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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20    will be archived in Figshare and the data DOI will be included at the end of the article.

## Abstract

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

## Introduction

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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   unprecedent 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).

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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

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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*

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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; Travnichek & 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; Lüdecke & 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

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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)*

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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

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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

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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; Messager *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; Lévêque *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

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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 $\pm$ 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

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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).

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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

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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

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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

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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.

**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

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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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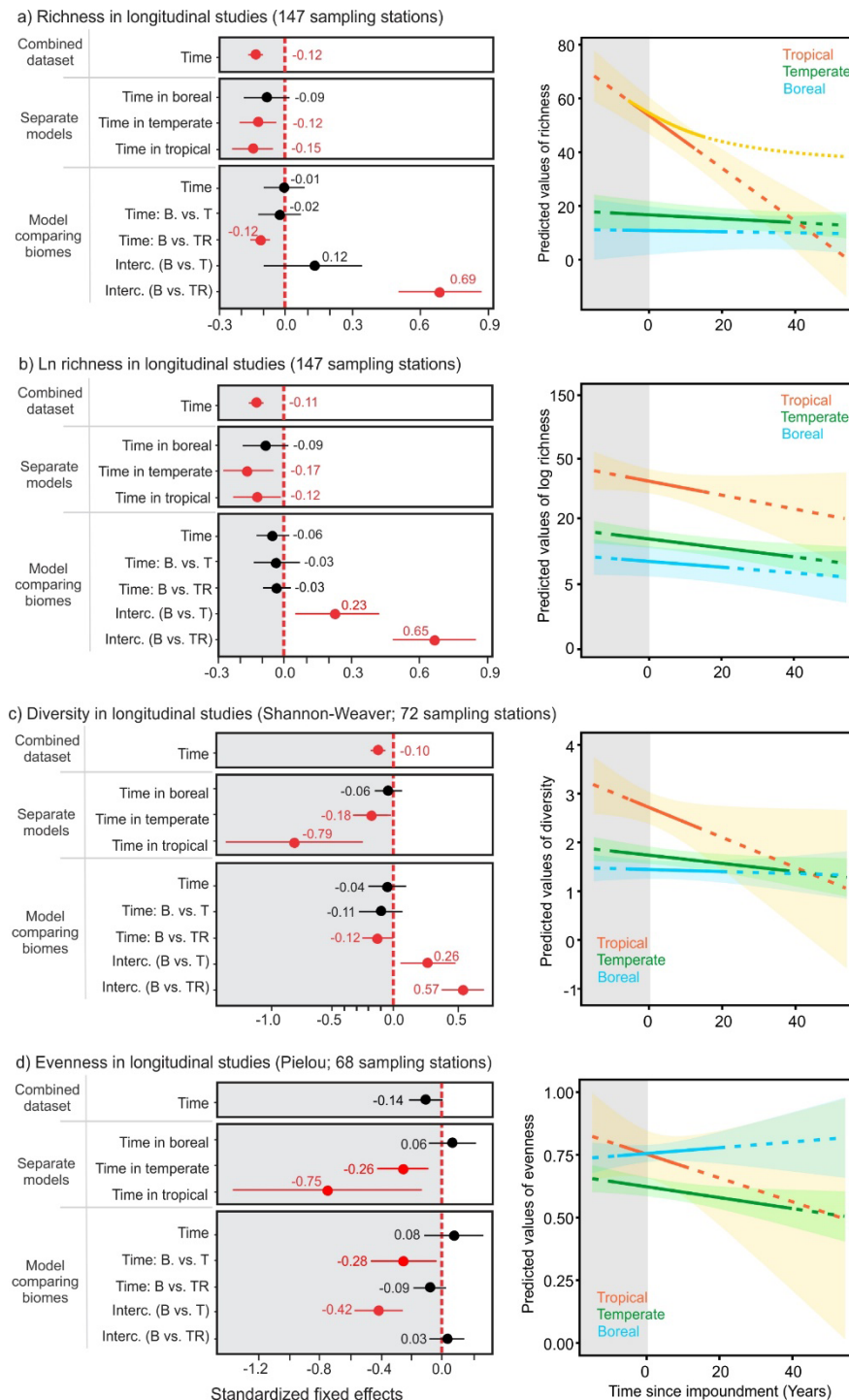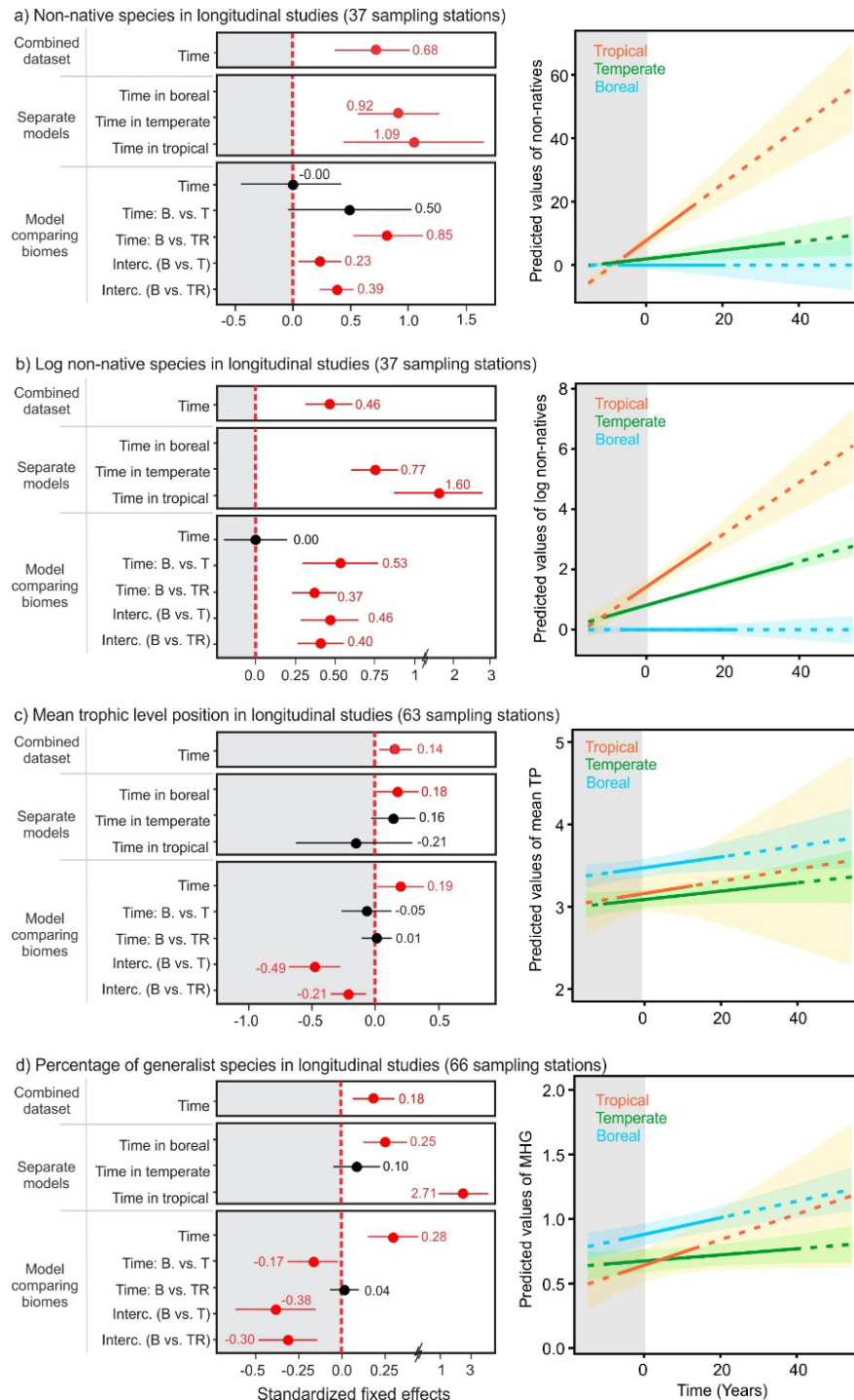865         Oklahoma. *Proc. Southeast. Assoc. Fish Wildl. Agencies*, 26, 530–540.

**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 li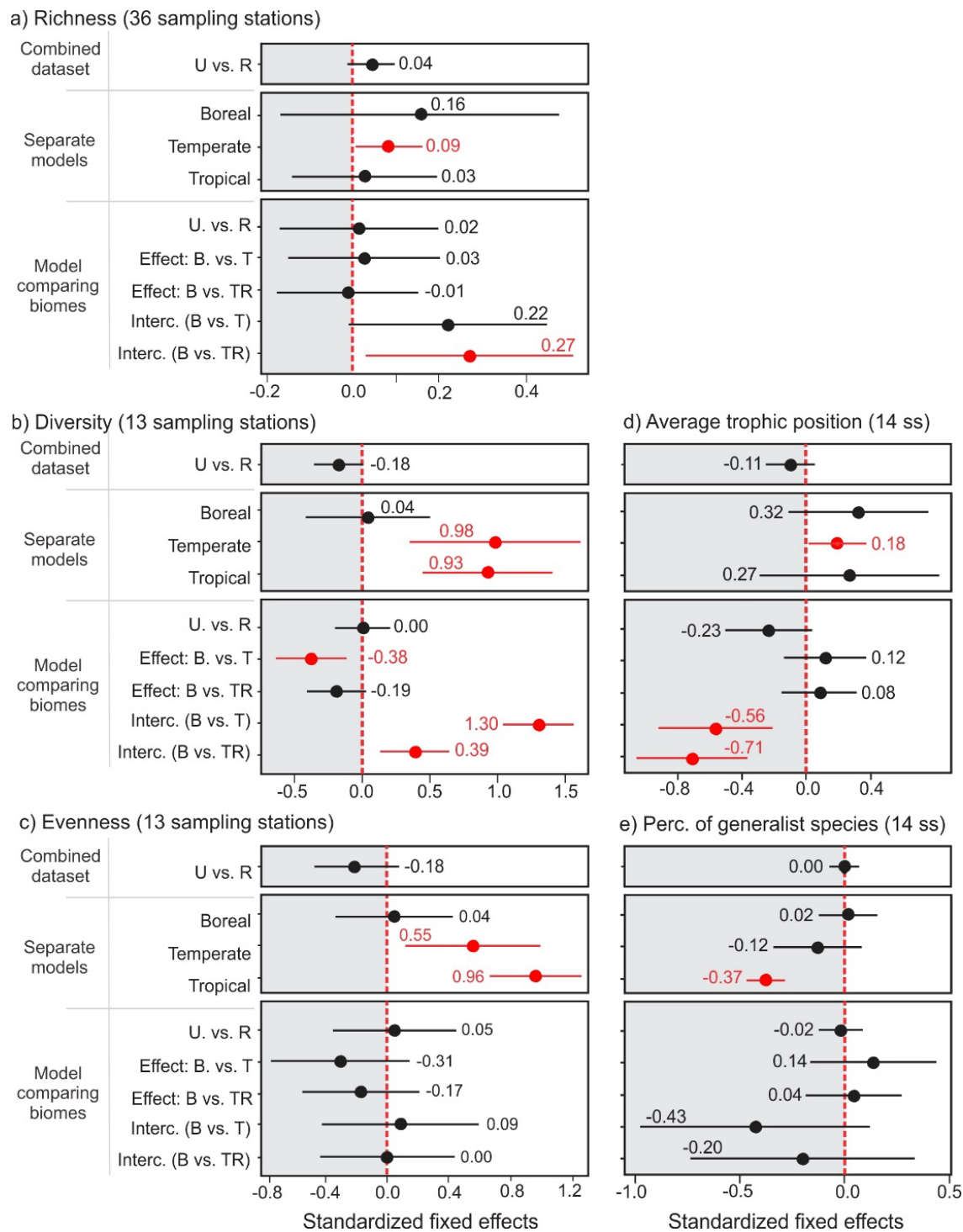nes represent model extrapolation. In a), the non-linear curve in the tropics is a more plausible pattern but cannot be modeled.

**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.
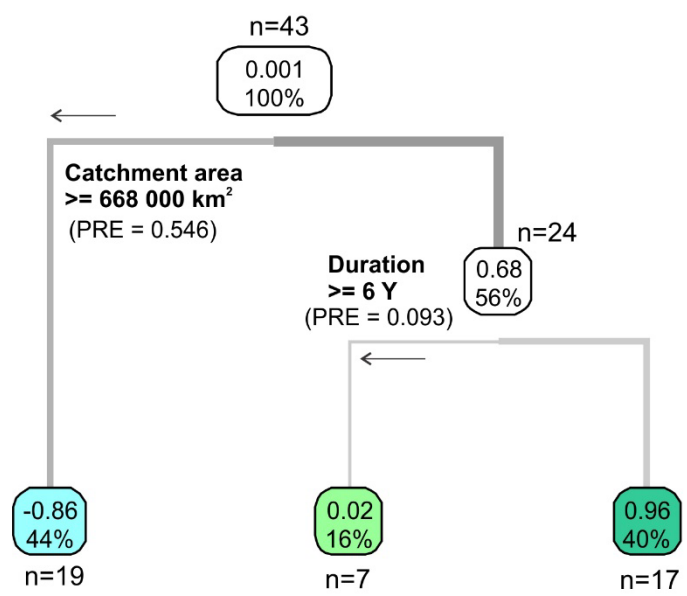
**Figure 3. Standardized effect size in cross-sectional studies for taxonomic and fish assemblage metrics.** Standardized fixed effects coefficients and standard error from the mixed effects models comparing the temporal trends in a) richness, b) diversity, c) evenness, d) mean trophic level position, 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.
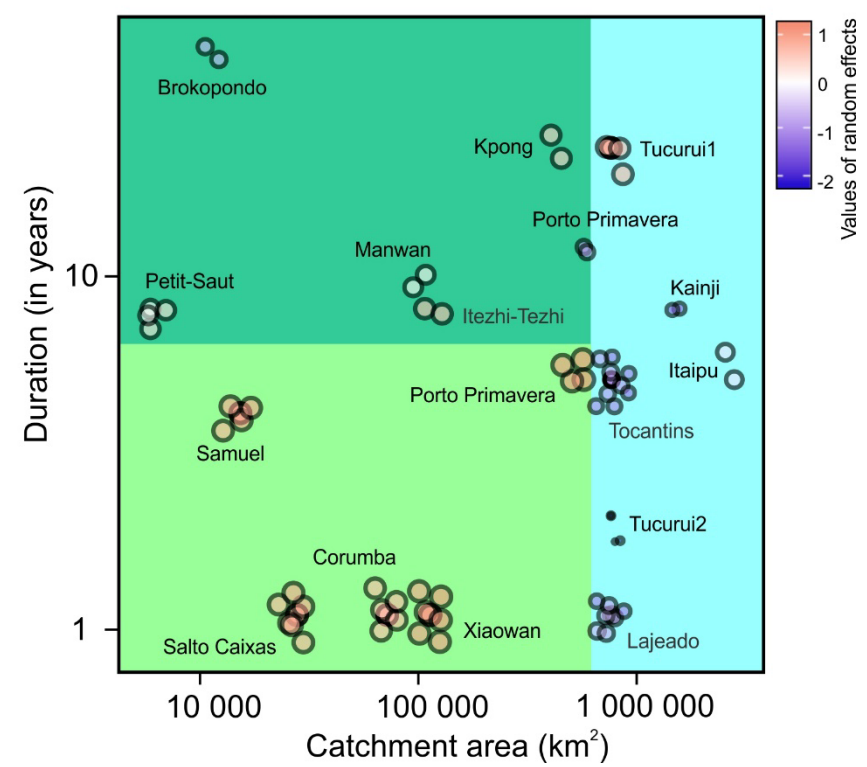
**Figure 4. Regression tree predicting the heterogeneity in random effect values (RE) from the mixed effect model examining the effect of time since impoundment on richness in the tropics.** a) plot of the pruned regression tree showing the mean value and proportion of the dataset in boxes at each step 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.
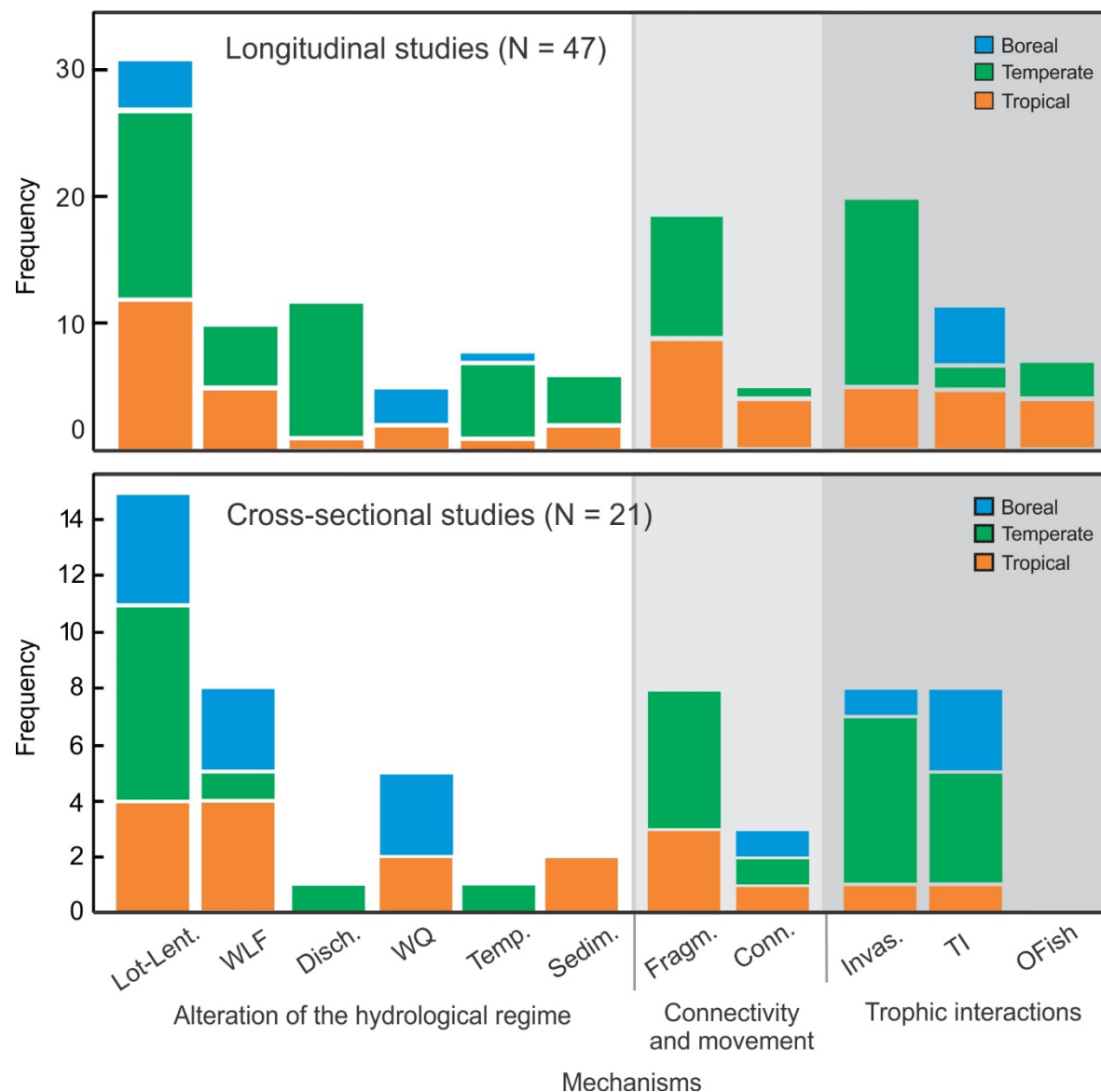
**Figure 5. Summary of the main mechanisms affecting fish biodiversity in a) longitudinal and b) cross-sectional studies.** Frequency distribution of the main mechanisms reported by the authors (in the abstract and/or conclusions) and potentially responsible for the change in fish assemblages observed 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, Fragm. = 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.