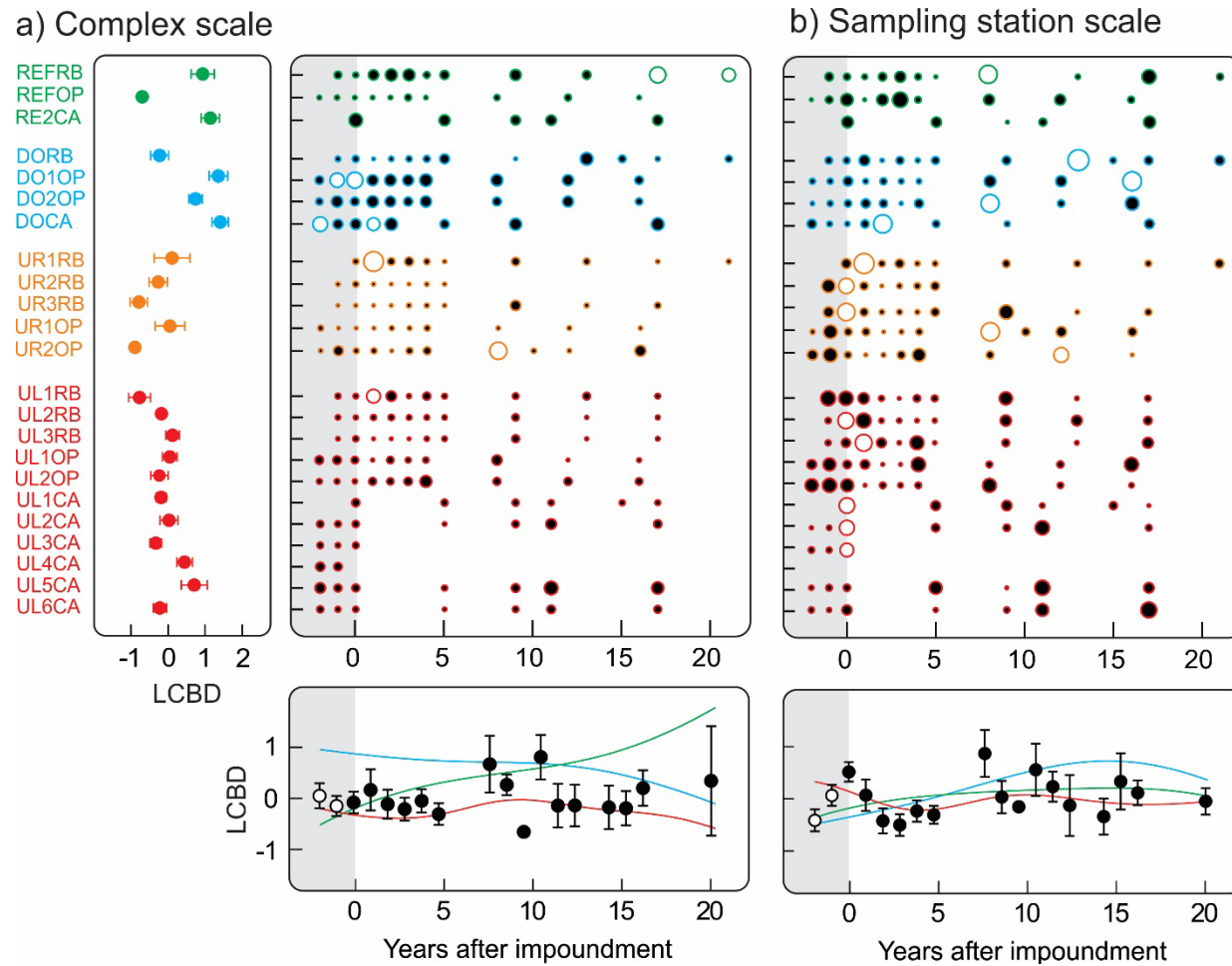
43

Figure 3. Local contribution to beta-diversity (LCBD) per station (24 stations) and year for beta-diversity analysis b) at the LG complex level and a) at the sampling station level. Circle surface areas are proportional to the LCBD values. Circles filled in white indicate significant LCBD indices at p<0.05. The lower panels represent mean values of LCBD per year. The right panel represents mean values of LCBD per station for the analysis at the complex level. Upstream stations are separated in two categories. Stations with a label starting with "UL" represent stations that were lakes before being a reservoir and the stations with a label starting with "UR" were rivers or stream before being a reservoir. Reference sites are labelled in green, downstream stations in blue and upstream stations in orange UR) and red (UL).
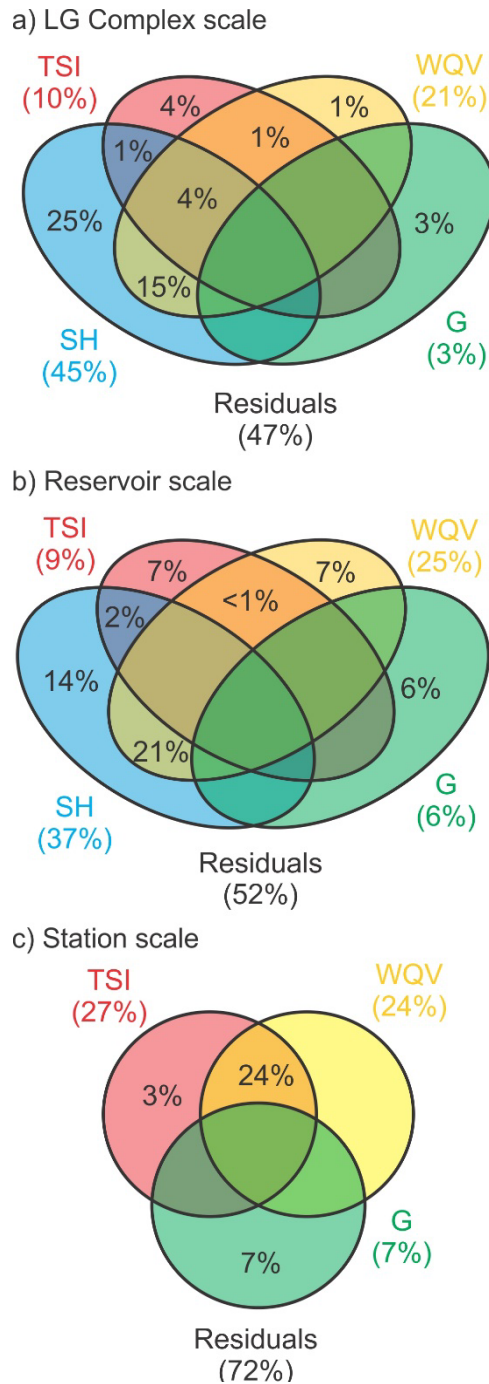
Figure 4. a) Variation partitioning analysis showing the contribution of four matrices (Time since impoundment [TSI], Spatial heterogeneity [SH], Water quality variables [WQ] and fishing gear [G]) to explained the variation in fish species assemblages at the a) LG complex level, b) at the reservoir level (the numbers are the average across reservoirs, see table B1 for the breakdown per reservoir), and c) at the sampling stations (the numbers are the average across sampling stations, see Appendix S4: table S2 for the breakdown per station). These analyses included reference sites.
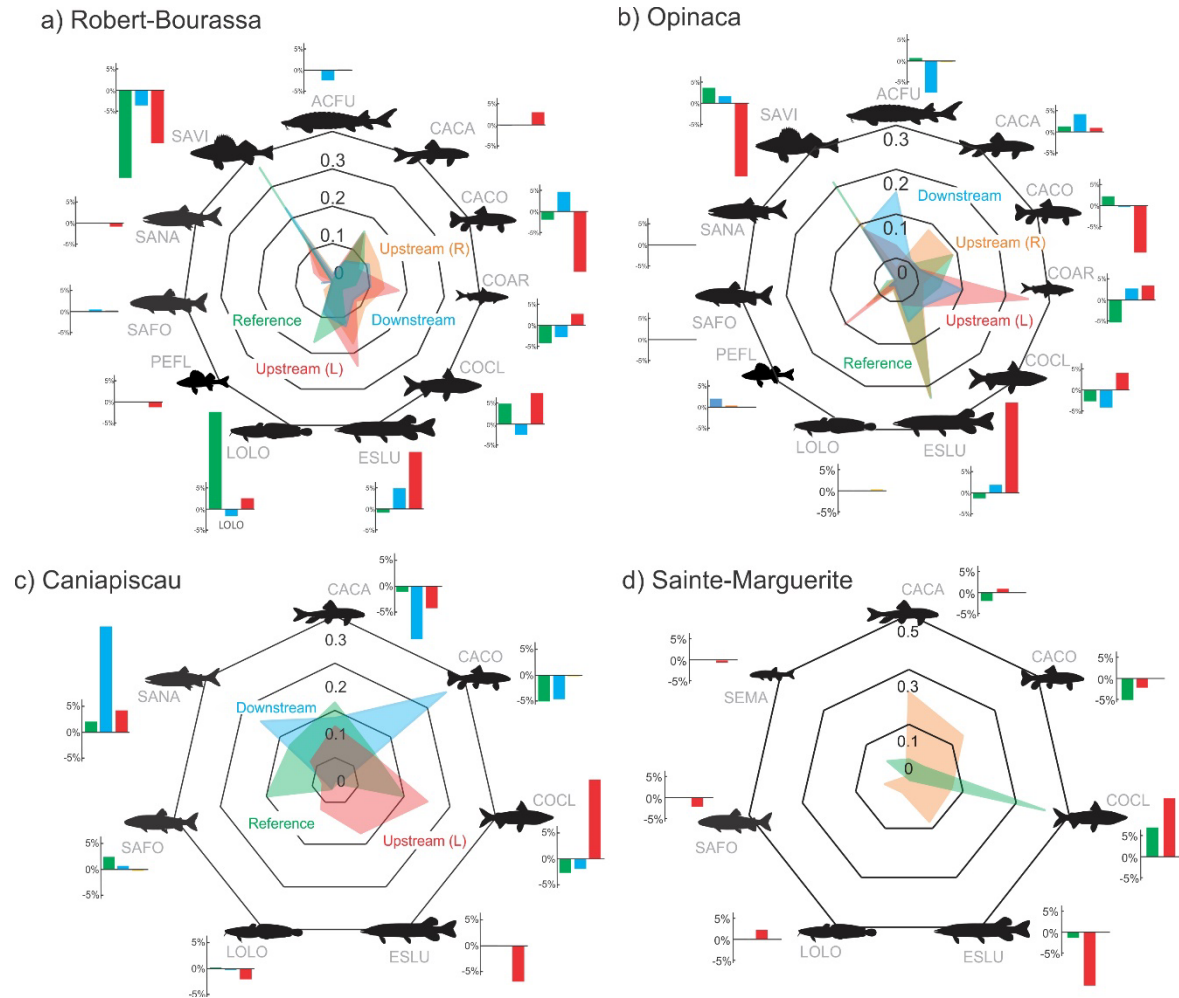
Figure 5. Radar chart graphs of species contributions to beta-diversity (SCBD) computed for each sampling stations, and pooled for a) Robert-Bourassa, b) Opinaca and c) Caniapiscau and d) Sainte-Marguerite. SCBDs determine which species exhibit large variations among year in each sampling stations. The absolute direction of a change for a given species, comparing % change in abundance before (average values) and after impoundment (average values) for each species is also presented beside each species. Green bars represent reference sites, blue bars represent downstream stations and red bars represents upstream stations (UL and UR combined). Only the ten most common species are pictured.