TITLE: Changes in freshwater macroinvertebrate richness due to river impoundment in the United States

Gabrielle Trottier^{1*}, Katrine Turgeon², Francesca Verones³, Daniel Boisclair⁴, Cécile Bulle^{1,5} and Manuele Margni¹

*Corresponding author: gabrielle.trottier@polymtl.ca; 514-340-4711 #2136

¹ CIRAG, Polytechnique Montréal, Département de mathématiques et génie industriel, C.P. 6079, succ. Centre-Ville, Montréal, Québec, Canada, H3C 3A7
manuele.margni@polymtl.ca

² ISFORT, Université du Québec en Outaouais, 58 rue Principale, Ripon, Québec, Canada, J0V1V0
katrine.turgeon@uqo.ca

³ Industrial Ecology Program, Department of Energy and Process Engineering, NTNU, Sem Sælands vei 7, Trondheim, Norway, 7491
francesca.verones@ntnu.no

⁴ Département des sciences biologiques, Université de Montréal, C.P. 6128 Succursale « Centre-ville », Montréal, Québec, H3C 3J7, Canada
daniel.boisclair@umontreal.ca

⁵ Département de stratégie, responsabilité sociale et environnementale, École des sciences de la gestion, Université du Québec à Montréal, Montréal, Québec, Canada, H3C 3P8
bulle.cecile@uqam.ca

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ABSTRACT

Whether it is for water supply, flood control or hydropower uses, the transformation of a river into a reservoir can impact freshwater ecosystems and their biodiversity. Using the National Lake Assessment (NLA; 148 reservoirs) and the National Rivers and Streams Assessment (NRSA; 2121 rivers and streams) of the United States Environmental Protection Agency (USEPA), we evaluated the impacts of river impoundment on macroinvertebrate biodiversity at three spatial scales (*i.e.*, reservoir, ecoregion and country scale). We used a space-for-time substitution approach to model the impact of impoundment (*i.e.*, we used rivers and streams as the before-impoundment conditions, and reservoirs as the after-impoundment conditions). We expressed the impact on biodiversity in terms of potentially disappeared fraction of species (PDF) to be used in the life cycle assessment (LCA) framework. To understand the role of regionalization, and some potentially influential variables, on changes in macroinvertebrate richness following impoundment in the United States, we used analyses of variance (ANOVAs) as well as variation partitioning, and developed empirical predictive models. Overall, 26% of macroinvertebrate taxa disappeared following impoundment in the United States, and PDFs followed a longitudinal gradient across ecoregions (*i.e.*, higher PDFs in the western part of the country, lower PDFs in the eastern part). We also observed that large and oligotrophic reservoirs, located in high elevation had high PDFs. This study provides the first empirical PDF values for macroinvertebrates to be used as characterization factors (CFs) by LCA practitioners. We also provide strong support for regionalization and a simple predictive model to be used by LCA modellers.

1. INTRODUCTION

Population growth in the last century has inevitably resulted in an increased need, and use of water by humans (WCD 2000, Strayer and Dudgeon 2010, Fang and Jawitz 2019). The extraction of water and the regulation of water flow by dams (*i.e.*, creation of storage reservoirs for drinking water, flood control, and energy production) or the water diversion by channels (*i.e.*, irrigation and navigation) has benefited human populations across the globe (Richter et al. 2003, Lehner et al. 2011, Chen et al. 2016). Despite some clear societal benefits, water use is often accompanied by a myriad of environmental impacts on freshwater ecosystems (Rosenberg et al. 2000, Vörösmarty 2005, Abell et al. 2008, Renöfalt et al. 2010, Gracey and Verones 2016).

The environmental impacts of a dam, and of transforming a river into a reservoir are particularly well documented (Agostinho et al. 2008). The geomorphology of a reservoir is different from the one of the original river. The water depth, as well as the hydrological regime (*i.e.*, lentic instead of lotic system), are notably altered. Water depth is known to affect ecological community structure and productivity, alongside with total dissolved solids (Ryder 1965, 1982, Ryder et al. 1974, Youngs and Heimbuch 1982, Jackson et al. 1990, Rempel and Colby 1991). A change in the hydrological regime affects several physical and biological processes (erosion/sedimentation; biological cue to life-history strategies), and the organisms' capacity to thrive and survive in these ecosystems. Those changes can ultimately impact ecosystem biodiversity, productivity, and the provision of ecosystem services (Poff et al., 1997; Bunn & Arthington, 2002; Dudgeon et al., 2006). If we wish to sustain these services and preserve the ecological

integrity of freshwater ecosystems, it is imperative to understand the potential impacts of dams and river impoundment on freshwater biodiversity.

The life cycle assessment (LCA) approach allows the evaluation of the potential environmental impacts of a product, process, or service throughout its entire life cycle (*i.e.*, from resource extraction to end of life; ISO, 2006). Emissions and resource extraction (*i.e.*, inventory flows) related to all activities involved in the life cycle of a product, process, or service are first inventoried and then characterized into potential environmental impacts through so-called characterization factors (CFs) (Curran et al. 2011). CFs are then modeled up to damages on different areas of protection, from an anthropocentric point of view, and traditionally include ecosystem quality, human health, and natural resources (Verones et al. 2017). The ecosystem quality area of protection typically aggregates multiple damage level indicators, such as eutrophication, acidification, ecotoxicity, as well as damages from climate change, water use and land use. Damage level indicators regarding the ecosystem quality area of protection are traditionally expressed in $\text{PDF} \cdot \text{m}^2 \cdot \text{yr}$ units, where PDF stands for potentially disappeared fraction of species, and can be aggregated into one common damage level indicator or kept disaggregated (Verones et al., 2017, Milà i Canals et al., 2007).

The impacts of transforming a river into a reservoir on ecosystem quality have received little attention in LCA. To our knowledge, only few attempts to evaluate changes in fish richness (*i.e.*, the number of taxa present) following impoundment have been made (see Turgeon et al., 2019 [submitted], available as a preprint and Dorber et al., 2019). In this study, we assessed the potential impacts of impoundment (*i.e.*, transforming a river into a reservoir) using empirical data on changes in freshwater

macroinvertebrate richness based on a dataset of 148 reservoirs and 2121 rivers and streams across the continental United States. Using a space-for-time substitution, we derived PDFs at three spatial scales: the scale of the United States, the scale of nine ecoregions, and the scale of reservoirs. Finally, we developed an empirical predictive model, built from the most influential variables affecting PDFs at the reservoir scale, to be used by LCA modellers.

2. MATERIAL AND METHODS

2.1 Impact characterization framework

CFs are determined by characterization models. These models are either based on the modelling of the environmental mechanisms that link environmental interventions to impact indicators, or on empirical observations of environmental interventions on impact indicators. Two categories of damage level indicators exist for the ecosystem quality area of protection. Traditionally, ecosystem quality damage assessment models used to quantify the temporary disappearance of species integrated in time and space, whether this was expressed in $\text{PDF} \cdot \text{m}^2 \cdot \text{yr}$ (*i.e.*, a potentially disappeared fraction of species over a given area and duration; Jolliet et al., 2003) or in $\text{species} \cdot \text{yr}$ (Goedkoop et al. 2009). More recently, some models focused on the regional or global disappearance of species expressed in PDF, that is quantifying the permanent disappearance of species at the continental or global scale (de Baan et al. 2013, Chaudhary et al. 2015). Both categories of indicators are relevant and should be considered complementary. The first one allows to assessment of temporary degradation of an ecosystem that will ultimately recover (*e.g.*, a toxic contamination that ultimately is degraded and after which the affected ecosystem

recovers). The second one allows the assessment of the absolute disappearance of species that will never be recovered (*e.g.*, endemic species that disappeared because of land transformation). The indicator developed in the current research corresponds to the first category of indicators and is meant to quantify the temporary damage on freshwater ecosystems, more specifically macroinvertebrates, due to impoundment, and integrated in time and in space.

The framework proposed by de Baan (2013) and Chaudhary (2015) for land occupation has been adopted and adapted to assess the occupation of a water body. In this approach, the indicator builds on an empirical model assessing land use impacts on biodiversity, and is expressed in $\text{PDF} \cdot \text{m}^2 \cdot \text{yr}$. In this case, the CF is expressed in PDF units, or implicitly $\text{PDF} \cdot \text{m}^2 \cdot \text{yr} / \text{m}^2 \cdot \text{yr}$ of water body occupied. This CF is the observed change in taxa richness, with respect to a reference ecosystem, and multiplies the environmental intervention, which is expressed in terms of $\text{m}^2 \cdot \text{yr}$ of water body occupied. In the current research, we did not quantify the damage due to water body transformation but only the damage of water body occupation. To be able to quantify the damage of water body transformation in compliance with the Milà i Canals framework (2007), the time needed by the water body to recover after the impoundment ends would be needed and we don't have this information. That's why we limited ourselves to the assessment of the impacts of occupation.

Here, we used an empirical space-for-time substitution approach to examine the difference in macroinvertebrate richness between a natural reference ecosystem and an impacted system to generate empirical PDFs representing the impacts of occupying a river, which has been transformed into a reservoir. To calculate CFs, we used the PDF; or

implicitly $\text{PDF} \cdot \text{m}^2 \cdot \text{yr} / \text{m}^2 \cdot \text{yr}$ of water body occupied) as a unit to express the proportional loss of macroinvertebrate taxa following impoundment, specific to nine ecoregions and 148 reservoirs in the United States.

2.2 Data collection

2.2.1 Macroinvertebrate richness

To extract data on macroinvertebrate richness in reservoirs (impacted sites; after impoundment), we used the 2012 National Lake Assessment (NLA), which is a United States Environmental Protection Agency (USEPA) effort to statistically survey numerous ponds, lakes and reservoirs in the United States and their associated biological, chemical, physical and recreational characteristics (USEPA 2015a). From this dataset, we retrieved macroinvertebrates richness (*i.e.*, RICHNESS; taxonomic resolution at the generic level, except for oligochaetes, mites, and polychaetes, which were identified to the family level, and ceratopogonids at the subfamily level; USEPA, 2017), a unique identifier (UID) for each reservoir, the latitude (LAT), longitude (LON), the ecoregion (ECO), and a suite of environmental variables (Table 1) from 148 reservoirs across the United States (Figure 1, reservoirs shown in black). It was impossible to get macroinvertebrate richness for the pre-impoundment period for the same ecosystem. To get an estimate of macroinvertebrates taxa richness from pre-impoundment conditions, we used the space-for-time substitution approach (Pickett 1989) and used the 2008-2009 National Rivers and Streams Assessment (NRSA). This dataset is also a USEPA initiative to survey U.S. rivers and streams' biological, chemical, physical, and recreational characteristics (USEPA 2015b). The NRSA dataset serves as reference for pre-impoundment characteristics, given the assumption that taxa richness in rivers and streams in the

169 **Table 1.** Table showing the four matrices used for variation partitioning, as well as the variables they included, a short definition, their
170 respective units and the type of variable they are (*i.e.*, N for numerical and F for categorical). Variables in bold are the variables
171 selected for the parsimonious variation partitioning.

MATRIX	VARIABLE	DEFINITION	UNITS	TYPE
SPATIAL	LATITUDE	LATITUDE OF RESERVOIR	DECIMAL DEGREES	N
	LONGITUDE	LONGITUDE OF RESERVOIR	DECIMAL DEGREES	N
	ECOREGION	NARS 9-LEVEL REPORTING REGIONS, BASED ON AGGREGATED OMERNIK LEVEL III ECOREGIONS	-	F
	TEMPERATURE	ANNUAL MEAN AIR TEMPERATURE, SPECIFIC TO ECOREGION	°C	N
	PRECIPITATION	ANNUAL MEAN PRECIPITATIONS, SPECIFIC TO ECOREGION	MM	N
	LC.FORESTED	PERCENTAGE OF LAND COVER IN ECOREGION THAT IS FORESTED	%	N
	LC.CULTIVATED.PASTURE	PERCENTAGE OF LAND COVER IN ECOREGION THAT IS CULTIVATED PASTURES	%	N
	LC.WETLANDS	PERCENTAGE OF LAND COVER IN ECOREGION THAT IS WETLANDS	%	N
	LC.GRASSLAND.SHRUBS	PERCENTAGE OF LAND COVER IN ECOREGION THAT IS GRASSLANDS AND SHRUBS	%	N
	LC.DEVELOPED	PERCENTAGE OF LAND COVER IN ECOREGION THAT IS DEVELOPED	%	N
	LC.WATER.BARREN	PERCENTAGE OF LAND COVER IN ECOREGION THAT IS WATER OR BARREN	%	N
PHYSICAL	AREA	SURFACE AREA OF RESERVOIR	HA	N
	ELEVATION	ELEVATION RESERVOIR COORDINATES	M	N
	MACROPHYTES	INDEX OF TOTAL COVER OF AQUATIC MACROPHYTES OF RESERVOIR	-	N
	SHALLOW.WATER	SHALLOW WATER HABITAT CONDITION INDICATOR	-	N
	RIP.VEG	RIPARIAN VEGETATION CONDITION INDICATOR	-	N

174 **Table 1. Continued**

MATRIX	VARIABLE	DEFINITION	UNITS	TYPE
CHEMICAL	TROPHIC.STATE	TROPHIC STATE OF RESERVOIR (<i>i.e.</i> , OLIGOTROPHIC AND EUTROPHIC)	-	F
	SECCHI	SECCHI DEPTH	M	N
	DOC	DISSOLVED ORGANIC CARBON LEVEL	MG/L	N
	PTL	TOTAL PHOSPHORUS LEVEL	UG/L	N
	COLOR	WATER COLOR	PCU	N
	COND	WATER CONDUCTIVITY LEVEL	US/CM	N
	NTL	TOTAL NITROGEN LEVEL	MG/L	N
	PH	PH LEVEL	PH SCALE	N
	METHYLMERCURY	TOP SEDIMENT METHYLMERCURY LEVEL	NG/L	N
	CHLA	CHLOROPHYLL-A MEASUREMENT RESULT OF RESERVOIR	UG/L	N
HUMAN	BUILDINGS	HUMAN INFLUENCE BY BUILDINGS AROUND RESERVOIR SHORELINE	-	N
	COMMERCIAL	HUMAN INFLUENCE BY COMMERCIAL ACTIVITIES AROUND RESERVOIR SHORELINE	-	N
	CROPS	HUMAN INFLUENCE BY CROPS AROUND RESERVOIR SHORELINE	-	N
	DOCKS	HUMAN INFLUENCE BY DOCKS AROUND RESERVOIR SHORELINE	-	N
	LANDFILL	HUMAN INFLUENCE BY LANDFILL AROUND RESERVOIR SHORELINE	-	N
	LAWN	HUMAN INFLUENCE BY LAWN AROUND RESERVOIR SHORELINE	-	N
	PARK	HUMAN INFLUENCE BY PARKS AROUND RESERVOIR SHORELINE	-	N
	PASTURE	HUMAN INFLUENCE BY PASTURES AROUND RESERVOIR SHORELINE	-	N
	POWERLINES	HUMAN INFLUENCE BY POWERLINES AROUND RESERVOIR SHORELINE	-	N
	ROADS	HUMAN INFLUENCE BY ROADS AROUND RESERVOIR SHORELINE	-	N
	WALLS	HUMAN INFLUENCE BY WALLS AROUND RESERVOIR SHORELINE	-	N
	OTHER	HUMAN INFLUENCE BY OTHER AROUND RESERVOIR SHORELINE	-	N

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surrounding area of a reservoir from the NLA dataset would be comparable to what would have been found in a river prior to its transformation into a reservoir. The same variables were collected (UID, LAT, LON, ECO and RICHNESS) for 2121 rivers and streams across the United States (Figure 1, rivers and streams shown in white).

Figure 1. Map of the USEPA-NLA, where reservoirs ($n = 148$) and the USEPA-NRSA rivers and streams data points ($n = 2121$), color-coded according to ecoregions.

2.2.2 Native riverine taxa definition

The taxa pool observed in rivers and streams was used as a baseline (reference; native riverine taxa) to compare taxa richness before and after impoundment. Using only native riverine taxa excluded all new taxa that would be encountered in a lake-like habitat (*i.e.*, reservoir), since they would most likely not be present in a pre-impoundment, river-like habitat. Comparing to a mean reference in each ecoregion, instead of a single

river/stream close to the reservoir, ensures that we are measuring the impacts from a set of reference conditions and not a singular pristine, or impacted, river or stream.

2.2.3 Ecoregions

Reservoirs and rivers/streams were distributed across nine terrestrial ecoregions to see if patterns varied across the United States; Coastal Plains (CPL), Northern Appalachians (NAP), Northern Plains (NPL), Southern Appalachians (SAP), Southern Plains (SPL) Temperate Plains (TPL), Upper Midwest (UMW), Western Mountains (WMT) and Xeric (XER; Figure 1). These ecoregions are the result of an aggregation (Omernik, 1987; Herlihy et al., 2008), based on similar environmental characteristics (*i.e.*, climate, vegetation, soil type and geology) and macroinvertebrate assemblages similarity of the level III ecoregions (Omernik 1987), which was adopted by the USEPA for both the NLA and NRSA surveys (USEPA 2016). For each ecoregion, we also extracted some land cover variables (USEPA, 2016; Table 1, spatial matrix) and variables related to human impacts (Table 1, human matrix).

2.2.4 PDFs calculation

We calculated PDFs as the difference in richness between reference river (x) and impacted reservoir richness (y), divided by the reference river richness (x). At the United States scale (PDF_{usa}), we compared overall United States mean native riverine richness in rivers and/or stream (one observation of richness per river and/or stream averaged over the United States; $\bar{x}_{usa}$) to the overall United States mean richness in reservoirs (one observation of richness per reservoir averaged over the United States; $\bar{y}_{usa}$) to get a United States specific change in richness, as per equation 1;

$$PDF_{usa} = \frac{\bar{x}_{usa} - \bar{y}_{usa}}{\bar{x}_{usa}} \quad \text{Eq. 1}$$

At the ecoregion scale (PDF_{eco}), we compared ecoregion mean native riverine richness of all rivers and/or stream (one observation of richness per river and/or stream averaged over each ecoregion; $\bar{x}_{eco}$) to the ecoregion mean richness in reservoirs (one observation of richness per reservoir averaged over each ecoregion; $\bar{y}_{eco}$) to get an ecoregion specific change in richness, as per equation 2;

$$PDF_{eco} = \frac{\bar{x}_{eco} - \bar{y}_{eco}}{\bar{x}_{eco}} \quad \text{Eq. 2}$$

At the reservoir scale (PDF_{res}), we compared ecoregion mean native riverine richness of all rivers and stream (one observation of richness per river and/or stream averaged over each ecoregion; $\bar{x}_{eco}$) to the richness of a specific reservoir within the same ecoregion (one specific richness observation per reservoir, no averaging; y_{res}) to get a reservoir specific change in richness, as per equation 3;

$$PDF_{res} = \frac{\bar{x}_{eco} - y_{res}}{\bar{x}_{eco}} \quad \text{Eq. 3}$$

2.3 Data analysis and empirical modelling

2.3.1 Regionalization and ANOVA

Regionalization refers to the integration of existing spatial variability to improve results' representativeness and reduce spatial uncertainties. Regionalization is a critical aspect in LCA (Patouillard et al. 2016, Yang 2016). CFs must be developed at an appropriate scale to capture the environmental impacts of a product, process, or service, and, to inform decision-makers. Here, we examined if PDFs differed across nine terrestrial ecoregions (Herlihy et al. 2008) that were adopted by both the NLA and NRSA surveys. As a first step, we ran an analysis of variance (ANOVA) to determine if PDFs differed across ecoregions (*i.e.*, ecoregion scale) and thus, test the relevance of this regionalization scale. To do so, we used a one-way randomized-group ANOVA. We

assessed the significance of regionalization at the ecoregion scale and identified which ecoregions were significantly different from each other based on the standardized mean difference and their confidence intervals (CIs). We conducted the ANOVA with the *ind.oneway.second* function in the *rpsychi* package version 0.8 (Okumura 2012).

2.3.2 Variation partitioning to explain the variation observed in our PDFs

As a second step, we were interested to understand which variables, associated to reservoirs or ecoregions, explained the variation observed in PDFs at the reservoir scale. To do so, we used variation partitioning (Legendre 2008). Variation partitioning describes how a set of explanatory matrices explains the shared variation observed in a response variable (*i.e.*, PDF). We built four explanatory matrices based on the availability of the descriptive variables, and selected relevant variables potentially influencing richness based on expert judgment, from the NLA and NRSA datasets; a spatial matrix (location of the reservoirs; *i.e.*, latitude, ecoregion, and types of land covers), a physical matrix (variables describing the reservoir; *i.e.*, reservoir area, elevation), a chemical matrix (biochemical state of the reservoir; *i.e.*, pH, trophic state, dissolved organic carbon) and a human activity matrix (human influence around the reservoir shoreline; *i.e.*, influence of crops, influence of docks). See Table 1 for a complete description of the variables included in each matrix. To achieve the most parsimonious analysis, we performed a stepwise selection procedure on each explanatory matrix to identify which variable, or combination of variables, best-explained the variation in PDFs (variables in bold; Table 1). Variation partitioning was conducted with the *varpart* function in the *vegan* package version 2.5-2 (Oksanen et al. 2019).

2.3.3 Empirical modelling

As a third step, we developed an empirical predictive model explaining the variation observed in our PDFs to be used by LCA modellers. We combined the variables identified by the variation partitioning analysis as the most influential variables to explain the variation in PDFs from the four above-mentioned explanatory matrices into one matrix and performed a model selection procedure. However, as opposed to the variation partitioning, ecoregion was not used in the empirical model to avoid constraining the model to the ecoregions of the United States and thus, allows extrapolation of the model. We use an automatic forward stepwise model selection procedure, which builds a model by maximizing adjusted R^2 , stopping the selection when it starts to decrease (Oksanen et al. 2019). We used the recommended information theoretic approach based on AIC (Burnham and Anderson 2004) and a Bayesian information criterion (BIC; Schwarz, 1978) to compare the candidate models, and select the model with the highest support. Predictive modelling was performed with the function *ordiR2step*, also from the *vegan* package. All statistical analyses were made using R version 3.0.2 (R Core Team 2013).

3. RESULTS

3.1 Variation in PDFs across ecoregions and scales

Empirical PDFs showed a loss in macroinvertebrate richness following impoundment in the United States, and this loss followed a longitudinal gradient associated with the ecoregions (Figure 2). At the scale of the United States, 26% of macroinvertebrate taxa disappeared in response to river impoundment ($\text{PDF} = 0.255 \pm 0.123$ [mean $\pm$ SE]; Table 2 and Figure 2). At the scale of the ecoregion, six out of nine ecoregions showed a significant loss of macroinvertebrate taxa, varying from $0.049 \pm$

0.048 to 0.472 ± 0.061 , and one ecoregion (CPL), showed a significant gain of macroinvertebrate taxa (*i.e.*, -0.242 ± 0.114 ; Table 2 and Figure 2). PDFs in most ecoregions significantly differed from each other except for NAP, NPL and UMW. Those ecoregions were characterized by small sample sizes (respectively, $n = 4, 8$ or 2 ; Figure 3). Results from the ANOVA suggest a longitudinal gradient of impact. At the reservoir scale, PDFs varied from -0.995 ± 0.640 (observation $\pm$ pooled SD) to 1.000 ± 0.323 , and 62% of the reservoirs showed a significant loss of macroinvertebrates taxa (Table A1).

Figure 2. Barplot showing a mean PDF ($\pm$ 95% confidence intervals) at the USA level (shown in dark grey) and at the ecoregion level (color-coded with ecoregions as a gradient of intensity). We used letter to identify which ecoregion mean PDF differ or not from each other. When two bars share the same letter, they are not significantly different from each other.

Table 2. Table showing the mean PDF ($\pm$ 95% confidence intervals) values for the USA and the nine ecoregions. Sample number is also shown (n).

Ecoregion	PDF.m ² .yr/m ² .yr	$\pm$ 95% CIs	n
USA	0.255	0.123	148
CPL	-0.242	0.182	13
SPL	-0.037	0.101	27
TPL	0.049	0.085	16
NAP	0.108	0.114	4
SAP	0.162	0.089	13
NPL	0.175	0.111	8
UMW	0.293	0.122	2
XER	0.334	0.143	32
WMT	0.472	0.157	34

3.2 Variables explaining the variation in PDFs

At the reservoir scale, the four matrices (*i.e.*, spatial, physical, chemical, and human) explained 50% of the total variation observed in PDFs (variation partitioning; Figure 3; Table A2 for details on the percentages). About 42% of the variation was explained by the combined effects of the spatial (*i.e.*, ecoregion) and physical (*i.e.*, area of the reservoir and its elevation) matrices. The ecoregion (in the spatial matrix) explained 27% of the variation, over which 25% of this variation was shared with the physical matrix, 12% was shared with the chemical matrix (*i.e.*, pH and trophic state) and 14% was shared with the human matrix (*i.e.*, presence of lawn and road adjacent to the reservoir shoreline). The physical matrix explained 40% of the variation. Elevation and reservoir area alone (variation not shared with the other matrices) explained 15% of the

variation. The chemical and human matrices explained respectively 18% and 19% of the variation.

Figure 3. Venn diagram of the variation partitioning of a response matrix (PDF) explained by four matrices, that is spatial matrix (ECO), physical matrix (ELE + AREA), chemical matrix (T.S + PH) and human matrix (LAWN + ROAD). Values < 0 not shown.

3.3 PDFs predictive model

According to the predictive models (Equations 4 and 5; Figure 4) 50% of the observed variation in PDFs (partial $R^2_{adj} = 0.434$; p -value < 0.001) was explained by elevation (33%), trophic state (*i.e.*, oligotrophic or eutrophic reservoir; 11%), and reservoir surface area (< 1%). PDF was positively related to reservoir elevation; the higher the elevation, the higher the PDF (Figure 4). PDF was also negatively related to eutrophication status. PDFs were higher in oligotrophic reservoirs (<10µg/l total

phosphorus), and lower in eutrophic reservoirs (>10µg/l total phosphorus). As for reservoir surface area, there was a positive relationship between reservoir surface area and PDF; bigger reservoir had a higher PDF than smaller ones (Figure 4). In other words, large oligotrophic reservoirs located at higher elevation were most likely to have higher macroinvertebrate PDF.

$$\text{PDF}_{\text{OLIGOTROPHIC}} = -0.054(\pm 0.155) + 0.015(\pm 0.002) \cdot \text{sqrt}(\text{ELEVATION}) + 0.121(\pm 0.038) \cdot \log_{10}(\text{AREA}) \quad \text{Eq. 4}$$

Values in parentheses are standard error (SE) of the estimate.

$$\text{PDF}_{\text{EUTROPHIC}} = -0.474(\pm 0.091) + 0.015(\pm 0.002) \cdot \text{sqrt}(\text{ELEVATION}) + 0.121(\pm 0.038) \cdot \log_{10}(\text{AREA}) \quad \text{Eq. 5}$$

Figure 4. Graphical representation of our best empirical model showing the relationship between potentially disappeared fraction of species (PDF.m².yr/m².yr) and reservoir elevation (square-rooted). Trophic state is color-coded and point size is representative of reservoir surface area.

4. DISCUSSION

From the analysis of 148 reservoirs and 2121 rivers and streams across the continental United States, our results showed a loss of about 26% of macroinvertebrate taxa following impoundment at the scale of the United States. This result is consistent with the literature estimates of the impacts of hydropower on macroinvertebrate richness across the world (Kraft 1988, Englund and Malmqvist 1996, Malmqvist and Englund 1996, Jackson et al. 2007, Valdovinos et al. 2007, Takao et al. 2008, Aroviita and Hämäläinen 2008, White et al. 2011, Behrend et al. 2012, Kullasoot et al. 2017). PDFs also varied across ecoregions. More than 25% of the total variation observed in PDFs was explained by the nine ecoregions, pressing the need for regionalized CFs. We provided evidence that the empirical PDFs values for macroinvertebrates were consistent across our three spatial scales (country, ecoregions and reservoirs). Overall, our empirical PDFs can be used as CFs by LCA practitioners to evaluate the potential impact of reservoir occupation on the ecosystem quality area of protection. We also provided a simple predictive model based on three explanatory variables (*i.e.*, elevation, trophic state and reservoir surface area), and explaining 50% of the variation in macroinvertebrate PDFs. Reservoirs at higher elevation, with lower levels of eutrophication and bigger surface area were most likely to have higher PDFs. This predictive model could be used by LCA modelers to extrapolate CFs based on few explicative variables.

4.1 United States taxa loss and regionalization

At the scale of the United States, 26% of macroinvertebrate taxa disappeared following impoundment. The observed loss of native riverine macroinvertebrate taxa is an expected consequence of transforming a river into a reservoir. Macroinvertebrate taxa

are highly adapted to their local habitat conditions (McCafferty 1983, Wetzel 2001). If flow regime is altered, which is a key characteristic of local riverine habitat, we can expect a substantial loss of these river specific taxa (Bunn & Arthington, 2002; Agostinho et al., 2008). The observed loss of taxa also followed a longitudinal gradient. PDFs are higher in the western than in the eastern ecoregions. The higher loss of taxa in the reservoirs of the “Western Mountains” (WMT) and “Xeric” (XER) ecoregions might be due to the higher water stress conditions. Reference rivers in these ecoregions are characterized by a higher proportion of intermittent streams, especially in dryer environment (Levick et al. 2008, USEPA 2013). This intermittent nature leads to highly variable environmental conditions, which increases taxonomic and functional biodiversity (Stubington et al. 2017) and can lead to a potentially higher loss of taxa in reservoirs. Another complementary explanation to this higher PDF in the west could be related to reservoir topography and elevation (Figure A1). Reservoirs created in low relief environment can connect more waterbodies and watercourse than higher relief environment and can result in smaller PDFs, or even gains in taxa following impoundment (Gido et al. 2002, Gubiani et al. 2010). This enhanced water body connectivity can lead to a higher colonization pool, a higher resilience of the community, and can result in a lower loss of taxa following reservoir creation. This is very likely the case in the CPL ecoregion, which appears to be dominated by flat plains and a low relief topography (USEPA 2016), and is also the only ecoregion showing a potential appearance of taxa following reservoir creation. This ecoregion is also characterized by a high percentage of wetlands (USEPA, 2016), which can also enhance water body connectivity, and lead to negative PDF (*i.e.*, gain of taxa). Because information regarding

these variables (*i.e.*, water stress/intermittence, waterbody connectivity, general topography and wetland presence) was not readily available from the datasets, we cannot statistically validate their relevance. Nonetheless, these significant differences in ecoregions' PDFs strengthen the need for regionalization and the examination of multiple scales when developing CFs.

4.2 Trophic state

While elevation explained most of the variation in PDF, oligotrophic reservoirs (trophic state) had higher PDFs. One plausible explanation for this difference can be related to the low productivity nature of oligotrophic water bodies (Wetzel 2001). Considering that oligotrophic ecosystems sustain relatively low diversity (Dodson et al. 2000), oligotrophic reservoir PDFs are expected to be higher than eutrophic ones when compared with a mean ecoregion reference. The seven oligotrophic reservoirs vary in elevation (221 m to over 3000 m) and in surface area (9 ha to over 1900 ha). Eutrophic reservoirs showed a similar range in elevation and surface area, respectively 13 m to 3105 m and 4 ha to 6559 ha. This difference in PDF between oligotrophic and eutrophic reservoirs seems independent of these two variables. However, this observation was based on only seven oligotrophic reservoirs, versus 135 eutrophic reservoirs, a rather small and unbalanced sample size. We also observed that all oligotrophic reservoirs were located in the western part of the United States, the majority (*i.e.*, six out of seven) in the WMT (4) and XER (2) ecoregions. This observation could then be the result of a statistical artifact regarding the importance of ecoregion and could impose a limitation on the robustness of our model. Thus, caution is in order when it comes to interpreting this result.

4.3 Surface area

Reservoir surface area was also identified as an influential variable explaining variation in PDFs. While most of the reservoir surface areas ranged between 0 to 1500 ha, six particularly big reservoirs, between 2000 and 6000 ha, show higher loss of macroinvertebrates. Even though this trend is significant, it is quite weak considering the unbalanced sample size of big reservoirs versus average-sized reservoirs and the small variation explained (1%). These big reservoirs were also not clustered in one particular region of the United States or ecoregion, but well distributed in north-south and west-east gradients (Figure 1). While the majority of averaged sized reservoir were located between zero to over 3000 m of elevation, the six big reservoirs were located between zero and 1500m. They did not share a similar water usage (*e.g.*, hydropower, irrigation, recreation, etc.) and thus, no hypotheses can be drawn from the potential water extraction dynamic (*i.e.*, timing, rate, magnitude and frequency) or reservoirs usage on biodiversity impacts. One last plausible explanation could be related to reservoir bathymetry. Big shallow reservoirs usually have a substantial littoral zone (Zohary et al. 2014), which typically sustains higher macroinvertebrate productivity and diversity than its pelagic counterpart (James et al. 1998, Wetzel 2001). Water levels management (*e.g.*, fluctuations) in big shallow reservoirs can especially affect the survival of the macroinvertebrate community, thus resulting in higher loss of taxa (Aroviita and Hämäläinen 2008, White et al. 2011, Zohary et al. 2014). No bathymetry data was available from the datasets.

4.4 Limitations

In this study, we defined richness as the number of native riverine taxa. We did not account for the potential gain of lentic specific taxa following impoundment. When a

river is transformed into a reservoir, some riverine species are lost, and some lentic taxa are gained. This gain in species, as well as gain in exotic and non-native invasive taxa should not be considered as an ecosystem improvement. Based on the habitat diversity hypothesis (Williams 1964), we can advocate that lotic environments are more diversified than lake-like ones (*i.e.*, reservoirs). This hypothesis states that the diversity of species is directly related to the diversity of habitats. Thus, because of their narrowness and longitude, rivers run through a greater range of geological formations as well as geographical regions per unit of surface area, and vary more in terms of substrate, water temperature and flow dynamics than lotic environment of comparable depth and size (Horwitz 1978, Moyle and Li 1979, Eadie et al. 1986). The increased environmental variability and productivity, as well as the presence of micro-habitat heterogeneity in rivers is likely to support more species per surface area (Gorman and Karr 1978, Matthews 1982, Eadie et al. 1986). We could then think that even after a lotic environment is transformed into and a lentic one, there would still be less taxa in the lentic environment. Moreover, gain of lentic species after impoundment is often considered a misleading argument because the littoral zone in reservoirs is less complex, differs in physico-chemical conditions (Walker et al. 1992) and is generally affected by varying water levels. Those characteristics can affect the productivity of littoral areas, which are crucial to reservoir productivity, and can, in turn, affect its biodiversity. Another limitation of this study is that our characterization model is not independent from other impact categories, namely eutrophication. Because trophic state was defined as a significant variable to predict PDF, we need to incorporate this information in our model. In the LCA framework, eutrophication is already taken into account and thus,

using it in our model could cause some bias in the overall compilation of impacts (*i.e.*, double-counting). Finally, one last limitation from this study is the use of space-for-time substitution. We do not have a real before-after control impact study design. It was impossible to have access to river richness before impoundment so our results and suggested PDFs must be interpreted with caution.

5. CONCLUSION

In this study, by using space-for-time substitution, we showed that the transformation of a river into a reservoir resulted in a loss of 26% of macroinvertebrate taxa in the continental United States. This loss of richness also varied across ecoregions, pressing the need for regionalized CFs. Patterns were also consistent across scales (the United States, nine ecoregions and 148 reservoirs) where we observed a general loss of macroinvertebrate richness. These PDFs are destined to be used by LCA practitioners as CFs. We also derived a predictive model to estimate PDFs as a function of three explanatory variables; reservoir elevation, trophic state (*i.e.*, oligotrophic or eutrophic) and surface area. Despite a few highlighted limitations, the empirical CFs developed through this study constitute a strong contribution to assess the impacts of river impoundment on the ecosystem quality area of protection. A natural follow-up to this study would be to integrate macroinvertebrate CFs with fish CFs, from Turgeon et al. (2019, *submitted*; available as a preprint) to build more robust CFs. Moreover, we also recommend evaluating the environmental relevance of the predictive models in other geographical contexts. These steps would be advances toward a more unified and global coverage of the impacts of reservoir occupation on its ecosystem biodiversity.

483

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493 6. REFERENCES

- 494 Abell, R., M. L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N.
495 Mandrak, S. C. Balderas, W. Bussing, M. L. J. Stiassny, P. Skelton, G. R. Allen,
496 P. Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J. V. Higgins,
497 T. J. Heibel, E. Wikramanayake, D. Olson, H. L. López, R. E. Reis, J. G.
498 Lundberg, M. H. Sabaj Pérez, and P. Petry. 2008. Freshwater Ecoregions of the
499 World: A New Map of Biogeographic Units for Freshwater Biodiversity
500 Conservation. *BioScience* 58:403–414.
- 501 Agostinho, A. A., F. M. Pelicice, and L. C. Gomes. 2008. Dams and the fish fauna of the
502 Neotropical region: impacts and management related to diversity and fisheries.
503 *Brazilian Journal of Biology* 68:1119–1132.
- 504 Aroviita, J., and H. Hämäläinen. 2008. The impact of water-level regulation on littoral
505 macroinvertebrate assemblages in boreal lakes. *Hydrobiologia* 613:45–56.
- 506 de Baan, L., C. L. Mutel, M. Curran, S. Hellweg, and T. Koellner. 2013. Land Use in Life
507 Cycle Assessment: Global Characterization Factors Based on Regional and
508 Global Potential Species Extinction. *Environmental Science & Technology*
509 47:9281–9290.
- 510 Behrend, R. D. L., A. M. Takeda, L. C. Gomes, and S. E. P. Fernandes. 2012. Using
511 oligochaeta assemblages as an indicator of environmental changes. *BRAZILIAN*
512 *JOURNAL OF BIOLOGY* 72:873–884.
- 513 Bunn, S. E., and A. H. Arthington. 2002. Basic Principles and Ecological Consequences
514 of Altered Flow Regimes for Aquatic Biodiversity. *Environmental Management*
515 30:492–507.
- 516 Burnham, K. P., and D. R. Anderson (Eds.). 2004. Model selection and multimodel
517 inference. Springer New York, New York, NY.

- Chaudhary, A., F. Verones, L. de Baan, and S. Hellweg. 2015. Quantifying Land Use Impacts on Biodiversity: Combining Species–Area Models and Vulnerability Indicators. *Environmental Science & Technology* 49:9987–9995.
- Chen, J., H. Shi, B. Sivakumar, and M. R. Peart. 2016. Population, water, food, energy and dams. *Renewable and Sustainable Energy Reviews* 56:18–28.
- Curran, M., L. de Baan, A. M. De Schryver, R. van Zelm, S. Hellweg, T. Koellner, G. Sonnemann, and M. A. J. Huijbregts. 2011. Toward Meaningful End Points of Biodiversity in Life Cycle Assessment. *Environmental Science & Technology* 45:70–79.
- Dodson, S. I., S. E. Arnott, and K. L. Cottingham. 2000. The Relationship in Lake Communities Between Primary Productivity and Species Richness. *Ecology* 81:2662–2679.
- Dorber, M., K. R. Mattson, O. T. Sandlund, R. May, and F. Verones. 2019. Quantifying net water consumption of Norwegian hydropower reservoirs and related aquatic biodiversity impacts in Life Cycle Assessment. *Environmental Impact Assessment Review* 76:36–46.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81:163–182.
- Eadie, J. M., T. A. Hurly, R. D. Montgomerie, and K. L. Teather. 1986. Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. *Environmental Biology of Fishes* 15:81–89.
- Englund, G., and B. Malmqvist. 1996. Effects of Flow Regulation, Habitat Area and Isolation on the Macroinvertebrate Fauna of Rapids in North Swedish Rivers. *Regulated Rivers: Research & Management* 12:433–445.
- Fang, Y., and J. W. Jawitz. 2019. The evolution of human population distance to water in the USA from 1790 to 2010. *Nature Communications* 10.
- Gido, K., C. Hargrave, W. Matthews, G. Schnell, D. Pogue, and G. Sewell. 2002. Structure of littoral-zone fish communities in relation to habitat, physical, and chemical gradients in a southern reservoir. *ENVIRONMENTAL BIOLOGY OF FISHES* 63:253–263.
- Goedkoop, M., R. Heijungs, M. Huijbregts, A. De Schryver, J. Struijs, and R. van Zelm. 2009. ReCiPe 2008. A life cycle impact assessment method which comprises harmonised category indicators at the midpoint and the endpoint level 1.
- Gorman, O. T., and J. R. Karr. 1978. Habitat Structure and Stream Fish Communities. *Ecology* 59:507–515.
- Gracey, E. O., and F. Verones. 2016. Impacts from hydropower production on biodiversity in an LCA framework—review and recommendations. *The International Journal of Life Cycle Assessment* 21:412–428.
- Gubiani, E. A., V. A. Frana, A. L. Maciel, and D. Baumgartner. 2010. Occurrence of the non-native fish *Salminus brasiliensis* (Cuvier, 1816), in a global biodiversity ecoregion, Iguacu River, Parana River basin, Brazil. *AQUATIC INVASIONS* 5:223–227.
- Herlihy, A. T., S. G. Paulsen, J. V. Sickie, J. L. Stoddard, C. P. Hawkins, and L. L. Yuan. 2008. Striving for consistency in a national assessment: the challenges of applying

- a reference-condition approach at a continental scale. *Journal of the North American Benthological Society* 27:860–877.
- Horwitz, R. J. 1978. Temporal Variability Patterns and the Distributional Patterns of Stream Fishes. *Ecological Monographs* 48:307–321.
- ISO. 2006. ISO 14040: Environmental management - Life cycle assessment. International Standards Organisation.
- Jackson, D. A., H. H. Harvey, and K. M. Somers. 1990. Ratios in Aquatic Sciences: Statistical Shortcomings with Mean Depth and the Morphoedaphic Index. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1788–1795.
- Jackson, H. M., C. N. Gibbins, and C. Soulsby. 2007. Role of discharge and temperature variation in determining invertebrate community structure in a regulated river. *River Research and Applications* 23:651–669.
- James, M. R., M. Weatherhead, C. Stanger, and E. Graynoth. 1998. Macroinvertebrate distribution in the littoral zone of Lake Coleridge, South Island, New Zealand—effects of habitat stability, wind exposure, and macrophytes. *New Zealand Journal of Marine and Freshwater Research* 32:287–305.
- Jolliet, O., M. Margni, R. Charles, S. Humbert, J. Payet, G. Rebitzer, and R. Rosenbaum. 2003. IMPACT 2002+: A new life cycle impact assessment methodology. *The International Journal of Life Cycle Assessment* 8:324–330.
- Kraft, K. J. 1988. Effect of Increased Winter Drawdown on Benthic Macroinvertebrates in Namakan Reservoir, Voyageurs National Park. Page 86. Michigan Technological University, Houghton, Michigan.
- Kullasoot, S., P. Intrarasattayapong, and C. Phalaraksh. 2017. Use of benthic macroinvertebrates as bioindicators of anthropogenic impacts on water quality of Mae Klong river, Western Thailand.
- Legendre, P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology* 1:3–8.
- Lehner, B., C. R. Liermann, C. Revenga, C. Vörösmarty, B. Fekete, P. Crouzet, P. Doll, M. Endejan, K. Frenken, J. Magome, and others. 2011. High-resolution mapping of the world’s reservoirs and dams for sustainable river-flow management. *Frontiers in Ecology and the Environment* 9:494–502.
- Levick, L., J. Fonseca, D. Goodrich, M. Hernandez, D. Semmens, J. Stromberg, R. Leidy, M. Scianni, D. P. Guertin, M. Tluczek, and W. Kepner. 2008. The Ecological and Hydrological Significance of Ephemeral and Intermittent Streams in the Arid and Semi-arid American Southwest. Page 116 pp. U.S. Environmental Protection Agency and USDA/ARS Southwest Watershed Research Center.
- Malmqvist, B., and G. Englund. 1996. Effects of hydropower-induced flow perturbations on mayfly (Ephemeroptera) richness and abundance in north Swedish river rapids. *Hydrobiologia* 341:145–158.
- Matthews, W. J. 1982. Small Fish Community Structure in Ozark Streams: Structured Assembly Patterns or Random Abundance of Species? *The American Midland Naturalist* 107:42–54.
- McCafferty, W. P. 1983. Aquatic entomology: The fishermen’s and ecologists’ illustrated guide to insects and their relatives. Jones & Bartlett Learning.
- Milà i Canals, L., C. Bauer, J. Depestele, A. Dubreuil, R. Freiermuth Knuchel, G. Gaillard, O. Michelsen, R. Müller-Wenk, and B. Rydgren. 2007. Key Elements in

610 a Framework for Land Use Impact Assessment Within LCA (11 pp). The
611 International Journal of Life Cycle Assessment 12:5–15.

612 Moyle, P. B., and H. W. Li. 1979. Community ecology and predator-prey relations in
613 warmwater streams. Pages 171–180 *Predator-prey Systems in Fisheries*
614 Management. H. Clepper, Sport Fishing Institute, Washington D. C.

615 Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, R. B.
616 O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H.
617 Wagner. 2019. Community Ecology Package.

618 Okumura, Y. 2012. Package “rpsychi.”

619 Omernik, J. M. 1987. Ecoregions of the Conterminous United States. *Annals of the*
620 *Association of American Geographers* 77:118–125.

621 Patouillard, L., C. Bulle, and M. Margni. 2016. Ready-to-use and advanced
622 methodologies to prioritise the regionalisation effort in LCA. *Matériaux &*
623 *Techniques* 104:105.

624 Pickett, S. T. A. 1989. Space-for-Time Substitution as an Alternative to Long-Term
625 Studies. Pages 110–135 in G. E. Likens (editor). *Long-Term Studies in Ecology*.
626 Springer New York, New York, NY.

627 Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E.
628 Sparks, and J. C. Stromberg. 1997. The Natural Flow Regime. *BioScience*
629 47:769–784.

630 R Core Team. 2013. R: a language and environment for statistical computing. R
631 Foundation for Statistical Computing, Vienna, Austria.

632 Rempel, R. S., and P. J. Colby. 1991. A Statistically Valid Model of the Morphoedaphic
633 Index. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1937–1943.

634 Renöfalt, B. M., R. Jansson, and C. Nilsson. 2010. Effects of hydropower generation and
635 opportunities for environmental flow management in Swedish riverine
636 ecosystems. *Freshwater Biology* 55:49–67.

637 Richter, B. D., R. Mathews, and R. Wigington. 2003. Ecologically sustainable water
638 management: Managing river flows for ecological integrity. *Ecological*
639 *Applications* 13:206–224.

640 Rosenberg, D. M., P. McCully, and C. M. Pringle. 2000. Global-Scale Environmental
641 Effects of Hydrological Alterations: Introduction. *BioScience* 50:746–751.

642 Ryder, R. A. 1965. A Method for Estimating the Potential Fish Production of North-
643 temperate Lakes. *Transactions of the American Fisheries Society* 94:214–218.

644 Ryder, R. A. 1982. The Morphoedaphic Index—Use, Abuse, and Fundamental Concepts.
645 *Transactions of the American Fisheries Society* 111:154–164.

646 Ryder, R. A., S. R. Kerr, K. H. Loftus, and H. A. Regier. 1974. The Morphoedaphic
647 Index, a Fish Yield Estimator — Review and Evaluation. *Journal of the Fisheries*
648 *Research Board of Canada* 31:663–688.

649 Schwarz, G. 1978. Estimating the dimension of a model. *The Annals of Statistics* 6:461–
650 464.

651 Strayer, D. L., and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent
652 progress and future challenges. *Journal of the North American Benthological*
653 *Society* 29:344–358.

654 Stubbington, R., M. T. Bogan, N. Bonada, A. J. Boulton, T. Datry, C. Leigh, and R.
655 Vander Vorste. 2017. Chapter 4.3 - The Biota of Intermittent Rivers and

Ephemeral Streams: Aquatic Invertebrates. Pages 217–243 in T. Datry, N. Bonada, and A. Boulton (editors). *Intermittent Rivers and Ephemeral Streams - Ecology and Management*. Academic Press.

Takao, A., Y. Kawaguchi, T. Minagawa, Y. Kayaba, and Y. Morimoto. 2008. The relationships between benthic macroinvertebrates and biotic and abiotic environmental characteristics downstream of the Yahagi dam, central Japan, and the state change caused by inflow from a tributary. *RIVER RESEARCH AND APPLICATIONS* 24:580–597.

Turgeon, K., G. Trottier, C. Turpin, C. Bulle, and M. Margni. 2019. Empirical characterization factors assessing the effects of hydroelectricity on fish richness across three large biomes. *bioRxiv*:678383.

USEPA. 2013. *Water: Rivers & Streams*. <https://archive.epa.gov/water/archive/web/html/streams.html>.

USEPA. 2015a. *National Lakes Assessment. Overviews and Factsheets*. <https://www.epa.gov/national-aquatic-resource-surveys/nla>.

USEPA. 2015b. *National Rivers and Streams Assessment. Overviews and Factsheets*. <https://www.epa.gov/national-aquatic-resource-surveys/nrsa>.

USEPA. 2016. *Ecoregions used in the National Aquatic Resource Surveys. Reports and Assessments*. <https://www.epa.gov/national-aquatic-resource-surveys/ecoregions-used-national-aquatic-resource-surveys>.

USEPA. 2017. *National Lake Assessment 2012: Technical Report*. U.S. Environmental Protection Agency, Washington, DC.

Valdovinos, C., C. Moya, V. Olmos, O. Parra, B. Karrasch, and O. Buettner. 2007. The importance of water-level fluctuation for the conservation of shallow water benthic macroinvertebrates: an example in the Andean zone of Chile. *Biodiversity and Conservation* 16:3095–3109.

Verones, F., J. Bare, C. Bulle, R. Frischknecht, M. Hauschild, S. Hellweg, A. Henderson, O. Jolliet, A. Laurent, X. Liao, J. P. Lindner, D. Maia de Souza, O. Michelsen, L. Patouillard, S. Pfister, L. Posthuma, V. Prado, B. Ridoutt, R. K. Rosenbaum, S. Sala, C. Ugaya, M. Vieira, and P. Fantke. 2017. LCIA framework and cross-cutting issues guidance within the UNEP-SETAC Life Cycle Initiative. *Journal of Cleaner Production* 161:957–967.

Vörösmarty, C. J. 2005. Chapter 7: Fresh Water in: *Millennium Ecosystem Assessment, Volume 1: Conditions and Trends Working Group Report*. Island Press.

Walker, K. F., M. C. Thoms, and F. Sheldon. 1992. Effects of weirs on the littoral environment of the River Murray, South Australia. *River conservation and management*:271–292.

WCD. 2000. *Dams and Development: A New Framework for Decision-making*. Earthscan, London and Sterling, VA.

Wetzel, R. G. 2001. *Limnology: Lake and river ecosystems*. Gulf Professional Publishing, California.

White, M. S., M. A. Xenopoulos, R. A. Metcalfe, and K. M. Somers. 2011. Water level thresholds of benthic macroinvertebrate richness, structure, and function of boreal lake stony littoral habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1695–1704.

Williams, C. B. 1964. *Patterns in the balance of nature and related problems of*

702 quantitative ecology.
703 Yang, Y. 2016. Two sides of the same coin: consequential life cycle assessment based on
704 the attributional framework. *Journal of Cleaner Production* 127:274–281.
705 Youngs, W. D., and D. G. Heimbuch. 1982. Another Consideration of the
706 Morphoedaphic Index. *Transactions of the American Fisheries Society* 111:151–
707 153.
708 Zohary, T., A. Sukenik, T. Berman, and A. Nishri. 2014. *Lake Kinneret: Ecology and*
709 *Management*. Springer.
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712 **8. APPENDICES**

713 **Table A1.** Raw data.

UID	LAT	LON	TROPHIC.STATE	ECO	N.REF	MEAN.REF.S	SD.REF.S	N.IMP	IMP.S	SD.IMP.S	DELTA.S	SD.POOLED	PDF	SD.PDF	LOW.CI	UP.CI
6243	38.50796545	-94.67326537	EUTROPHIC	TPL	16	30.2	14.5	1	42	0	-11.77	3.62	-0.39	-0.22	-0.61	-0.17
6252	40.1117666	-75.8615303	EUTROPHIC	SAP	13	43.8	17.5	1	35	0	8.77	4.86	0.2	0.14	0.06	0.34
6267	31.62154629	-88.35373896	EUTROPHIC	CPL	13	27.6	17.1	1	32	0	-4.43	4.74	-0.16	-0.2	-0.36	0.04
6270	35.17438787	-99.07748881	EUTROPHIC	SPL	27	25.9	13.3	1	14	0	11.85	2.57	0.46	0.26	0.2	0.72
6281	35.28501346	-112.1541634	EUTROPHIC	WMT	34	39.4	12.5	1	15	0	24.42	2.15	0.62	0.2	0.41	0.82
6319	36.83163302	-104.2263032	EUTROPHIC	WMT	34	39.4	12.5	1	16	0	23.42	2.15	0.59	0.2	0.4	0.79
6342	39.99496234	-105.112227	EUTROPHIC	SPL	27	25.9	13.3	1	26	0	-0.15	2.57	-0.01	-0.1	-0.11	0.09
6404	39.63835365	-95.45681141	EUTROPHIC	TPL	16	30.2	14.5	1	22	0	8.23	3.62	0.27	0.18	0.1	0.45
6437	39.0001536	-95.77964833	EUTROPHIC	TPL	16	30.2	14.5	1	34	0	-3.77	3.62	-0.12	-0.13	-0.26	0.01
6451	40.16178738	-79.05238419	EUTROPHIC	SAP	13	43.8	17.5	1	43	0	0.77	4.86	0.02	0.11	-0.09	0.13
6481	39.48435525	-118.7235713	EUTROPHIC	XER	32	30.7	11.9	1	19	0	11.69	2.1	0.38	0.16	0.22	0.54
6482	41.92898525	-119.1790015	EUTROPHIC	XER	32	30.7	11.9	1	16	0	14.69	2.1	0.48	0.2	0.28	0.68
6501	35.98082795	-108.9316434	EUTROPHIC	WMT	34	39.4	12.5	1	14	0	25.42	2.15	0.64	0.21	0.43	0.86
6525	35.99293158	-96.87367696	EUTROPHIC	SPL	27	25.9	13.3	1	40	0	-14.15	2.57	-0.55	-0.3	-0.85	-0.25
6550	34.95361555	-96.71815923	EUTROPHIC	SPL	27	25.9	13.3	1	27	0	-1.15	2.57	-0.04	-0.1	-0.15	0.06
6556	35.41220255	-95.92927589	EUTROPHIC	SPL	27	25.9	13.3	1	25	0	0.85	2.57	0.03	0.1	-0.07	0.13
6570	37.65556473	-98.26098551	EUTROPHIC	SPL	27	25.9	13.3	1	39	0	-13.15	2.57	-0.51	-0.28	-0.79	-0.23
6575	40.72381895	-109.183908	EUTROPHIC	XER	32	30.7	11.9	1	21	0	9.69	2.1	0.32	0.14	0.18	0.46
6586	31.7872742	-96.06449217	EUTROPHIC	CPL	13	27.6	17.1	1	28	0	-0.43	4.74	-0.02	-0.17	-0.19	0.16
6599	46.54392165	-104.028258	EUTROPHIC	NPL	8	28.5	11.2	1	33	0	-4.52	3.97	-0.16	-0.15	-0.31	-0.01
6606	37.39088653	-99.78483802	EUTROPHIC	SPL	27	25.9	13.3	1	28	0	-2.15	2.57	-0.08	-0.11	-0.19	0.03
6617	41.75740963	-115.7220267	EUTROPHIC	XER	32	30.7	11.9	1	26	0	4.69	2.1	0.15	0.09	0.06	0.24

6618	41.19805974	-115.8922956	EUTROPHIC	XER	32	30.7	11.9	1	26	0	4.69	2.1	0.15	0.09	0.06	0.24
6622	31.88917209	-97.70249202	EUTROPHIC	SPL	27	25.9	13.3	1	35	0	-9.15	2.57	-0.35	-0.21	-0.56	-0.15
6667	43.37681333	-123.2640104	NA	WMT	34	39.4	12.5	1	30	0	9.42	2.15	0.24	0.09	0.15	0.33
6668	36.82300133	-96.04758798	EUTROPHIC	SPL	27	25.9	13.3	1	38	0	-12.15	2.57	-0.47	-0.26	-0.73	-0.21
6695	36.70544343	-96.4191085	EUTROPHIC	TPL	16	30.2	14.5	1	40	0	-9.77	3.62	-0.32	-0.2	-0.52	-0.13
6719	38.39816173	-115.117053	EUTROPHIC	XER	32	30.7	11.9	1	23	0	7.69	2.1	0.25	0.12	0.13	0.37
6731	41.70168986	-113.9596706	EUTROPHIC	XER	32	30.7	11.9	1	26	0	4.69	2.1	0.15	0.09	0.06	0.24
6735	32.94442993	-96.45375244	EUTROPHIC	SPL	27	25.9	13.3	1	34	0	-8.15	2.57	-0.32	-0.19	-0.51	-0.12
6742	47.76171554	-108.4328294	EUTROPHIC	NPL	8	28.5	11.2	1	30	0	-1.52	3.97	-0.05	-0.14	-0.19	0.09
6753	39.93104164	-104.9732957	EUTROPHIC	SPL	27	25.9	13.3	1	20	0	5.85	2.57	0.23	0.15	0.07	0.38
6762	33.51617531	-94.12513187	EUTROPHIC	CPL	13	27.6	17.1	1	43	0	-15.43	4.74	-0.56	-0.39	-0.95	-0.17
6774	46.82604195	-100.6342083	EUTROPHIC	NPL	8	28.5	11.2	1	16	0	12.48	3.97	0.44	0.22	0.22	0.66
6795	38.99724122	-108.0511795	EUTROPHIC	WMT	34	39.4	12.5	1	32	0	7.42	2.15	0.19	0.08	0.11	0.27
6796	37.19334598	-95.98897607	EUTROPHIC	SPL	27	25.9	13.3	1	36	0	-10.15	2.57	-0.39	-0.23	-0.62	-0.17
6806	38.49141175	-79.31478115	EUTROPHIC	SAP	13	43.8	17.5	1	43	0	0.77	4.86	0.02	0.11	-0.09	0.13
6823	43.16587842	-115.6524756	EUTROPHIC	XER	32	30.7	11.9	1	24	0	6.69	2.1	0.22	0.11	0.11	0.33
6825	37.25249786	-113.7781188	EUTROPHIC	XER	32	30.7	11.9	1	2	0	28.69	2.1	0.93	0.37	0.57	1.3
6868	38.23508748	-112.4630091	EUTROPHIC	WMT	34	39.4	12.5	1	26	0	13.42	2.15	0.34	0.12	0.22	0.46
6869	38.8475374	-111.9613903	EUTROPHIC	XER	32	30.7	11.9	1	16	0	14.69	2.1	0.48	0.2	0.28	0.68
6874	39.03670301	-107.9111308	EUTROPHIC	WMT	34	39.4	12.5	1	30	0	9.42	2.15	0.24	0.09	0.15	0.33
6875	40.94491896	-106.0119684	EUTROPHIC	XER	32	30.7	11.9	1	26	0	4.69	2.1	0.15	0.09	0.06	0.24
6923	40.03999071	-81.01388786	EUTROPHIC	SAP	13	43.8	17.5	1	24	0	19.77	4.86	0.45	0.21	0.24	0.66
6940	44.32909632	-116.1841073	EUTROPHIC	WMT	34	39.4	12.5	1	29	0	10.42	2.15	0.26	0.1	0.16	0.36
6944	39.1695073	-111.4507206	EUTROPHIC	WMT	34	39.4	12.5	1	29	0	10.42	2.15	0.26	0.1	0.16	0.36
6959	44.96411515	-116.4630194	EUTROPHIC	WMT	34	39.4	12.5	1	32	0	7.42	2.15	0.19	0.08	0.11	0.27
6966	39.14241052	-111.452546	EUTROPHIC	WMT	34	39.4	12.5	1	9	0	30.42	2.15	0.77	0.25	0.52	1.02
6970	44.79670477	-116.7326881	OLIGOTROPHIC	WMT	34	39.4	12.5	1	13	0	26.42	2.15	0.67	0.22	0.45	0.89

6971	43.1914128	-116.9598035	EUTROPHIC	XER	32	30.7	11.9	1	8	0	22.69	2.1	0.74	0.29	0.44	1.03
6976	38.7911491	-105.1063606	EUTROPHIC	WMT	34	39.4	12.5	1	4	0	35.42	2.15	0.9	0.29	0.61	1.19
7001	42.2158744	-83.58440358	EUTROPHIC	TPL	16	30.2	14.5	1	48	0	-17.77	3.62	-0.59	-0.31	-0.89	-0.28
7020	38.07832575	-122.7433592	EUTROPHIC	XER	32	30.7	11.9	1	36	0	-5.31	2.1	-0.17	-0.1	-0.27	-0.08
7057	39.20473742	-111.6689123	EUTROPHIC	WMT	34	39.4	12.5	1	30	0	9.42	2.15	0.24	0.09	0.15	0.33
7097	38.78818748	-111.7748779	EUTROPHIC	WMT	34	39.4	12.5	1	15	0	24.42	2.15	0.62	0.2	0.41	0.82
7100	43.96521803	-122.6839683	EUTROPHIC	WMT	34	39.4	12.5	1	37	0	2.42	2.15	0.06	0.06	0	0.12
7105	41.11051556	-82.08387214	EUTROPHIC	NAP	4	44.6	15.7	1	28	0	16.58	7.87	0.37	0.22	0.15	0.59
7108	30.9634384	-95.90350405	EUTROPHIC	CPL	13	27.6	17.1	1	27	0	0.57	4.74	0.02	0.17	-0.15	0.19
7109	32.0726955	-97.12977293	EUTROPHIC	SPL	27	25.9	13.3	1	24	0	1.85	2.57	0.07	0.11	-0.03	0.18
7136	41.6332907	-118.3893572	EUTROPHIC	XER	32	30.7	11.9	1	23	0	7.69	2.1	0.25	0.12	0.13	0.37
7168	48.27818524	-116.8311247	NA	WMT	34	39.4	12.5	1	35	0	4.42	2.15	0.11	0.07	0.05	0.18
7205	32.24025447	-101.3133027	OLIGOTROPHIC	SPL	27	25.9	13.3	1	2	0	23.85	2.57	0.92	0.49	0.44	1.41
7207	42.15782464	-122.6076343	EUTROPHIC	WMT	34	39.4	12.5	1	26	0	13.42	2.15	0.34	0.12	0.22	0.46
7226	42.13001338	-122.4782769	EUTROPHIC	WMT	34	39.4	12.5	1	19	0	20.42	2.15	0.52	0.17	0.34	0.69
7228	34.22781586	-86.84344912	EUTROPHIC	SAP	13	43.8	17.5	1	44	0	-0.23	4.86	-0.01	-0.11	-0.12	0.11
7229	40.63158462	-120.00287	EUTROPHIC	XER	32	30.7	11.9	1	20	0	10.69	2.1	0.35	0.15	0.2	0.5
7232	40.70340664	-83.37874497	EUTROPHIC	TPL	16	30.2	14.5	1	17	0	13.23	3.62	0.44	0.24	0.2	0.68
7276	41.16858314	-119.8174513	OLIGOTROPHIC	XER	32	30.7	11.9	1	9	0	21.69	2.1	0.71	0.28	0.42	0.99
7294	39.05604224	-82.69067345	EUTROPHIC	SAP	13	43.8	17.5	1	47	0	-3.23	4.86	-0.07	-0.12	-0.19	0.04
7304	31.58749658	-98.62250327	EUTROPHIC	SPL	27	25.9	13.3	1	36	0	-10.15	2.57	-0.39	-0.23	-0.62	-0.17
7306	39.24114932	-117.1658183	EUTROPHIC	XER	32	30.7	11.9	1	19	0	11.69	2.1	0.38	0.16	0.22	0.54
7325	40.33707955	-105.1266943	EUTROPHIC	SPL	27	25.9	13.3	1	19	0	6.85	2.57	0.27	0.17	0.1	0.43
7367	40.58885713	-111.5899784	OLIGOTROPHIC	WMT	34	39.4	12.5	1	0	0	39.42	2.15	1	0.32	0.68	1.32
7368	32.51586852	-87.86108477	EUTROPHIC	CPL	13	27.6	17.1	1	29	0	-1.43	4.74	-0.05	-0.17	-0.23	0.12
7369	41.03542015	-96.83772744	EUTROPHIC	TPL	16	30.2	14.5	1	26	0	4.23	3.62	0.14	0.14	0	0.28
7375	33.36486204	-88.16688028	EUTROPHIC	CPL	13	27.6	17.1	1	45	0	-17.43	4.74	-0.63	-0.43	-1.06	-0.2

7392	34.53435079	-92.26882632	EUTROPHIC	CPL	13	27.6	17.1	1	26	0	1.57	4.74	0.06	0.18	-0.12	0.23
7394	31.62154629	-88.35373896	EUTROPHIC	CPL	13	27.6	17.1	1	28	0	-0.43	4.74	-0.02	-0.17	-0.19	0.16
7402	34.28477821	-97.17097192	EUTROPHIC	SPL	27	25.9	13.3	1	39	0	-13.15	2.57	-0.51	-0.28	-0.79	-0.23
7405	40.32809914	-96.53200107	EUTROPHIC	TPL	16	30.2	14.5	1	25	0	5.23	3.62	0.17	0.15	0.03	0.32
7409	33.07556301	-92.66059625	EUTROPHIC	CPL	13	27.6	17.1	1	31	0	-3.43	4.74	-0.12	-0.19	-0.31	0.06
7459	33.88200988	-85.9316179	EUTROPHIC	SAP	13	43.8	17.5	1	39	0	4.77	4.86	0.11	0.12	-0.01	0.23
7471	46.04062349	-110.6921749	EUTROPHIC	NPL	8	28.5	11.2	1	23	0	5.48	3.97	0.19	0.16	0.03	0.35
7472	46.6246241	-110.7383363	EUTROPHIC	NPL	8	28.5	11.2	1	25	0	3.48	3.97	0.12	0.15	-0.03	0.27
7533	43.07839868	-112.6936589	EUTROPHIC	XER	32	30.7	11.9	1	14	0	16.69	2.1	0.54	0.22	0.32	0.77
7572	40.37248248	-84.34011043	EUTROPHIC	TPL	16	30.2	14.5	1	22	0	8.23	3.62	0.27	0.18	0.1	0.45
7579	39.60815568	-84.97150743	EUTROPHIC	TPL	16	30.2	14.5	1	21	0	9.23	3.62	0.31	0.19	0.12	0.49
7587	42.26037727	-111.4707171	NA	WMT	34	39.4	12.5	1	19	0	20.42	2.15	0.52	0.17	0.34	0.69
7588	42.89525373	-111.9638056	NA	XER	32	30.7	11.9	1	36	0	-5.31	2.1	-0.17	-0.1	-0.27	-0.08
7590	44.21474968	-111.6155136	EUTROPHIC	XER	32	30.7	11.9	1	44	0	-13.31	2.1	-0.43	-0.18	-0.62	-0.25
7596	40.86163552	-75.61191223	NA	SAP	13	43.8	17.5	1	46	0	-2.23	4.86	-0.05	-0.11	-0.16	0.06
7643	39.70682362	-111.2933692	EUTROPHIC	WMT	34	39.4	12.5	1	29	0	10.42	2.15	0.26	0.1	0.16	0.36
7652	40.17663921	-84.26522022	EUTROPHIC	TPL	16	30.2	14.5	1	29	0	1.23	3.62	0.04	0.12	-0.08	0.16
7684	37.67328141	-107.1127777	EUTROPHIC	WMT	34	39.4	12.5	1	19	0	20.42	2.15	0.52	0.17	0.34	0.69
7686	37.31623199	-107.1129943	EUTROPHIC	WMT	34	39.4	12.5	1	34	0	5.42	2.15	0.14	0.07	0.07	0.21
7698	41.15233931	-110.8249531	EUTROPHIC	XER	32	30.7	11.9	1	8	0	22.69	2.1	0.74	0.29	0.44	1.03
7713	46.11821631	-113.37464	EUTROPHIC	WMT	34	39.4	12.5	1	26	0	13.42	2.15	0.34	0.12	0.22	0.46
7769	30.97184148	-88.0527428	EUTROPHIC	CPL	13	27.6	17.1	1	55	0	-27.43	4.74	-0.99	-0.64	-1.63	-0.35
7800	41.67757315	-73.14469782	EUTROPHIC	NAP	4	44.6	15.7	1	51	0	-6.42	7.87	-0.14	-0.18	-0.33	0.04
7810	43.41399799	-119.4104723	EUTROPHIC	XER	32	30.7	11.9	1	10	0	20.69	2.1	0.67	0.27	0.4	0.94
7812	35.5624593	-93.63756822	EUTROPHIC	SAP	13	43.8	17.5	1	28	0	15.77	4.86	0.36	0.18	0.18	0.54
7994	32.66237175	-97.61238491	EUTROPHIC	SPL	27	25.9	13.3	1	47	0	-21.15	2.57	-0.82	-0.43	-1.25	-0.38
8016	33.8293043	-109.090421	EUTROPHIC	WMT	34	39.4	12.5	1	17	0	22.42	2.15	0.57	0.19	0.38	0.76

8121	36.06720319	-91.14242843	EUTROPHIC	SAP	13	43.8	17.5	1	26	0	17.77	4.86	0.41	0.2	0.21	0.6
8144	35.58318947	-90.96294056	EUTROPHIC	CPL	13	27.6	17.1	1	21	0	6.57	4.74	0.24	0.23	0.01	0.46
8151	41.08846075	-82.7290152	EUTROPHIC	TPL	16	30.2	14.5	1	26	0	4.23	3.62	0.14	0.14	0	0.28
8184	40.05558648	-105.7470802	EUTROPHIC	WMT	34	39.4	12.5	1	17	0	22.42	2.15	0.57	0.19	0.38	0.76
8207	39.65347461	-82.47378134	EUTROPHIC	SAP	13	43.8	17.5	1	44	0	-0.23	4.86	-0.01	-0.11	-0.12	0.11
8250	48.38062147	-110.9852659	EUTROPHIC	NPL	8	28.5	11.2	1	20	0	8.48	3.97	0.3	0.18	0.12	0.48
8256	39.77597099	-81.52247236	EUTROPHIC	SAP	13	43.8	17.5	1	36	0	7.77	4.86	0.18	0.13	0.05	0.31
8278	48.02656863	-109.6237599	EUTROPHIC	NPL	8	28.5	11.2	1	27	0	1.48	3.97	0.05	0.14	-0.09	0.19
8325	37.4167824	-108.4056506	EUTROPHIC	WMT	34	39.4	12.5	1	14	0	25.42	2.15	0.64	0.21	0.43	0.86
8342	32.05630851	-96.73178299	EUTROPHIC	SPL	27	25.9	13.3	1	34	0	-8.15	2.57	-0.32	-0.19	-0.51	-0.12
8360	40.67460225	-110.9706993	OLIGOTROPHIC	WMT	34	39.4	12.5	1	15	0	24.42	2.15	0.62	0.2	0.41	0.82
8395	40.88926752	-109.8461084	EUTROPHIC	WMT	34	39.4	12.5	1	24	0	15.42	2.15	0.39	0.14	0.26	0.53
8409	39.72076713	-86.72022287	EUTROPHIC	TPL	16	30.2	14.5	1	30	0	0.23	3.62	0.01	0.12	-0.11	0.13
8413	31.91034371	-95.30185594	EUTROPHIC	CPL	13	27.6	17.1	1	38	0	-10.43	4.74	-0.38	-0.29	-0.67	-0.09
8414	40.12169493	-104.9459108	EUTROPHIC	SPL	27	25.9	13.3	1	6	0	19.85	2.57	0.77	0.41	0.36	1.18
8416	38.93934838	-91.28285684	EUTROPHIC	TPL	16	30.2	14.5	1	37	0	-6.77	3.62	-0.22	-0.16	-0.38	-0.06
8427	44.69847871	-87.49992572	EUTROPHIC	UMW	2	38.9	13.3	1	30	0	8.87	9.44	0.23	0.26	-0.03	0.48
8435	47.87668819	-107.1252315	EUTROPHIC	NPL	8	28.5	11.2	1	14	0	14.48	3.97	0.51	0.24	0.26	0.75
8437	42.64690672	-72.21849668	EUTROPHIC	NAP	4	44.6	15.7	1	40	0	4.58	7.87	0.1	0.18	-0.08	0.28
8443	41.81248656	-70.63822658	EUTROPHIC	CPL	13	27.6	17.1	1	42	0	-14.43	4.74	-0.52	-0.37	-0.89	-0.16
8480	30.00697302	-96.70980987	EUTROPHIC	SPL	27	25.9	13.3	1	39	0	-13.15	2.57	-0.51	-0.28	-0.79	-0.23
8487	39.66169251	-84.64620693	EUTROPHIC	TPL	16	30.2	14.5	1	20	0	10.23	3.62	0.34	0.2	0.14	0.54
8494	41.98955896	-71.20506636	EUTROPHIC	NAP	4	44.6	15.7	1	40	0	4.58	7.87	0.1	0.18	-0.08	0.28
8495	46.94126809	-119.27853	EUTROPHIC	XER	32	30.7	11.9	1	34	0	-3.31	2.1	-0.11	-0.08	-0.19	-0.03
8504	38.07061898	-111.3751268	EUTROPHIC	WMT	34	39.4	12.5	1	9	0	30.42	2.15	0.77	0.25	0.52	1.02
8614	36.04444348	-85.58629482	EUTROPHIC	SAP	13	43.8	17.5	1	22	0	21.77	4.86	0.5	0.23	0.27	0.73
8627	48.687922	-121.6679362	OLIGOTROPHIC	WMT	34	39.4	12.5	1	6	0	33.42	2.15	0.85	0.28	0.57	1.12

8635	40.49553571	-83.89988027	EUTROPHIC	TPL	16	30.2	14.5	1	21	0	9.23	3.62	0.31	0.19	0.12	0.49
8765	37.59556184	-112.2546686	EUTROPHIC	WMT	34	39.4	12.5	1	25	0	14.42	2.15	0.37	0.13	0.24	0.49
8766	40.86378075	-109.8118146	EUTROPHIC	WMT	34	39.4	12.5	1	13	0	26.42	2.15	0.67	0.22	0.45	0.89
8777	39.36035119	-111.9637079	EUTROPHIC	XER	32	30.7	11.9	1	3	0	27.69	2.1	0.9	0.36	0.55	1.26
8811	31.33182559	-97.26843785	EUTROPHIC	SPL	27	25.9	13.3	1	41	0	-15.15	2.57	-0.59	-0.32	-0.9	-0.27
1000019	43.46019017	-116.1413012	EUTROPHIC	XER	32	30.7	11.9	1	25	0	5.69	2.1	0.19	0.1	0.09	0.28
1000025	43.19840666	-114.5997261	EUTROPHIC	XER	32	30.7	11.9	1	27	0	3.69	2.1	0.12	0.08	0.04	0.2
1000029	42.67704536	-113.4072962	EUTROPHIC	XER	32	30.7	11.9	1	12	0	18.69	2.1	0.61	0.25	0.36	0.85
1000030	42.20637168	-114.8788521	EUTROPHIC	XER	32	30.7	11.9	1	20	0	10.69	2.1	0.35	0.15	0.2	0.5
1000062	33.27090609	-98.15099199	EUTROPHIC	SPL	27	25.9	13.3	1	9	0	16.85	2.57	0.65	0.35	0.3	1
1000068	46.20607125	-116.8343671	EUTROPHIC	XER	32	30.7	11.9	1	22	0	8.69	2.1	0.28	0.13	0.15	0.41
1000073	35.58232959	-101.7171387	EUTROPHIC	SPL	27	25.9	13.3	1	9	0	16.85	2.57	0.65	0.35	0.3	1
1000084	41.03740677	-100.7757749	EUTROPHIC	SPL	27	25.9	13.3	1	15	0	10.85	2.57	0.42	0.24	0.18	0.66
1000086	41.32198742	-98.90067497	EUTROPHIC	SPL	27	25.9	13.3	1	15	0	10.85	2.57	0.42	0.24	0.18	0.66
1000088	41.76432182	-98.65979155	NA	SPL	27	25.9	13.3	1	27	0	-1.15	2.57	-0.04	-0.1	-0.15	0.06
1000122	42.26425757	-116.3104956	EUTROPHIC	XER	32	30.7	11.9	1	25	0	5.69	2.1	0.19	0.1	0.09	0.28
1000126	42.53147462	-116.3645133	EUTROPHIC	XER	32	30.7	11.9	1	23	0	7.69	2.1	0.25	0.12	0.13	0.37
1000137	42.1873061	-113.92408	OLIGOTROPHIC	XER	32	30.7	11.9	1	11	0	19.69	2.1	0.64	0.26	0.38	0.9
1000223	43.53712279	-90.95935275	EUTROPHIC	UMW	2	38.9	13.3	1	25	0	13.87	9.44	0.36	0.27	0.08	0.63

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719 **Table A2.** Variation partitioning fractions (*i.e.*, percentages) explained.

%	[a]	[b]	[c]	[d]	[e]	[f]	[g]	[h]	[i]	[j]	[k]	[l]	[m]	[n]	[o]	Value
50	0.022	0.151	0.057	0.032	0.039	<0	0.003	<0	<0	0.006	0.094	0.06	<0	<0	0.053	0.517
42	0.022	0.151			0.039		0.003				0.094	0.06			0.053	0.422
27	0.022				0.039		0.003				0.094	0.06			0.053	0.271
25					0.039						0.094	0.06			0.053	0.246
12							0.003					0.06			0.053	0.116
14											0.094				0.053	0.147
40		0.151			0.039						0.094	0.06			0.053	0.397
15		0.151														0.151
18			0.057				0.003			0.006		0.06			0.053	0.179
19				0.032						0.006	0.094				0.053	0.185

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722 **Figure A1.** Heatmaps of PDF, elevation and surface area of reservoir is proportional to

723 the point size.