

1 **Reviews and Syntheses**

2 **Running title:** Changes in fish biodiversity in regulated ecosystems

3 **Dams have varying impacts on fish communities across latitudes: A quantitative**
4 **synthesis**

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21 **Abstract**

22 Dams are recognized to impact aquatic biodiversity and ecosystem functions, but the
23 magnitude of effects vary across studies. By using a meta-analytical approach, we examined the
24 effects of impoundment on fish community across three large biomes. The impacts of dams on
25 richness and diversity differed across biomes, with significant declines in the tropics, lower
26 amplitude but similar directional changes in temperate reservoirs, and no changes in boreal
27 reservoirs. Our analysis also showed that non-native species increased significantly in tropical
28 and temperate reservoirs, but not in boreal reservoirs. In contrast, temporal trajectories in fish
29 assemblage metrics were common across regions, with all biomes showing an increase in mean
30 trophic position and in the proportion of generalist species after impoundment. Such changes in
31 fish assemblages may affect food web stability and merit closer study. Across the literature
32 examined, predominant factors or mechanisms that render fish assemblages susceptible to
33 impacts from dams were: 1) the transformation of the lotic environment into a lentic
34 environment; 2) habitat fragmentation and 3) invasive or non-native species. Collectively our
35 results highlight that an understanding of the regional context and a suite of metrics are needed to
36 make robust predictions about how fish will respond to river impoundments.

37 **Introduction**

38 Dams are becoming a pervasive feature of the landscape around the globe (Stickler *et al.*
39 2013; Grill *et al.* 2015) and hydropower has been identified by many as a clean energy source
40 (Teodoru *et al.* 2012; Liu *et al.* 2013) that could be a major catalyst for driving the move to
41 decarbonize our global economy (Figueres *et al.* 2017; Potvin *et al.* 2017). However, there is a
42 clear need to identify where, and by how much dams alter the environment, particularly sensitive
43 aquatic communities (Strayer & Dudgeon 2010). This is especially important given the
44 unprecedented boom in dam construction in emerging economies that are mostly located in
45 species-rich regions (Ziv *et al.* 2012; Stickler *et al.* 2013; Winemiller *et al.* 2016).

46 Large dams (*i.e.*, higher than 15 metres) transform large rivers into storage reservoirs,
47 changing at least part of the ecosystem from a lotic to a lentic one (Ward & Stanford 1995; Friedl
48 & Wüest 2002). Upstream and downstream of the dam, the alteration of the hydrological regime
49 may generate variation in water levels and discharge far beyond natural amplitudes, with changes
50 varying in magnitude depending on dam purpose and management (Kroger 1973; Zohary &
51 Ostrovsky 2011). Dams can also fragment rivers by creating partial barriers to migratory
52 organisms (Nilsson *et al.* 2005; Pelicice *et al.* 2015), or can connect aquatic ecosystems that were
53 spatially isolated before (Gido *et al.* 2002; Gubiani *et al.* 2010). Thus, the modification of the
54 quality, diversity, distribution and access of some key habitats should detrimentally affect some
55 species and favor others (Stanford *et al.* 1996; Zohary & Ostrovsky 2011; Turgeon *et al.* 2018).
56 Ultimately, dams can affect the biodiversity, ecosystem services, and the functions of the
57 associated regulated ecosystems (Nilsson *et al.* 2005; Dudgeon *et al.* 2006; Poff *et al.* 2007;
58 Vörösmarty *et al.* 2010).

59 The effects of dams on fish have been extensively studied, but divergent effects have
60 been reported. At regional and global scales, dams can lead to fish fauna homogenization (*i.e.*,
61 the process by which ecosystems lose their biological uniqueness; Rahel 2000; Poff *et al.* 2007;
62 Gido *et al.* 2009; Villéger *et al.* 2011; Liermann *et al.* 2012; Vitule *et al.* 2012). At a more local
63 scale, empirical evidence exists to show that richness and diversity decrease after impoundment,
64 or are lower in reservoirs (Reyes-Gavilán *et al.* 1996; Pyron *et al.* 1998; Gehrke *et al.* 2002; de
65 Mérona *et al.* 2005; Sá-Oliveira *et al.* 2015; Lima *et al.* 2016). Conversely, other studies and a
66 recent meta-analysis (Liew *et al.* 2016) found either no change or an increase in richness and
67 diversity after impoundment in reservoirs (Martinez *et al.* 1994a; Guenther & Spacie 2006; Irz *et*
68 *al.* 2006). An increase in non-native species have been observed in several studies, suggesting
69 that non-natives can made up the difference in total species richness in reservoirs (Martinez *et al.*
70 1994b; Johnson *et al.* 2008; Gido *et al.* 2009; Clavero & Hermoso 2010; Liew *et al.* 2016).
71 Convergences among studies also suggest a general decrease in rheophilic species, an increase in
72 limnophilic and generalist species (Bonner & Wilde 2000a; Taylor *et al.* 2001, 2014), and an
73 increase in piscivorous fish in reservoirs (Quist *et al.* 2005; Guenther & Spacie 2006; Pelicice &
74 Agostinho 2008; Winters & Budy 2015; Turgeon *et al.* 2018).

75 Earlier works have provided valuable information regarding the effects of dams on fish
76 communities, but the divergences observed regarding fish responses to impoundment call for a
77 global assessment that goes beyond taxonomic indices to include assemblage metrics and
78 functional indices (Mérona and Vigouroux 2012, Mims and Olden 2013, Lima *et al.* 2017b). The
79 effects might also vary across latitudes according to the inherent adaptability of fish communities
80 to respond to the physico-chemical and biological changes brought about by dams and newly
81 created reservoirs (Rosenberg *et al.* 1997; Gomes & Miranda 2001; Vörösmarty *et al.* 2010).

82 Here, by using meta-analytic approach examining both taxonomic (richness, diversity and
83 evenness) and fish assemblage metrics (number of non-native species, trophic level position and
84 macrohabitat flow guild), across latitudes covering three large biomes, we found significant loss
85 in richness in the tropics and relatively little change in boreal region. We also found a general
86 change in fish assemblages toward a more generalist and predatory community, globally.

87 **Methods**

88 **Literature search process**

89 For this study, we used the guidelines and followed the checklist suggested by PRISMA
90 (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Moher *et al.* 2009). The
91 studies presented in this synthesis were compiled from journals indexed in Thomson ISI's Web
92 of Knowledge (mostly peer-reviewed articles; resulting in 668 publications) and from Google
93 Scholar (*i.e.* peer-reviewed articles and textbooks, as well as government and industry reports,
94 non-peer reviewed journals and conference proceedings). We searched for references including
95 the following keywords, individually or in combination: “reservoir*”, “dam*”, “impound*”,
96 “regulat*” but the search included “fish*” at all times. Extensive searches were performed
97 between October 2014 and June 2017 on the references available at that time and published
98 between 1900 and 2017. In addition, the reference lists and bibliographies of relevant sources
99 were also scanned to find literature that was not identified through Thomson ISI's Web of
100 Knowledge and Google Scholar (mostly reports from the grey literature).

101 We then screened our database to refine our selection criteria to include only references that
102 had quantitative data of the effects of impoundment on fish community. We thus excluded
103 modelling and simulation exercises. A total of 67 references met our selection criteria (see

104 Appendix S1; Table S1.1). We then classified each reference as being longitudinal (*i.e.*, one or a
105 few reservoirs with data before and after impoundment; No. of references = 47, No. of sites =
106 147) or cross-sectional (*i.e.*, study presenting data on numerous reservoirs and unregulated
107 aquatic ecosystems sampled at a single point in time; No. of references = 21, No. of sites = 37).

108 **Data extraction**

109 Data were mostly extracted from tables or from datasets available in appendices and
110 supplemental material. When data were presented in figures, they were extracted using the
111 WebPlotDigitizer software (Rohatgi 2018). From longitudinal references, we extracted data for
112 each reservoir and/or each sampling stations separately (*e.g.*, downstream and upstream of the
113 dam) which sometimes resulted in more than one study site per reference (147 studies from 47
114 references; Table S1.1). The analysis was performed at the study site level for longitudinal
115 studies. From each longitudinal study, in addition to fish data over time, we consistently
116 recorded: 1) the archetype of the reservoir visually assessed (lake-shaped, dendritic and canyon;
117 Appendix S2, Fig. S2.1), 2) the geographic location (longitude and latitude), 3) the freshwater
118 ecoregion (Abell *et al.* 2008; <http://www.feow.org/>), 4) the location of the sampling station
119 (downstream, upstream of the dam or upstream of the reservoir), 5) the distance from the dam, 6)
120 the duration of the study, 7) the area of the reservoir at full pool, 8) the flooded terrestrial area, 9)
121 the catchment area (or watershed area), 10) the main reservoir usage (hydroelectricity, water
122 storage, irrigation, flood control, multi-purpose) and 11) the main mechanisms reported by the
123 authors to be responsible of the observed change in diversity or fish assemblages (Table S1.1).
124 We aimed to collect a similar set of data from the 47 cross-sectional studies, including: 1) the
125 geographic location (longitude and latitude), 2) the freshwater ecoregion(s), 3) the location of the
126 sampling stations, 4) the area of the reservoir and reference lakes when available, 5) key dates

127 including the date at which the reservoir was created, the date at which the river or lake was
128 impounded and the date at which the reservoir reached its full pool, and 6) the main mechanisms
129 responsible of the observed change in assemblages (Table S1.1). In cases where these data were
130 not presented in the original references, we attempted to find these data from alternative sources
131 (e.g., Google Earth or other published studies focused on the same target ecosystem). See
132 Appendix S2 (Fig. S2.2) for a graphical summary of the dataset.

133 *Calculation of the taxonomic metrics*

134 *Richness* – Richness values (i.e., the number of fish species) were provided in all studies.
135 We also used \ln values of richness, where trends can be interpreted as an estimation of
136 proportional changes per biome when values lie between -1 and 1. *Diversity* – Values of
137 diversity were directly provided in only three studies. However, many references had data on
138 relative abundance of the species in the community (24/47 studies for longitudinal and 17/37
139 studies in cross-sectional studies). We used these relative abundance data to calculate diversity,
140 evenness, the mean trophic level position and macrohabitat flow guild. We calculated diversity
141 by using the Shannon's H' diversity index ($H' = -\sum_{i=1}^R p_i \ln p_i$), The Shannon's H' takes
142 evenness and species richness into account and quantifies the uncertainty in predicting the
143 species identity of an individual that is taken at random from the dataset and where p_i is the
144 proportion of individuals belonging to the i^{th} species in the dataset. *Evenness* – We calculated
145 evenness by using the Pielou's J' Evenness index. Pielou's J' ($J' = \frac{H'}{\ln S}$) ranges from near 0
146 (indicating pronounced dominance) to near 1 (indicating an almost equal abundance of all
147 species) and H' is the Shannon's H' diversity index where S is the total number of species.

148 *Calculation of the change in fish assemblages' metrics*

149 *Non-native species* – When provided, we extracted the number of non-native species
150 observed. In this contribution, a non-native species consisted of a species that is introduced
151 beyond its native range as a direct (*e.g.*, stocking angling, bait fish) or indirect result of human
152 action (elimination of the barrier that connects adjacent aquatic ecosystems through “natural”
153 dispersal; Jeschke *et al.* 2014). *Trophic level position* - We extracted the mean trophic level
154 position for each species from FishBase (Froese & Pauly 2015), and we calculated a mean
155 trophic level position metric using: $TP = \sum_{i=1}^R p_i TP_i$, where p_i is the proportion of individuals
156 belonging to the i^{th} species and TP_i is the average reported trophic level position for species i .
157 *Macrohabitat flow guild* – We first categorized fish species based on their macrohabitat flow
158 guild (generalist, fluvial facultative or fluvial specialist) by using FishBase (Froese & Pauly
159 2015) and other articles and books (Scott & Crossman 1973; Travnicek & Maceina 1994;
160 Quinn & Kwak 2003; Guenther & Spacie 2006; Baumgartner *et al.* 2014; Buckmeier *et al.* 2014;
161 Lima *et al.* 2017a). Generalists species were coded 1, whereas fluvial facultative taxa were coded
162 0.5 and fluvial specialists coded 0. We then used this formula to generate an index of
163 macrohabitat flow guild, $MFG = \sum_{i=1}^R p_i MFG_i$, where p_i is the proportion of individuals
164 belonging to the i^{th} species and MFG_i is the macrohabitat guild for species i (the MFG metrics
165 varies from 0 to 1).

166 **Data analysis**

167 We ran separate analyses for longitudinal (data before and after impoundment) and cross-
168 sectional datasets (data comparing reservoirs and unregulated aquatic ecosystems). For
169 longitudinal studies, our main goal was to extract trends regarding the impacts of impoundment
170 over time on fish metric across studies (*i.e.*, metrics ~ time since impoundment). Conventional
171 meta-analyses rely on the assumption that sampling distributions have known conditional

172 variances (*i.e.*, weight assigned to both the variances and sample sizes from original studies) and
173 that effect size estimates from different studies are independent (Borenstein *et al.* 2009; Hedges
174 *et al.* 2010; Gurevitch *et al.* 2018). In our synthesis, we could not satisfy the assumption of
175 known conditional variance because for many of our longitudinal studies (39%), sample size
176 variance was unknown or could not be calculated. We were also interested to use sampling
177 station as our statistical unit (called “studies”) and thus our studies were not independent (some
178 stations came from the same reservoir). Because of these limitations, we ran Linear Mixed
179 Effects Models (LMM; lmer function in the lme4 library v.1.1-18-1, Bates *et al.* 2018) that were
180 weighted by the number of observation in the time series (and assumes that sample size is
181 inversely related with variance). In addition, the application of LMM allowed us to increase our
182 power (Hillebrand & Cardinale 2010) and to add a complex structure of covariates in the fixed
183 effects that cannot be easily implemented in most meta-analysis packages. All analyses were
184 performed in R (v. 3.3.2; R Core Team 2017).

185 We ran three sets of models to fully understand the observed patterns because we were
186 really interested in how taxonomic and fish assemblage metrics varied across biomes. We first
187 ran a model for the combined dataset (where all biomes were combined). Secondly, we ran a
188 model comparing biomes among each other and used the interaction between time and biome in
189 the LMM (covariates). Finally, we ran separate models per biome to examine how richness
190 changes over time per biome, without drawing comparisons among biomes. For the three sets of
191 models, we used (years | study_ID/Reservoir_ID) as random factors, controlling for the effect of
192 time per study, and where each study was nested in its reservoir (to control for the spatial non-
193 independence of the studies; similar approaches have been used in Liao *et al.* 2007; Rey Benayas
194 *et al.* 2009; Vilà *et al.* 2011). The mean effect size for the fixed effects was estimated with

195 Restricted Maximum Likelihood and calculated with Kenward-Roger approximation to
196 approximate degrees of freedom in mixed effect models (Kenward & Roger 1997) by using the
197 sjPlot package in R (v. 2.6.0; Lüdtcke & Schwemmer 2018).

198 For the cross-sectional studies, since both variances and sample sizes were available, we
199 ran conventional weighted meta-analyses. We weighted effect size estimates by their inverse
200 variance weights, such that studies with higher sample sizes were given more weight by using
201 (*i.e.*, weights = $((1/SD)*N)$, following Borenstein *et al.* 2009; Hedges *et al.* 2010). We assessed
202 differences in the overall effect size (*e.g.*, if the mean of each metrics differs between regulated
203 or unregulated ecosystems) by using the Standardized Mean Difference (SMD). For each
204 biodiversity metric considered in the cross-sectional studies, we also ran three sets of models
205 (one for the combined effect, one with the interaction term (biome*effect), and separate models
206 per biomes). Unfortunately, not enough information was provided for non-native species in
207 cross-sectional studies.

208 We used regression trees (rpart package, v. 4.1-10, Therneau *et al.* 2018) to explore and
209 explain the variability observed and residual variance in random effects values (RE) of the mixed
210 models based on reservoir or sampling station characteristics (when relevant, see Table S1.1 and
211 Fig. S2.2). Regression trees were pruned by minimizing the cross-validated error to avoid
212 overfitting (De'ath & Fabricius 2000).

213 **Publication bias**

214 We explored the possibility of publication bias by using funnel plots (Appendix S5),
215 which allow for a visual assessment of whether studies with small effect sizes are missing from
216 the distribution of all effect sizes (*i.e.*, asymmetry). We also ran Spearman rank correlations to

217 examine the relationship between the standardized effect size and the sample size across studies,
218 and the relationship between the standardized effect size and the duration of the studies for
219 longitudinal studies (Rosenberg *et al.* 2000). A significant correlation would indicate a
220 publication bias whereby larger effect sizes are more likely to be published than smaller effect
221 sizes, when sample size is small or duration of the study is short.

222 **Results**

223 **How do impoundments affect fish biodiversity and assemblages? Longitudinal studies**

224 *Taxonomic metrics (Richness, Diversity and Evenness)*

225 Richness and diversity decreased significantly over time when all studies and regions were
226 combined, but this pattern is observed only in temperate and tropical regions when biomes were
227 modeled separately (Fig. 1 a, c). Richness and diversity decreased at a much faster rate in
228 tropical reservoirs when compared to boreal and temperate reservoirs (Time: B vs. TR, boreal
229 used as the contrast in the model; Fig. 1 a, c). Using \ln richness, we still observed a decrease
230 over time in the combined dataset, as well as in temperate and tropical regions (Fig. 1 b), but the
231 proportional rate of change in richness over time is comparable across biomes (interaction terms
232 between Time and Biomes are not significant; Fig. 1 b). Evenness did not significantly decrease
233 over time for the combined dataset. However, we did find that evenness declined significantly in
234 tropical and temperate regions when biome-specific models were performed (Fig. 1 d).
235 Compared to boreal reservoirs, evenness was lower and decreased faster in temperate regions
236 (Fig. 1 d).

237 *Species assemblage metrics (Non-native, Trophic level position and Macrohabitat flow guild)*

238 Across all analyses of species assemblage metrics, we detected different results when the
239 combined datasets (studies across all biomes) were contrasted with the regionally-specific
240 analyses. For example, no non-native species were observed in any of the boreal reservoirs
241 following impoundment, but some invaded tropical and temperate reservoirs (Fig. 2 a). The
242 number of non-native species increased for the combined dataset, but this was driven by tropical
243 and temperate regions (Fig. 2 a). We found that the rate of change in non-native species
244 increased much faster in tropical reservoirs than in temperate reservoirs (Fig. 2 a), and this was
245 still true when the proportional rate of increase in non-native species was considered (Fig. 2 b).
246 The average trophic level position increased following impoundment for the combined dataset,
247 as well as in boreal reservoirs, but not in temperate and tropical reservoirs (Fig. 2 c). The mean
248 trophic level position was lower in temperate and tropical regions when compared to the boreal,
249 and the rate of change did not differ across regions (Fig. 2 c). We observed an increase in
250 generalist species over time in boreal and tropical regions as well as in the combined dataset (but
251 did not in temperate region alone; Fig. 2 d). Compared to boreal reservoirs, temperate and
252 tropical reservoirs had a higher proportion of rheophilic species originally (Fig. 2 d) and the rate
253 of change in the proportion of generalist species increased more slowly in temperate than in
254 tropical regions (Fig. 2 f).

255 *Study specific effects (random effect values; RE)*

256 The examination of the study specific effects as random effect values (RE; forest plot)
257 from the mixed effects models showed a much higher variability in richness in the tropics than in
258 temperate and boreal regions and showed that residual variances across studies (at the sampling
259 station level) were comparable within a given reservoir (Appendix S3; Figs. S3.3, and S3.5).
260 Using a regression tree on the RE of the model built with tropical data only, we found that

261 variation in RE was significantly associated with the catchment area of the reservoirs
262 (Proportional reduction in error (PRE) = 54.6% of the variation explained) and the duration of
263 the study (PRE = 9.3%; Fig. 4). Reservoirs with large catchment area showed a tendency to
264 experience a higher loss of species relative to the mean loss of richness in this region, whereas
265 young reservoirs with smaller catchment area experienced a lower loss of species, and sometimes
266 even an increase in richness (Fig. 4). RE values for diversity and evenness did not show this
267 amount of variability (Fig. S3.6). The examination of the RE values for the number of non-native
268 species showed some variability in the tropics but very little in boreal and temperate regions
269 (Fig. S3.7). Variability across studies was not significant in the other species assemblage metrics
270 (Figs. S3.7 and S3.8).

271 **How do impoundments affect fish biodiversity and assemblages? Cross-sectional studies**

272 *Diversity metrics (Richness, Diversity and Evenness)*

273 Across the different diversity metrics, we could obtain a substantially larger number of
274 observations for richness, relative to diversity and evenness. Based on our analyses of the cross-
275 sectional studies, richness did not differ between regulated (reservoirs and regulated rivers and
276 streams) and unregulated aquatic ecosystems when all studies and regions were combined.
277 However, when using separate models, we found higher richness in regulated ecosystems
278 relative to unregulated ecosystems in temperate region (Fig. 3 a). Diversity was higher in
279 regulated ecosystems compared to in unregulated ones when tropical and temperate ecosystems
280 were considered separately (Fig. 3 b). The difference in diversity between regulated and
281 unregulated ecosystems was greater in temperate region when compared to boreal and tropical
282 regions (Fig. 3 b). Evenness did not differ between regulated and unregulated aquatic ecosystems
283 for the combined dataset but was higher in regulated tropical and temperate ecosystems when

284 each biome was considered separately (Fig. 3 c). The examination of the RE values for
285 taxonomic metrics did not show significant heterogeneity across individual studies (Appendix
286 S3).

287 *Assemblages metrics (Non-native species, Trophic level and Macrohabitat flow guild)*

288 Regarding species assemblage metrics in cross-sectional studies, few patterns were
289 significant. The average trophic level position did not differ between regulated and unregulated
290 aquatic ecosystems for the combined dataset, nor did it for the boreal or tropical regions when
291 examined separately, but was higher in regulated ecosystems in temperate region (Fig. 3 d). The
292 percentage of generalist species did not differ between regulated and unregulated ecosystems for
293 the combined dataset, for boreal and temperate regions, but was lower in tropical regulated
294 ecosystems (Fig. 3 e). We did not have enough data to examine if the number of non-native
295 species differ between regulated and unregulated ecosystems across all biomes. The examination
296 of the RE values for species assemblage metrics also did not show significant heterogeneity
297 across individual studies (Appendix S3).

298 **Discussion**

299 **Gradient of impacts on biodiversity across latitudes**

300 The impacts of dams on fish biodiversity followed a clear gradient across latitudes, from
301 a general lack of apparent changes in boreal regions to substantial ones in the tropics. A previous
302 meta-analysis by Liew *et al.* (2016) suggested that dams have similar effect across regions, but
303 their analyses did not consider the boreal region. In addition, we report on a substantially larger
304 pool of information, representing 60% increase in number of references considered by Liew *et*
305 *al.* (2016). As such, the gradient of effects we report on here clearly underscores the need for an

306 understanding of regional fish assemblages, and the context of stressors when evaluating the
307 impacts of damming rivers on fish biodiversity.

308 Fish from tropical rivers and temperate prairie streams have evolved in fluvial
309 ecosystems and most lack the morphological, behavioural and reproductive traits, as well as
310 plasticity needed to successfully occupy the new lentic habitats created upstream of the dam
311 (Gomes & Miranda 2001; Dodds *et al.* 2004; Agostinho *et al.* 2008; Durham & Wilde 2011).
312 Such a lack of traits and plasticity can partly explain the decrease in richness observed over time
313 in longitudinal studies in tropical and temperate ecosystems. On the other hand, boreal reservoirs
314 from this synthesis have minimal anthropogenic impacts other than dams due to their remote
315 locations, and have no reports of non-native species (Sutela & Vehanen 2008; Turgeon *et al.*
316 2018). Large lakes are also much more common in the boreal region than in temperate and
317 tropical regions (Verpoorter *et al.* 2014; Messenger *et al.* 2016), and fish have been colonized
318 boreal aquatic ecosystems from refugia after glaciers began retreating about 15 000 years ago
319 (Schluter & Rambaut 1996; Griffiths 2006). For these reasons, boreal freshwaters fish fauna is
320 depauperate and characterized by large body size species that are generally able dispersers and
321 ecologically-tolerant species (Dynesius & Jansson 2000; Griffiths 2006; L  v  que *et al.* 2008).
322 Collectively, these characteristics make boreal fish communities potentially quite resilient to
323 river impoundment.

324 Given the differences in the length of available time series across biomes and the
325 substantial heterogeneity observed across reservoirs within the tropics, it is important to
326 scrutinize the data before drawing generalizations about the sensitivity of fish richness and
327 diversity in impounded tropical systems. Tropical reservoirs are much younger than temperate
328 and boreal reservoirs, and therefore time series available for the tropics are shorter (*i.e.*, on

329 average 6 years, as opposed to 18 or 19 years as found with boreal regions and temperate
330 regions, respectively; Fig. S2.2). For completeness, we truncated the time series in temperate and
331 boreal regions to only keep richness data spanning up to 5 y post-impoundment, and re-analysed
332 the data (Appendix S4, Fig. S4.10). Even with comparable study periods (5y), richness still
333 decreased faster in the tropics (Fig. S4.10). We must still be careful with predictions that extend
334 beyond 10 years in duration in the tropics because they could well be overestimating loss in
335 richness (Fig. 2 a; dashed line). An alternative and more plausible trajectory would be a
336 decreasing non-linear curve that stabilizes at some point (Fig. 2 a; saturating curve illustrated),
337 but the short time series did not allow us to test for non-linear patterns over time. Furthermore,
338 we observed significant heterogeneity across studies in the tropics when compared to temperate
339 and boreal regions (Figs. S3.3 and S3.5). This variability across studies was significantly
340 associated with the size of the catchment area and the duration of the study (Fig 4). A higher
341 decrease in richness relative to the mean loss of species was observed in reservoirs located in
342 large catchment area. Rivers in larger catchment areas usually have higher richness (Welcomme
343 2000; in this study: LMM, estimate \pm SE = 0.242 ± 0.078 , $P = 0.003$, $R^2 = 0.17$), and thus had a
344 higher potential to lose species. A lower loss in richness relative to the mean loss of species or an
345 increase in richness was observed mostly in short duration time series and can partly be
346 explained by the short term and rapid increase in non-native species (supported by this meta-
347 analysis) that were better adapted to the newly created lentic habitats (Rahel 2002; Clavero &
348 Hermoso 2010; Vitule *et al.* 2012) and may result in biotic homogenisation at larger scales (Poff
349 *et al.* 2007; Gido *et al.* 2009; Vitule *et al.* 2012). These non-native species can come from newly
350 connected drainages by the flooding of natural barriers (direct effect; Júlio *et al.* 2009; Clavero &
351 Hermoso 2010; Vitule *et al.* 2012), or by intentional or unintentional species introduction

352 (indirect effect through propagule pressure; Johnson *et al.* 2008; Pelicice & Agostinho 2008).
353 However, this increase in richness in the tropics is suggested to be transient because some studies
354 demonstrated a rise and fall in richness (humped-shaped non-linear pattern) after impoundment
355 in the tropics (Agostinho *et al.* 1994; Lima *et al.* 2016), stressing for the need of longer time
356 series.

357 **Impacts on the food web: Less rheophilic, more non-native and predatory species**

358 Our meta-analytic approach suggested a global decrease in rheophilic species (more
359 pronounced in tropical region), an increase in non-native (except in the boreal region) and an
360 increase in mean trophic level position (Fig. 2). A decrease in rheophilic species was expected
361 following the transformation of a lotic to a lentic ecosystem (Gomes & Miranda 2001; Agostinho
362 *et al.* 2008) due to strong selective pressures in these newly created lentic habitats that should
363 favor generalists over rheophilic and fluvial specialist species (Li *et al.* 2013). Interestingly, the
364 strength of trophic interactions and the observed increase in predatory fish in reservoirs can also
365 contribute to the decrease of rheophilic species. Increased predator densities have been suggested
366 to reduce migration success of small-bodied stream fishes (Matthews & Marsh-Matthews, 2007;
367 Franssen, 2012).

368 The general increase in the trophic level position can be due to an increase in predatory
369 fish (higher trophic level position), a decrease in benthivorous and planktivorous fish (lower
370 trophic position) or to both mechanisms. Because reservoirs are frequently larger and more
371 accessible to humans relative to natural lakes, they attract significant numbers of recreational
372 fisherman. Likewise, reservoirs have been subject to intense fish stocking and species
373 introduction, mainly for piscivores and sport/game fish species (Pelicice & Agostinho 2008).

374 Water drawdown in reservoirs can also favor piscivores by concentrating prey fish (Hulsey 1956;
375 Ploskey 1986; Nordhaus 1989; Sutela & Vehanen 2008), which can increase the feeding activity
376 and growth of young and adult piscivores (Heman *et al.* 1969; Zweiacker *et al.* 1972; Johnson &
377 Andrews 1973; Heisey *et al.* 1980; Herrington *et al.* 2005). Moreover, the trophic surge
378 following impoundment can also benefit predators by the boom of productivity during and
379 shortly after impoundment, but this effect might be transient. Lastly, the cannibalism observed in
380 many large predators in reservoirs might keep reservoirs in a predator-dominated state
381 (McCauley *et al.* 2018) and might confer some stability to the food web (Claessen *et al.* 2004;
382 McCann 2011).

383 These changes in species assemblages, and how they can impact the structure and the
384 stability of food webs in reservoirs deserve closer investigation, especially in the tropics where
385 alterations to species-rich food web are greater, on-going, and not well-understood (Layman *et*
386 *al.* 2005; Rooney *et al.* 2006). Reservoirs seem to have longer food chains (Hoeinghaus *et al.*
387 2008; Mercado-Silva *et al.* 2009) and more “weblike” interactions, especially in the presence of
388 omnivory (Stein *et al.* 1995). The potential impacts of dams on food web stability call for a
389 better integration of taxonomic, functional and life history trait responses to impoundment at a
390 global scale (Mérona & Vigouroux 2012; Mims & Olden 2013; Lima *et al.* 2017b) because their
391 relative importance can change across latitude and in a spatio-temporal context.

392 **Mechanistic understanding of the effects of impoundment on fish assemblages**

393 Several hypotheses regarding the mechanisms responsible for the change in biodiversity
394 and fish assemblages following impoundment have been suggested. As a first exploratory step to
395 develop a general mechanistic understanding, we extracted the main mechanisms reported by the

396 authors from our 67 references (Fig. 5; Table S1.1). We then classified the 11 identified
397 mechanisms into three categories: 1) alteration of the hydrological regime, 2) impacts on
398 connectivity and fish movement and 3) change in food web and trophic interactions (Fig. 5).

399 The alteration of the hydrological regime can affect fish communities by shifting the
400 ecosystem from a lotic to a lentic one, through changes in discharge and water levels, and by
401 changing water quality, temperature and sedimentation regimes (Fig. 5). The transformation of
402 the lotic environment into a lentic environment was the most commonly cited mechanism (69%
403 of the studies; Fig. 5). The new lentic conditions upstream of the dam and a change in discharge
404 downstream can adversely affect fluvial specialists and large-river species (Winston *et al.* 1991;
405 Bonner & Wilde 2000b; Franssen & Tobler 2013; Taylor *et al.* 2014); this mechanism was
406 clearly illustrated in our meta-analysis by the general decrease in rheophilic species and an
407 increase in generalists. Water levels fluctuations and winter drawdown can affect fish that
408 depend on the littoral zone through modification of their feeding, growth and reproduction
409 (freezing of eggs and larvae, lost of spawning substrate; June 1970; Gafny *et al.* 1992; Kahl *et al.*
410 2008; Probst *et al.* 2009) and also indirectly through changes in prey availability and quality
411 (Paller 1997; Furey *et al.* 2006; Aroviita & Hämäläinen 2008; Zohary & Ostrovsky 2011; Stoll
412 2013). Information on the proportion of benthophages or species inhabiting the littoral zone
413 would help inform this later mechanism.

414 The modification of the riverscape connectivity by dams can also alter fish assemblages
415 by limiting the movement of migratory species, by affecting metapopulation dynamics, or by
416 facilitating invasions by connecting aquatic ecosystems (Dynesius & Nilsson 1994; Fullerton *et*
417 *al.* 2010). The fragmentation of rivers through the construction of barriers to migration was
418 another mechanism commonly cited (39% of the studies, Fig. 5). Populations isolated in

419 upstream areas by dams can be subject to extirpation when reproductive failure or high mortality
420 cannot be counterbalanced by recolonization from downstream sources (Winston *et al.* 1991). On
421 the other hand, some authors have observed increased colonization of non-native species in
422 impounded streams (Havel *et al.* 2005; Johnson *et al.* 2008). To capture this mechanism in future
423 meta-analyses, the proportion of species undergoing migration (anadromous, potamodromous)
424 needs to be reported more frequently.

425 In addition to a higher susceptibility to propagule pressure, reservoirs are particularly
426 vulnerable to successful establishment of non-native species (40% of the studies, Fig. 5) because
427 they are in a perturbed state after impoundment compared to natural lakes (Thornton *et al.* 1990;
428 Pringle *et al.* 2000; Davis 2003; Didham *et al.* 2007). Several studies have found an increase in
429 non-native species after impoundment, and often these taxa are piscivorous species that become
430 quite abundant post-impoundment (Martinez *et al.* 1994b; Quist *et al.* 2005; Guenther & Spacie
431 2006; Johnson *et al.* 2008; Gido *et al.* 2009; Clavero & Hermoso 2010; Franssen & Tobler
432 2013). When introduced, they compete with, and can prey upon native species (Li *et al.* 1987,
433 Minckley *et al.* 1991). Basses are well known to homogenize fish assemblages by eliminating
434 small-bodied prey species (Jackson 2002) and are very often introduced in temperate reservoirs.
435 Quist *et al.* (2005) found that the Great Plains river fish assemblage switched from a catostomids
436 and cyprinids (*i.e.* river specialists) dominated system prior to impoundment to an non-native
437 species assemblage, mainly dominated by piscivores (*e.g.*, smallmouth bass, walleye, yellow
438 perch and brown trout).

439 The above-mentioned mechanisms are mostly based on authors opinions and not on
440 strong quantitative evidence because replication in longitudinal studies is rare. The dominant
441 mechanisms can also differ according to the location and scale (biomes, location of the sampling

442 station), may be dynamic over time (*i.e.*, differ among the filling phase vs. shortly after or many
443 years after impoundment) and can be influenced by the particularities of reservoir management
444 and confounding factors (*i.e.*, stocking, fishing). This summary also enlightens the importance of
445 moving toward a trait-based approach to get a mechanistic understanding of the effects of
446 impoundment on fish communities, which needs to be more thoroughly reported in original
447 research studies.

448 **Limitations and publication bias**

449 The main limitations and/or biases in our synthesis that could affect the interpretation and
450 strength of evidence are: 1) publication bias, 2) variation in fishing effort and gears, 3) variation
451 in the duration of the studies, 4) assumption of a linear relationship between time and richness, 5)
452 calculation of the trophic position in a changing habitat, 6) defining an adequate reference
453 ecosystem for a reservoir, and 7) the difference in ecosystems size. We addressed the issue of
454 publication bias with the visual inspection of funnel plots and Spearman rank correlation
455 examining the effect size in relation to the sample size and duration of the study (Appendix S5).
456 Funnel plots show an absence of a clear sampling/publication bias in most cases, but we found
457 few significant Spearman r values suggesting a bias toward publishing large effect sizes when
458 sample size is small or study duration is short (Appendix S5). Second, the effort and the fishing
459 gears used varied across studies, but also among years in some studies. Roughly 41% of the
460 studies did not have similar effort across years (See Table S1.1) – sometimes using different
461 fishing gears - and only 23% of the studies reported rarefied richness (*i.e.*, controlling for the
462 number of samples). Most studies used gill nets, resulting in an underestimation of small littoral
463 and pelagic species. Third and fourth, the duration of the study also varied among studies and
464 was much shorter in the tropics. The consequences and implications of these limitations were

465 discussed earlier. Given the predominance of shorter time series, particularly in the tropics, we
466 assumed a linear relationship between time and richness; with longer time series, nonlinear
467 modeling would be worth exploring. Fifth, we assumed that the change in habitat brought about
468 by dam would not change the trophic level position for a given species. However, some studies
469 have demonstrated that, in altered habitats or those invaded with non-native species, the trophic
470 level position can change for a species (Vander Zanden *et al.* 1999; Tewfik *et al.* 2016). Our goal
471 was simply to develop a general assessment of a change in fish assemblages, and we considered
472 the trophic position provided by Fishbase (Froese & Pauly 2015) as a reasonable proxy to
473 evaluate if fish get more predatory over time in reservoirs. Follow up studies using more direct
474 approaches (*e.g.*, stable isotopes) would be worthwhile to investigate this observation more fully.
475 Finally, what constitutes an adequate reference ecosystem for a reservoir, and the potential
476 differences in ecosystem sizes among studies and biomes need consideration. In cross-sectional
477 datasets, the unregulated sites for boreal ecosystems were all lakes whereas unregulated sites
478 were mainly rivers and streams in temperate (5% lakes, 95% rivers or streams) and tropical
479 ecosystems (11% lakes, 89% rivers or streams). We need appropriate reference ecosystems to
480 control for stochasticity and climatic events, but comparing reservoirs to only reference lakes or
481 only rivers might be inadequate because reservoirs are neither a lake nor a river. Only one study
482 compared reservoir fish communities with those in rivers and lakes in temperate systems and
483 found that reservoir communities were more similar to lake vs. river communities (Irz *et al.*
484 2006). Differences in ecosystem size between reservoirs and lakes is another plausible
485 explanation for the trophic position and diversity results presented herein, as there is certainly a
486 well-established body of literature showing that these metrics scale with ecosystem size (Post *et*
487 *al.* 2000). Similarly, geographic location is known to influence fish richness in lakes (Matuszek

488 & Beggs 1988; Samarasin *et al.* 2014). We clearly see that fish diversity metrics are higher in
489 tropical sites (even before impoundment), which is consistent with the expected trend. We
490 believe that part of the effect of ecosystem size is reflected in the regression tree that explores
491 what variables might explain differences in RE among studies, where we found that catchment
492 area was the strongest predictor. Awareness of the potential effects associated with ecosystem
493 size is particularly relevant when investigators are comparing reservoirs to natural lakes. Boreal
494 reservoirs used in this synthesis were on average 158 times bigger than adjacent reference lakes.
495 Therefore, richness should be higher in reservoir relative to adjacent reference lakes just based
496 on their respective size. Empirical and experimental studies going forward would be well advised
497 to take these factors into consideration.

498 **Concluding remarks**

499 Based on an analysis of 147 longitudinal and 37 cross-sectional studies from a total of 67
500 references, we present a comprehensive synthesis that quantitatively evaluates the effects of
501 impoundment on fish biodiversity and species assemblages across three globally-dominant
502 biomes. Four major insights emerge from our synthesis. First, predictions regarding the impact of
503 dams on fish communities require a regional perspective. Tropical regions were more affected
504 and characterized by stronger changes in richness and diversity, and marked increases in non-
505 native species following impoundment. In contrast, lower amplitude changes were observed in
506 temperate and boreal reservoirs. Second, the full extent of fish communities' dynamics in
507 tropical regions remains to be determined as time series here are short. Tropical reservoirs are
508 young and novel ecosystems, and are still in the non-equilibrium phase. Third, a lack of change
509 in richness does not mean no change in native species richness. We observed a sharp increase in
510 non-native species in the tropics that was not observed in boreal ecosystems, and this effect

511 masked changes in the whole fish assemblage. Finally, changes in fish assemblages is a common
512 feature across regulated ecosystems. We detected a global increase in the trophic level position
513 and a general decrease in the percentage of rheophilic species. Collectively, we conclude that the
514 changes in fish assemblages and diversity detected in reservoirs could potentially impact the
515 stability of the food web, the productivity of these ecosystems, the sustainability of artisanal
516 fisheries, and the function and ecosystems services (Hoeinghaus *et al.* 2009; Toussaint *et al.*
517 2016). In light of this global quantitative synthesis, hydropower may be part of the solution to
518 decarbonize our global economy but will come at substantially higher ecological cost to the
519 tropics (Ziv *et al.* 2012; Winemiller *et al.* 2016; Pelicice *et al.* 2017). When planning
520 hydropower development, strategic and transboundary actions should be taken to protect,
521 conserve and restore fish biodiversity, particularly in the sensitive regions like the tropics.

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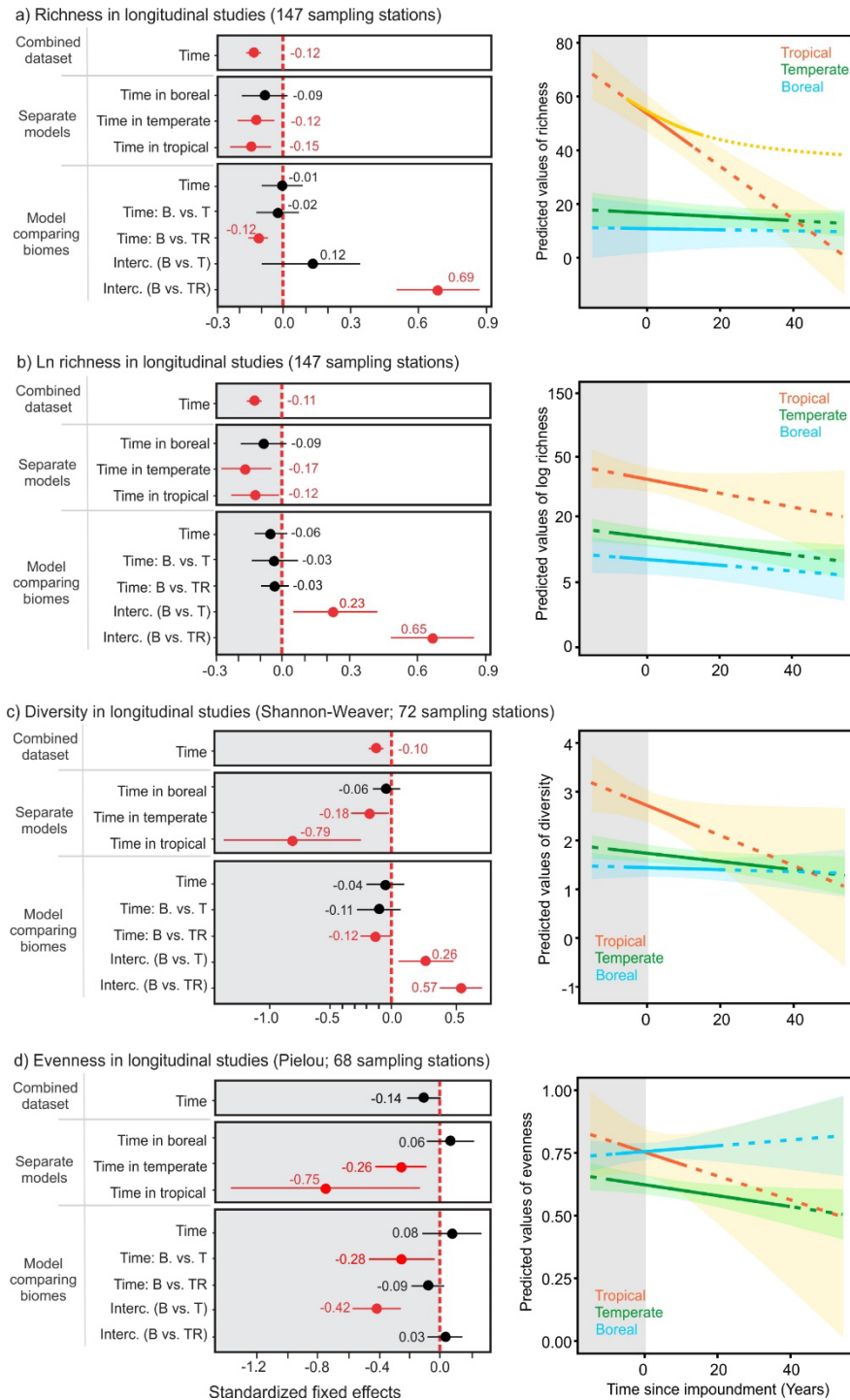


Figure 1. Standardized effect size in longitudinal studies for taxonomic metrics. *Left panels:* Standardized fixed effects coefficients and standard error from the mixed effects models comparing the temporal trends in a) richness, b) *ln* richness, c) diversity, and d) evenness across biomes. For each taxonomic metric, we showed the effect of time since impoundment on the metrics for the combined dataset, for each biome modelled separately, and we also compared biomes in the model by using an interaction between biome and time (Time: B vs. T and Time: B vs. TR, using boreal (B) as the contrast). The 95% CI were evaluated with the Kenward Roger approximation. Coefficients in red represent significant patterns for a given fixed effect. *Right panels:* Models predictions from the model comparing the effect of time since impoundment on taxonomic metrics across biomes (model with the interaction). The solid lines represent the predictions where we have actual data and the dotted lines represent model extrapolation. In a), the non-linear curve in the tropics is a more plausible pattern but cannot be modeled.

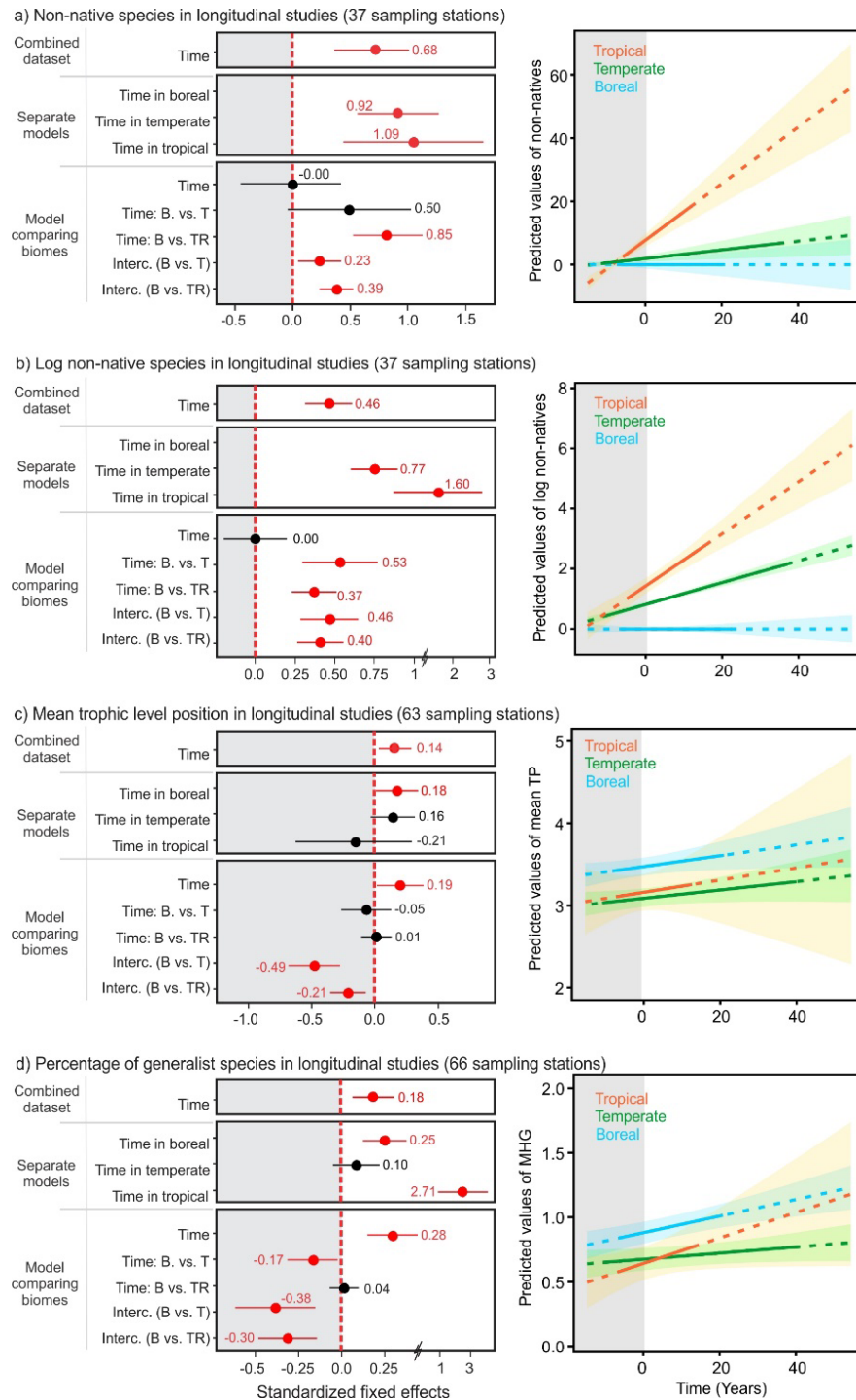


Figure 2. Standardized effect size in longitudinal studies for taxonomic metrics. *Left panels:* Standardized fixed effects coefficients and standard error from the mixed effects models comparing the temporal trends in a) number of non-native species, b) \ln number of non-native species, c) mean trophic level position, and d) percentage of generalist species across biomes. For each taxonomic metric, we showed the effect of time since impoundment on the metrics for the combined dataset, for each biome modelled separately, and we also compared biomes in the model by using an interaction between biome and time (Time: B vs. T and Time: B vs. TR, using boreal (B) as the contrast). The 95% CI were evaluated with the Kenward Roger approximation. Coefficients in red represent significant patterns for a given fixed effect. *Right panels:* Models predictions from the model comparing the effect of time since impoundment on taxonomic metrics across biomes (model with the interaction). The solid lines represent the predictions where we have actual data and the dotted lines represent model extrapolation.

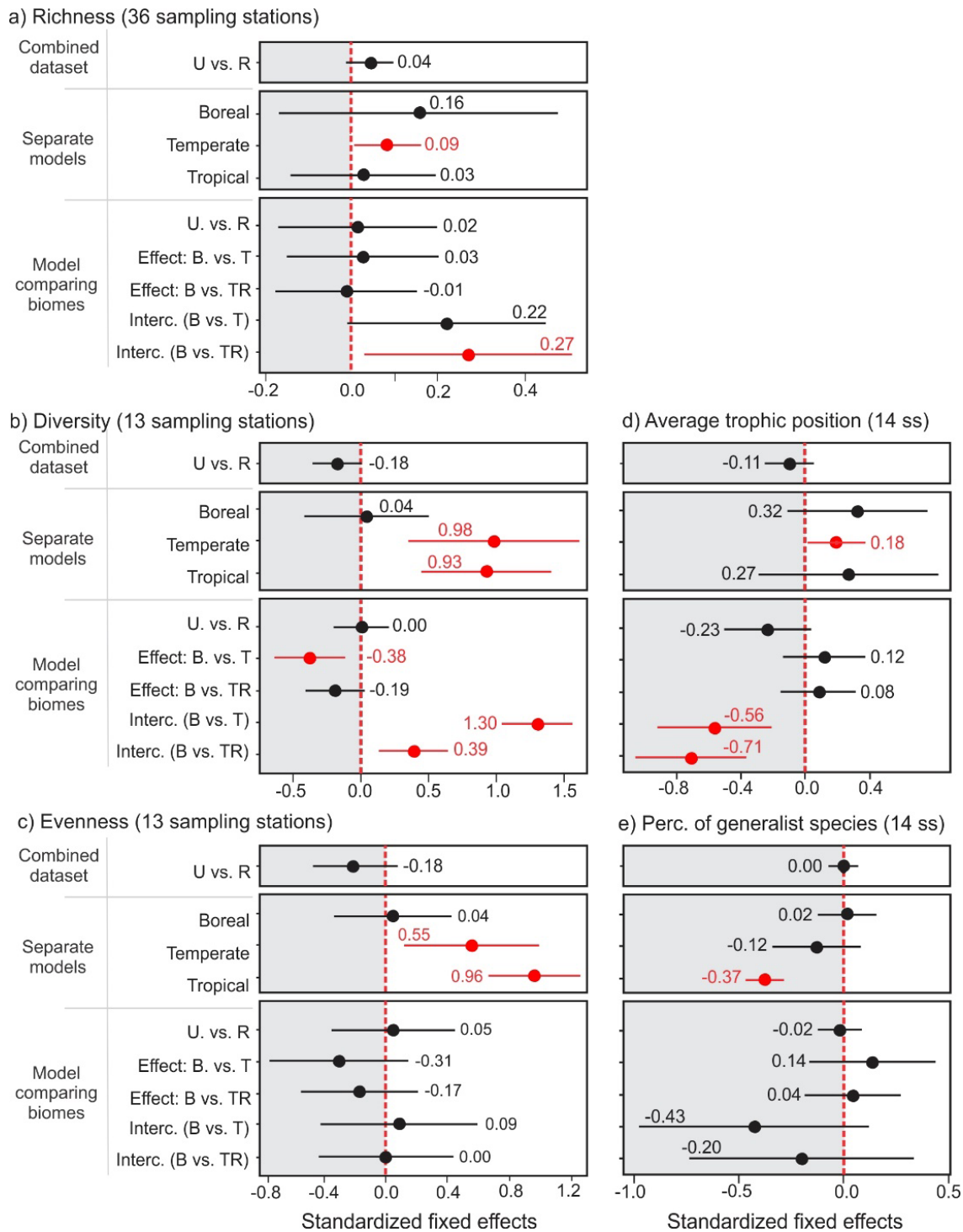
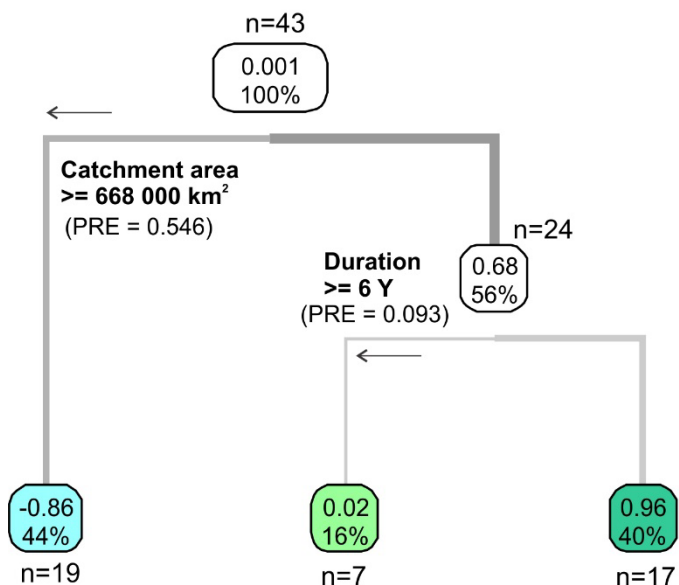


Figure 3. Standardized effect size in cross-sectional studies for taxonomic and fish assemblage metrics.

Standardized fixed effects coefficients and standard error from the mixed effects models comparing the temporal trends in a) richness, b) diversity, c) evenness, d) mean trophic level position, and e) percentage of generalist species across biomes. Positive deviations in standardized fixed effects represent cases where the regulated ecosystems had higher values relative to the unregulated ecosystems. For each metric, we showed the difference between regulated (R) and unregulated ecosystems (U) on the metrics for the combined dataset, for each biome modelled separately, and we also compared biomes in the model by using an interaction between biome and effect (Effect: B vs. T and Effect: B vs. TR, using boreal (B) as the contrast). The 95% CI were evaluated with the Kenward Roger approximation. Coefficients in red represent significant patterns for a given fixed effect. Coefficients in red represent significant patterns for a given fixed effect.

a) Pruned regression tree



b) Distribution of the sampling stations

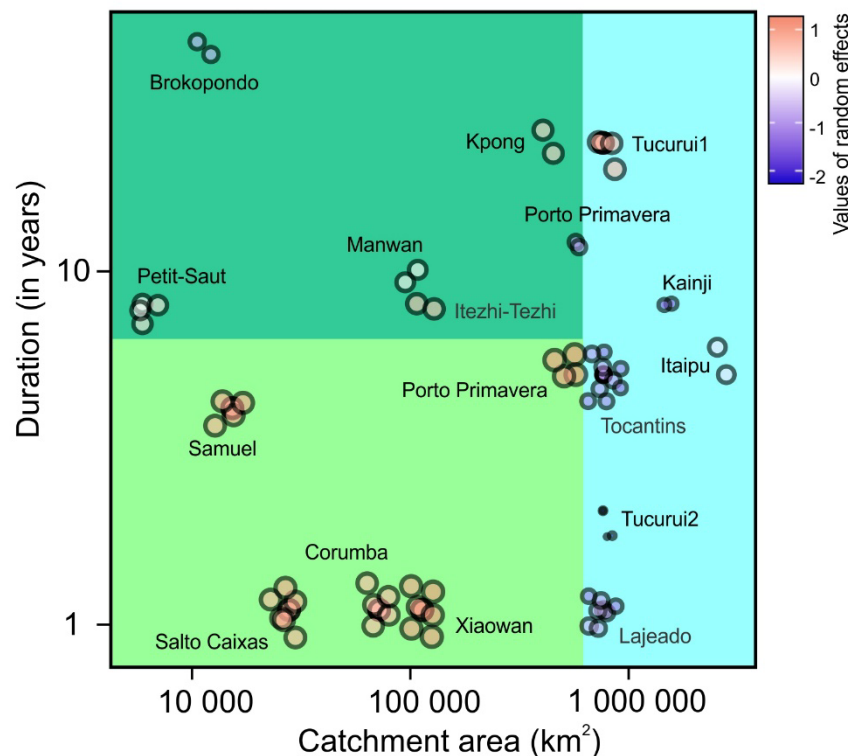


Figure 4. Regression tree predicting the heterogeneity in random effect values (RE) from the mixed effect model examining the effect of time since impoundment on richness in the tropics. a) plot of the pruned regression tree showing the mean value and proportion of the dataset in boxes at each step of the tree, and b) distribution of the sampling stations and reservoirs in the catchment area and duration of the studies space. The size and color of the circle represent the RE values of the model (i.e., variation relative to the mean loss of richness in this region). Red means a lower loss in richness relative to the mean loss of richness in this region and an increase in richness in some cases, blue means a higher decrease in richness relative to the mean loss of richness in this region. The different shades area in panel b correspond to data range covered by the three final nodes in the pruned regression tree.

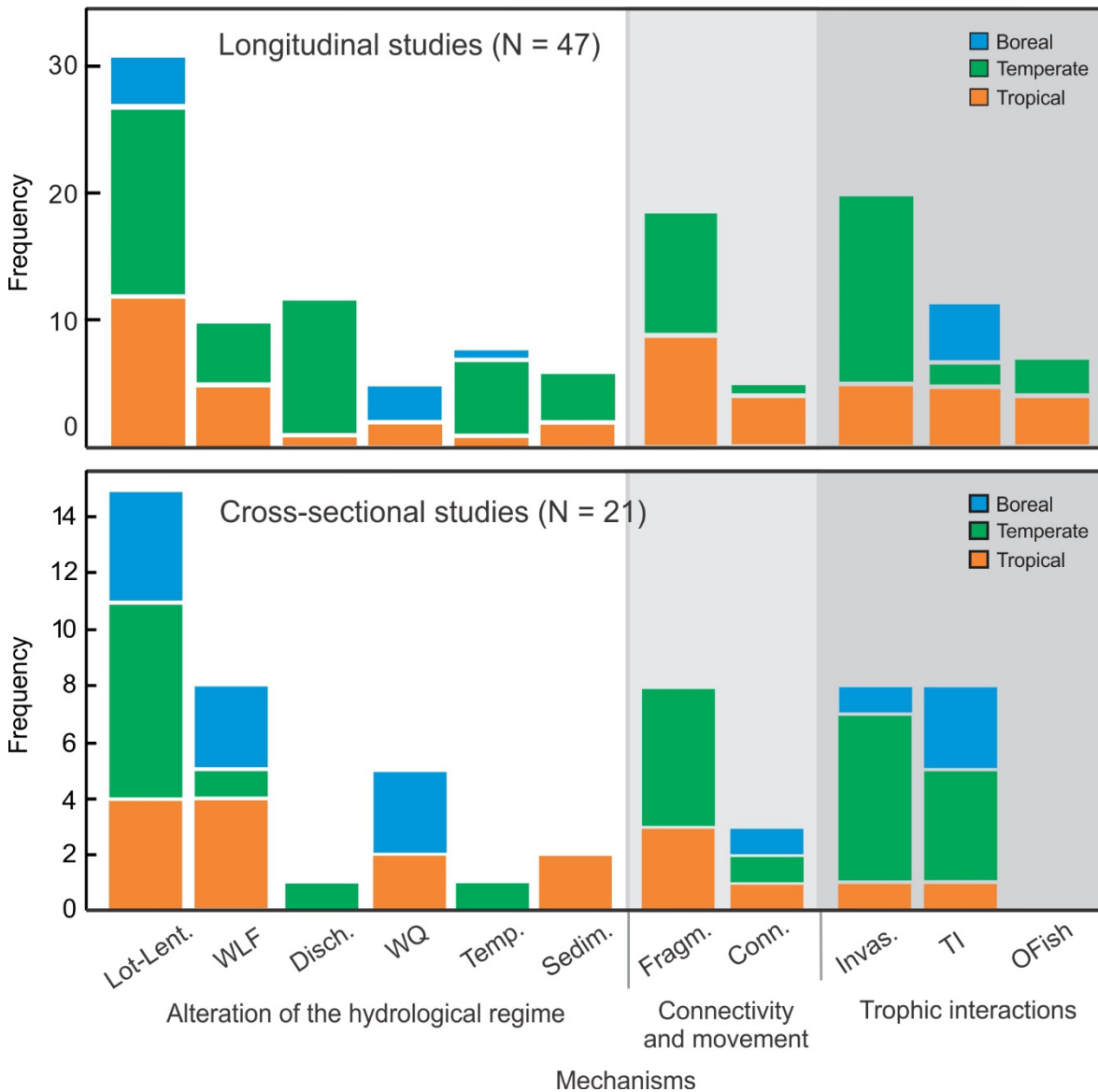


Figure 5. Summary of the main mechanisms affecting fish biodiversity in a) longitudinal and b) cross-sectional studies. Frequency distribution of the main mechanisms reported by the authors (in the abstract and/or conclusions) and potentially responsible for the change in fish assemblages observed in the 67 references. The mechanisms were classified into three main classes: Alteration of the hydrological regime, alteration of the connectivity and fish movement, and impacts on the trophic interactions. Lot-Lent. = change from a lotic to lentic condition, WLF = water level fluctuation in the reservoir, Disch. = change in discharge downstream of the dam, WQ = change in water quality excluding temperature, Temp. = change in temperature upstream and downstream of the dam, Sedim. = change in sedimentation regime, Fragn. = dams fragment river dynamics and can create a barrier to movement, Conn. = increased connectivity of the drainage basins, Invas. = increase in the number of invasive species, TI = change in the strength of the trophic interactions (predation and competition), OFish = overfishing of some species.