ORIGINAL ARTICLE

Freshwater Biology WILEY

Effects of small hydropower dams on macroinvertebrate and fish assemblages in southern Brazil

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico; H Mason Keeler Endowed; National Geographic Society; Rufford Foundation; Society for Conservation Biology

Abstract

- Hydropower dams affect freshwater biodiversity by virtue of modifying flow regimes and degrading habitat conditions both above and below the water impoundment and diversion structure. In recent decades, there has been a global proliferation of Small Hydropower Plants (SHPs) propelled by incentive policies and a general perception that small dams are less harmful to the environment. However, limited science is available on the effects of SHPs on freshwater biodiversity, which is concerning considering their sheer numbers and the high variability in the size and operation of dams classified as SHPs.
- 2. We investigated the ecological effects of 12 SHPs on macroinvertebrate and fish assemblages of the Chapecó River Basin, Brazil. Our study included sites located upstream of the SHPs and sites directly affected by their operations (i.e., reservoir, dewatering section and downstream of the powerhouse). This design allowed us to quantify shifts in taxonomic composition and examine the relative role of different SHP attributes (e.g., dam height, reservoir area, age) in explaining these changes.
- 3. Our results reveal that SHPs modify the composition of both macroinvertebrate and fish assemblages, but the magnitude of such changes vary widely among dams. Both assemblages exhibited directionality in taxonomic shifts, resulting in a gradual replacement of taxa associated with fast-flowing habitats by other groups more commonly associated with standing waters. We also found that changes in assemblage structureare related to structural (dam height, reservoir area) and spatial attributes (distance from headwaters) of SHPs, although the predictive power of these attributes varied taxonomically and among reservoir, dewatering and downstream sites.
- 4. Overall, our results demonstrate that SHPs have important and heterogeneous effects on freshwater assemblages, which may manifest individually or cumulatively across the riverscape. This suggests that it is unlikely that a priori classifications of dams based on their structural attributes can replace site-specific and cumulative impact assessments. The results also shed light on the need for better understanding of how SHP attributes shape their ecological effects, so that a full

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assessment of the potential environmental impacts of the wide range of "small" dams is possible.

KEYWORDS

dam cascades, flow regulation, lentification, run-of-river, water diversion

1 | INTRODUCTION

Accelerating losses of freshwater biodiversity is a global crisis (Tickner et al., 2020), and the longstanding and continued expansion of hydropower dams is considered a primary cause (Thieme et al., 2021). The conservation challenge imposed by dam development is particularly evident in developing countries, where riverine ecosystems host a diverse aquatic biota upon which millions of people rely directly for their livelihoods (Flecker et al., 2022; Winemiller et al., 2016; Zarfl et al., 2014). While research attention often focuses on understanding and mitigating the ecological impacts of large hydropower dams, the vast majority of present-day and planned dams are, in fact, relatively smaller in size; these are collectively classified as Small Hydropower Plant (SHP; Couto & Olden, 2018).

The definition of SHP is ambiguous and quite inconsistent, but it broadly refers to dams with low generation capacity (<10 megawatts) that operate in low- to medium-order rivers (Couto & Olden, 2018; Kelly-Richards et al., 2017). The "small" modifier has been used as a beacon to guide environmental policies that support incentives and licensing exemptions for SHPs, although little evidence exists that "small" necessarily equates to lower environmental impacts (Couto & Olden, 2018; Kibler & Tullos, 2013; Lange et al., 2019). Furthermore, the sheer number of SHPs is far from small (11 SHPs for every large hydropower dam in operation), with current and planned future constructions estimated in the order of hundreds of thousands globally (Couto & Olden, 2018).

Dams can impact essential geomorphological, hydrological and ecological processes in rivers, including nutrient cycling, primary productivity, sediment transportation, and thermal and hydrological regimes (Olden, 2016; Olden & Naiman, 2010; Poff et al., 1997). These effects are not restricted to large dams, and mounting evidence suggests that SHPs also impact distinct ecosystem processes and facets of biodiversity (Hayes et al., 2008; Stanley et al., 2002; Wu et al., 2010). Firstly, dams and weirs impound upstream water in reservoirs in a process termed river lentification (Falasco et al., 2018; Sabater, 2008). The degree of conversion of flowing rivers to nearly standing-water varies from large storage structures to "run-of-river" schemes that have lower storage capacity and shorter water residence times (Anderson et al., 2015). Secondly, water is diverted to the powerhouse to produce hydroelectricity, resulting in reduced discharge and dewatered river sections immediately below the dam (McManamay et al., 2016). The amount of water diverted and how far downstream the water is returned to the river from the powerhouse dictates the degree and spatial extent of dewatering; such impacts

can be disproportionally high for small dams (Anderson, Freeman, & Pringle, 2006; Kibler, 2017; Kuriqi et al., 2021). Thirdly, flow regulation caused by both storage and diversion can extend far downstream, leading to reduced high-flow events, damped hydrologic variability, and more stable base flows downstream of powerhouse outflows (Figueiredo et al., 2021; Kibler, 2017; Meier et al., 2003).

Scientific studies have consistently demonstrated shifts in the composition of freshwater communities in response to dam-induced flow alteration. Lentification of riverine habitats commonly increases the abundance of generalist species at the expense of fluvial specialists with more complex life histories (Freeman & Marcinek, 2006; Haxton & Findlay, 2008)-a process that is often reported as a facilitator for the establishment of invasive species (Turgeon et al., 2019). These shifts in community composition are not restricted to newly created lentic habitats such as reservoirs, but also propagate downstream of dams as a response to flow regulation (Mims & Olden, 2013). For example, water-level fluctuations during peaking operations or water drawdown during periods of low flow may result in exposed or dewatering of the river channel, affecting algae, invertebrates and fish communities below SHPs (Jesus et al., 2004; Jumani et al., 2018; Wu et al., 2010). These ecological alterations, however, have been shown to be variable (Haxton & Findlay, 2008; Mbaka & Mwaniki, 2015), and in some instances result in negligible or even enhanced biodiversity (Anderson et al., 2017; Izagirre et al., 2013; Lessard & Hayes, 2003).

Considering the marked variability in the attributes of SHPs in terms of dam height, reservoir area and dewatering distance, greater knowledge of the direction and magnitude of ecological effects caused by SHPs remains a priority (Couto & Olden, 2018; Poff & Hart, 2002). Enhancing this understanding has important implications for hydropower policy and regulations as a consequence of the central importance of differentiating "small" and "large" during the environmental licensing process (Couto & Olden, 2018; Kelly-Richards et al., 2017). Currently, size classifications of hydropower are arbitrary and primarily based on thresholds of energy generation capacity, thus failing to describe other meaningful descriptors of the likely ecological effects of these structures (Couto & Olden, 2018; Kibler, 2017). Moreover, it is expected that the cascading effects of multiple dams play a major role in dictating their ecological impacts (Loures & Pompeu, 2018; Miranda & Dembkowski, 2016; Ward & Stanford, 1983), fuelling concerns that overlooking the cumulative effects of SHPs is a significant limitation of current policies (Athayde et al., 2019; Couto et al., 2021; Lange et al., 2018). A better understanding of the associations between dam attributes, their

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longitudinal positioning and different dimensions of freshwater biodiversity is a necessary precursor to improve environmental policies and regulations currently being applied to SHPs.

The pace of SHP development in tropical and sub-tropical regions demands new science that informs rapidly evolving environmental policy (Couto & Olden, 2018; Jumani et al., 2017; Kibler & Tullos, 2013). Here, we investigated the ecological effects of SHPs on biological assemblages of the Chapecó River Basin (Brazil)—a region where the SHP sector has been expanding rapidly in recent decades, with 22 SHPs operating and several new others under licensing or construction. Firstly, we examined and compared the response of fish and benthic macroinvertebrate assemblages to lentification by SHPs via three mechanisms: (a) water storage associated with the impoundment upstream of the dam or weir, (b) channel dewatering associated with water diversion between the dam and the powerhouse, and (c) flow modification caused by regulated water releases downstream of the powerhouse. We expected that each one of these three mechanisms would produce detectable changes in taxonomic composition in both macroinvertebrate and fish assemblages in comparison to control sites. Secondly, we tested for consistent directionality in shifts in assemblage composition across multiple SHPs and taxonomic groups. As a consequence of lentification, we expected that assemblage composition in the different SHPs would follow similar directional trends of taxonomic replacement. Thirdly, we explored whether the structural attributes of each SHP and their longitudinal position in the watershed predict the magnitude of observed shifts in assemblage composition. Considering that SHP classifications accommodate dams with a wide range of sizes and modes of operation, we predicted that shifts in taxonomic composition would be directly correlated with structural attributes associated with flow regulation (e.g., dam height, reservoir area, longitudinal position) and impoundment age.

2 | METHODS

2.1 | Study area

The study area is the mainstem habitats of the Chapecó and Chapecozinho Rivers in the upper Chapecó River Basin, Brazil (Figure 1a). The Basin is part of the Uruguay River system, draining an area of $8,302 \,\mathrm{km}^2$ and with a monthly mean discharge of $238 \,\mathrm{m}^3/\mathrm{s}$ (Estado de Santa Catarina, 2017). The Basin overlaps with an extensive basaltic flood province known as the Serra Geral formation, characterised by a combination of basaltic plateaus and acidic volcanic rocks in a highly dissected terrain (Crósta et al., 2012; MMA, 2010). The vegetation is classified as Araucaria moist forest, a critically threatened ecoregion of the Atlantic Forest Biome (WWF, 2020). Land use in the Chapecó River Basin primarily comprises forestry activities and cattle ranching, although riparian zones in the study area are fairly well-preserved, especially in the surrounding areas of the Araucárias National Park (MMA, 2010). The steep, sinuous valleys form a series of rapids and waterfalls in both rivers, creating suitable conditions for hydropower development. Altogether, there are 23 mainstem hydropower installations currently in operation in both rivers, and an additional 23 are under different stages of licensing or construction (Desenvolver, 2016). Most of these installations are diversion schemes classified as SHPs (<30MW), of which 12 were considered in this study (Figure 1a; Table 1). These SHPs were selected to include the full sequence of dams within and upstream of our study area, all of them being located in the upper portion of the Basin. The Cachoeirinha and Abrasa SHPs were considered a single dam given their very close proximity. Most SHPs sampled have moderate-to-low water storage, but a few have considerably large reservoirs relative to the size of the rivers, and their dewatering sections can extend over 8 km (Table 1). SHP development is a source



FIGURE 1 (a) Map depicting the 22 small hydropower plants (SHPs) and the one large hydropower plant (LHP) operating in the mainstems of Chapecó and Chapecozinho rivers. Sampled SHPs are represented by purple squares and unsampled dams are represented in lilac. Green polygons represent the protected areas and indigenous territories. (b) The Rondinha SHP illustrates the sampling design that included surveys of fish and benthic macroinvertebrates in upstream (light blue), reservoir (red), dewatering (orange) and downstream (dark blue) sites.

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Freshwater Biology –WILEY with 120 ml volume of dry dog food. This also is a passive fishing technique, but it targets small-sized fish (<10 cm). Two sets of four regularly spaced minnow traps (2.0 m apart) connected by cords were placed nearshore in depths that ranged from 0.1 to 2.0 m. The captured fish were measured, weighed and identified in the field at the species level, based on field guides for the Upper Uruguay River and taxonomic keys published (Zaniboni-Filho, 2004). Most specimens were released at the same sites where they were captured, but some individuals were collected for further validation of identification. Collected specimens were euthanised with lethal doses of eugenol, fixed in formalin solution and then transferred to 70% ethanol (AVMA, 2020). The voucher specimens were deposited at the fish collection of the Universidade de Brasília. Data analysis Patterns in invertebrate and fish assemblage composition were investigated using unconstrained ordination techniques based on Principal Coordinates Analysis (PCoA; Gower, 1966). Count data (i.e., number of individuals belonging to each taxon) from the different methods and locations within a sampling site were pooled and log-transformed $-\log_2(x)+1$ (based on Anderson, Ellingsen, & McArdle, 2006)---and then summarised using a PCoA on Bray-Curtis dissimilarity distances. Distance matrices then were corrected using the minimum additive constant method to ensure that no negative eigenvalues were generated (Borcard et al., 2011). Ordination axes were overlaid with a broken-stick randomisation model as a stopping rule (Jackson, 1993), and we retained just the first two PCoA axes (PC1 and PC2) for all subsequent invertebrate and fish analyses. Differences in assemblage composition between the four site groups (upstream, reservoir, dewatering, downstream) were tested using a permutational multivariate analysis of variance (PERMANOVA) with 9,999 permutations (Anderson, 2001) and a Bonferroni-corrected statistical significance level. We also tested for differences in multivariate data dispersion between the site groups (Anderson, 2006). All multivariate analyses were conducted using the functions "de-

2.3

Circular statistics were used to quantify the magnitude and direction of assemblage compositional change from the least-impacted (upstream) site to each of the dam-affected sites (reservoir, dewatering, downstream) according to their location in the PCoA ordination space. These three groups of assemblage compositional shifts are referenced as Δ -Reservoir, Δ -Dewatering and Δ -Downstream. Based on the Cartesian coordinates of PC1 and PC2, we calculated Euclidian distances (i.e., magnitude) and θ angles (i.e., direction) for vectors connecting upstream to reservoir site, upstream to dewatering site, and upstream to downstream site for each SHP. Angles were then converted to polar coordinates and submitted to Rayleigh's test for circular uniformity (Jammalamadaka & Sengupta, 2001). This test assesses whether the distribution of angles representing directional shifts in assemblage structure for reservoir, dewatering and

costand", "cmdscale", "envfit", "adonis" and "betadisper" from the R

package vegan (Oksanen et al., 2022).

of ongoing conflict in the region, being listed as one of the primary threats to conservation in the Basin (MMA, 2010).

2.2 Sampling design

The 12 SHPs were surveyed during the low-flow season in the Chapecó River (3 March to 15 April 2018) and the Chapecozinho River (2 February to 22 March 2019). Four sampling sites were selected for each SHP: one "least-impacted" site and three sites under influence of the SHP (Figure 1b). The least-impacted site upstream of the reservoir created by SHP is characterised by flowing water habitats. This site typically was located at a minimum of two rapids/riffles complexes above the upstream extent of the reservoir to avoid any direct effects of the dam on site-level flows. Near the dam structure, the "reservoir site" is a lentic or quasi-lentic river section created by the SHP impoundment. The "dewatering site" is in the dewatering section downstream of the dam structure and upstream of the confluence with the powerhouse outlet. The "downstream site" represents flowing-water habitat located at least two rapids/riffles below the powerhouse outlet where water is returned to the river. The exact locations of each sampling site depended on accessibility and were selected to accommodate the wide range of micro- and mesohabitats available. At each site, we delimited a ~250-m river section, where benthic macroinvertebrates and fish were surveyed.

We collected three samples of benthic invertebrates in each site to represent the diversity of microhabitats available at the site-level (i.e., water velocity, depth and subtract type). Each sample was collected with a Surber sampler with an area of 1 m^2 and a 250- μ m mesh size, and preserved in the field in 70% ethanol (Pérez, 1988). In the laboratory, the collected material was carefully washed using 500um sieves and processed using a stereomicroscope. All macroinvertebrates were identified to the lowest taxonomic resolution possible (mostly family level) using appropriate taxonomic keys (Hamada et al., 2014; Pérez, 1988). Studies conducted in the Brazilian Atlantic Forest have demonstrated consistently that ecological assessments based on family-level identifications are suitable to detect the response of macroinvertebrate assemblages to distinct sorts of environmental change (Buss & Vitorino, 2010; Rezende et al., 2019; Suriano et al., 2011).

Fish assemblages were sampled using three sets of gill nets and eight minnow traps deployed within the 250-m section of the river, always installed in both margins and covering varied microhabitats present in the site. Both nets and traps were placed overnight, typically from 16:00 to 10:00 hr (mean set time of 17.9 ± 3 hr). We installed three sets of 25 m-long gill nets with multiple mesh sizes in parallel to the shores, following proposed methods for standardised fish sampling in large rivers (Oliveira et al., 2014; Tejerina-Garro & de Mérona, 2010). Each set was composed of a combination of 5-m-long nets of five different mesh-sizes (15, 30, 40, 55, 80mm between opposed knots), varying from 1.44 to 2.00m in height. Fish also were sampled with eight wire-mesh Gee minnow traps (0.42 m long × 0.21 m diameter with two 35-mm openings) baited

SHP name	Sub-basin	Generation capacity (MW)	Annual average discharge (m ³ /s)	Distance to Headwater (km)	Number of dams upstream	Dam height (m)	Dam length (m)	Reservoir area (km²)	Dewatering distance (m)	Opening date
Flor do Mato	Chapecozinho	4.80	11.9	50.9	0	13.2	267	5.77	280	6 Dec 1946
Adami Quimica	Chapecozinho	3.00	5.2	37.6	0	8.0	124	0.26	370	1 Jan 1970
Rio do Mato	Chapecozinho	1.20	14.7	62.9	1	0.5	38	0.01	360	26 Jun 2014
Dalapria	Chapecozinho	1.44	29.1	87.1	e	2.0	40	0.15	380	1 Feb 1985
Cachoeirinha- Abrasa	Chapecozinho	2.14	31.3	92.5	4	3.0	140	0.65	80	1 Jan 2007
Tonet	Chapecó	0.76	4.0	23.9	0	3.5	30	0.13	30	May 1, 1975
Contestado	Chapecó	5.60	17.5	47.9	1	3.0	234	0.85	3,760	1 Nov 2007
Coronel Araujo	Chapecó	5.80	19.2	53.9	2	5.0	183	0.86	470	1 Nov 2007
Das Pedras	Chapecó	5.60	21.4	59.9	c	17.0	145	0.46	4,300	23 Dec 2017
Salto Santo Antonio	Chapecó	6.24	23.5	64.4	4	2.0	06	0.05	500	1 Jan 1963
Passos Maia	Chapecó	25.00	30.4	82.8	5	28.0	199	1.75	7,950	18 Feb 2012
Rondinha	Chapecó	9.60	38.3	98.1	6	17.0	172	0.62	4,350	4 Jun 2014

TABLE 1 List of attributes of the 12 small hydropower plants (SHPs) sampled in this study.

Note: Average annual discharge and distance to headwater were sourced from Linke et al. (2019), dewatering distances were measured in Google Earth, and the remaining attributes were retrieved from federal and state-level databases and licensing reports (ANEEL, 2020a, 2020b).

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downstream sites (referenced to upstream) across SHPs significantly depart from uniformity in which angles occur in all directions with equal frequency (Landler et al., 2018). Watson's two-sample test of homogeneity (Jammalamadaka & Sengupta, 2001) was conducted to test for differences between mean angle of directional change between reservoir, dewatered and downstream sites. Angular data were used to construct circular histograms that depict the mean and frequency of directional shifts in assemblage structure. All analyses were performed using the R package *CircStats* (Lund & Agostinelli, 2022).

Relationships between shifts in taxonomic composition and basic attributes of SHPs were investigated through multiple linear regression models. We compiled a set of attributes of potential ecological relevance from energy/environmental agency databases, hydrological data and licensing reports (Table 1). Multicollinearity among attributes was tested through Pearson correlations, and a threshold of 0.70 was adopted for variables selection (Dormann et al., 2013). As distance to headwaters (source), river discharge and number of dams upstream were highly correlated (>0.95), only distance to headwaters was adopted as a metric of longitudinal position. Dam length is highly correlated with reservoir area (0.72) and was removed from the analysis. Dam height, dewatering distance and generation capacity also showed high multicollinearity (ranging from 0.83 to 0.87), so we opted to retain dam height owing to its overall relevance in the ecological literature as a proxy of dam impacts on flow (Poff & Hart, 2002). All SHP attributes were then log-transformed (natural logarithm) before subsequent analyses.

We tested the relative importance of different subsets of dam attributes for predicting magnitude and direction of assemblage compositional change from the least-impacted (upstream) site to each of the dam-affected sites (reservoir, dewatered, downstream) using an information-theoretic approach to model selection (Burnham & Anderson, 2002). We considered 52 candidate general linear regression models containing all possible combination of covariates drawn from the following global model:

$$\begin{aligned} & \mathsf{Faxonomic shift} \left(\Delta_i \right) = \quad \beta_0 + \beta_1 \mathsf{River}_i + \beta_2 \mathsf{Height}_i + \beta_3 \mathsf{Area}_i + \\ & \beta_4 \mathsf{Distance}_i + \beta_5 \mathsf{Age}_i + \beta_6 \mathsf{Height}_i * \mathsf{Distance}_i + \\ & \beta_7 \mathsf{Area}_i * \mathsf{Distance}_i \end{aligned}$$

where Δ_i is the site-comparison taxonomic shift for a given SHP *i*, β_0 is the intercept, and β_1 - β_7 are the coefficients associated with the five covariates and the two interaction terms. The variables used to fit the global model were the river sub-basin (Chapecó vs. Chapecozinho), dam height, reservoir area, distance to upstream headwater, and dam age attributed to each SHP *i* (Table 1). The two interaction terms represent theoretical expectations of the relative role of dam size and river discharge on the ecological effects of flow regulation (Kibler, 2017; Lehner et al., 2011; Ward & Stanford, 1983). Three sets of response variables were fitted independently in the models representing site-comparison taxonomic shifts (Δ_i): the magnitude of the shift (i.e., Euclidian distance) and the direction of the shift (i.e., θ angle) decomposed along each one of the two PCoA axes. The two metrics describing directions, Direction

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PC1 and Direction PC2, were calculated through sine and cosine equations, and reflect independent taxonomic changes along each axis.

Regression diagnostics from the global model with all variables indicated a reasonable statistical fit with no significant deviations from the parametric assumptions. Consequently, we ranked our candidate models using the Akaike information criterion (AICc) corrected for small sample sizes (Burnham & Anderson, 2002) to evaluate the relative support (given the data) for each model. We also calculated the difference between the best approximating model value and all remaining model values (ΔAIC_i). Maximum log-likelihood estimates and Akaike weights (w_i), representing the relative likelihood of a model against all candidate models, were calculated. Evidence ratios were computed to quantify the relative support for each model by dividing the w_i of the best approximating model by the w_i for each individual model. All of the analyses were conducted in R version 4.2.2 (R Core Team, 2022).

3 | RESULTS

3.1 | Macroinvertebrate assemblages

Our surveys revealed the presence of 71 macroinvertebrate taxa, belonging to Platyhelminthes, Nematoda, Annelida, Mollusca, Crustacea, Arachnida, Entognatha and Insecta (Table S1). The two first axes of the PCoA (PC1 and PC2) explained 31% of the total variation, and 16 invertebrate taxa demonstrated statistically significant loadings (eigenvectors) on one or both axes (Figure 2a, p < 0.05). Macroinvertebrate assemblages differed among groups of sites (PERMANOVA Pseudo-F = 2.77, $R^2 = 0.16$, p < 0.001), reflecting significant differences in species composition between upstream (least-impacted) and reservoir sites (Pseudo-F = 6.38, $R^2 = 0.22$, p = 0.001), and between upstream and dewatering sites (Pseudo-F = 3.15, R^2 = 0.13, p = 0.003). Macroinvertebrate taxa considered fluvial specialists (e.g., Baetidae, Leptophlebiidae, Philopotamidae, Elmidae) were more prevalent in upstream sites, and showed decreased abundance and occurrence in dam-affected sites (reservoir, dewatered and downstream). Assemblage composition was less variable in upstream sites than in dam-affected sites (F = 7.28, p < 0.001). Macroinvertebrate assemblage composition varied the most in reservoir sites, being generally dominated by taxa associated with standing waters (e.g., Caenidae, Euthyplociidae, Oligochaeta and Hirudinea) and devoid of fluvial specialists. Dewatering and downstream sites showed intermediate variability in comparison to upstream and reservoir sites. In general, dewatering and downstream sites supported more fluvial specialists compared to reservoir sites (but not upstream sites), but also contained taxa associated with standing waters in some instances.

We detected directional (non-uniform) shifts in macroinvertebrate species composition from the least-impacted (upstream) site to each of the dam-affected sites (reservoir, dewatered, downstream), generally moving from left to right along the first ordination axis (Figure 3; Table 2). Directionalities were stronger for



FIGURE 2 Ordination biplots of Principal Coordinate Analysis (PCoA) for (a) macroinvertebrate and (b) fish assemblages of the Chapecó River Basin, Brazil. PC1 and PC2 are the first two axes of each ordination (variation explained in parenthesis). Coloured circles represent the site scores and the black arrows represent the correlation of each axis with taxon vectors (only significant correlations shown; p < 0.05). Colours distinguish upstream (light blue), reservoir (red), dewatering (orange) and downstream (dark blue) sites.

 Δ -Reservoir (Rayleigh's test, $\rho = 0.78$, p < 0.001) and Δ -Dewatering ($\rho = 0.50$, p = 0.05), but were not significant for Δ -Downstream ($\rho = 0.36$, p = 0.23). Directionalities of change for all dam-affected sites were not significantly different (Watson's test statistic, $U_{\text{reservoir-dewatering}} = 0.06$, p > 0.10; $U_{\text{reservoir-downstream}} = 0.12$, p > 0.10; $U_{\text{dewatering-downstream}} = 0.02$, p > 0.10), suggesting similar compositional shifts in macroinvertebrate assemblages associated with a decrease and increase in the relative abundance of fluvial specialists and standing-waters taxa, respectively, in dam-affected sites (Figure 2a for reference).

The overall variance in magnitude and direction of shifts in composition indicate heterogeneous effects of SHPs, which were correlated, in part, with structural and spatial attributes (Table 3; Figure 4a-f). The most supportive model for the magnitude of shifts in upstream-reservoir assemblage incorporated dam height (AICc = 0.11, $w_i = 0.31$); this model was twice as likely as the next most competitive model (Table 3). Taller dams were found to have larger effects on the magnitude of Δ -Reservoir (Figure 4a; $R^2 = 0.30$, F = 5.67, p = 0.04). Longitudinal position and dam height were the most supportive predictors of the direction of shifts in the sites located in reservoirs, with longitudinal position alone supporting the best model describing direction of shifts along PC1 (AICc = 11.25, $w_i = 0.36$), and dam height together with longitudinal position and the river sub-basin fitting the best model for direction of shifts along PC2 (AICc = 2.28, $w_i = 0.17$). Both models indicated positive effects of distance to headwaters on the direction of shifts in Δ -Reservoir along the PC1 (Figure 4b; $R^2 = 0.38$, F = 7.70, p = 0.02) and PC2 axes (Figure 4d; $R^2 = 0.16$, F = 5.53, p = 0.05). For directional shifts along

PC2, dam height was found to have a negative effect, with taller dams producing larger negative shifts along PC2 in Δ -Reservoir (Figure 4c; $R^2 = 0.44$, F = 10.25, p = 0.01).

None of the candidate models outperformed the null model for Δ -Dewatering, indicating that the attributes tested are not good predictors of composition shifts or that there is little variability in the magnitude and directionality of shifts among SHPs to be explained (Table 3). SHP longitudinal position was the most supportive predictor of the magnitude of shifts in the sites located downstream of the dams (AICc = 6.40, $w_i = 0.31$), with greater Δ -Downstream shifts occurring further downstream of the headwaters (Figure 4e; $R^2 = 0.28$, F = 5.24, p = 0.05). Likewise, longitudinal position was the best predictor of the direction of shifts in Δ -Downstream along PC1 axis (AICc = 10.28, $w_i = 0.36$), with larger shifts in macroinvertebrate assemblages manifested further downstream of the headwaters (Figure 4f; $R^2 = 0.28$, F = 5.32, p = 0.04).

3.2 | Fish assemblages

We recorded a total of 16 fish species, belonging to five families and four orders (Table S2; Figure S1), all of them native to the Upper Uruguay System. Together, PC1 and PC2 explained 31% of the variation of the PCoA, in which eight fish species showed significant loadings (Figure 2b; p < 0.05). Fish composition did not change among groups of sites (PERMANOVA Pseudo-F = 1.25, $R^2 = 0.08$, p = 0.24), and variation in data dispersion was homogeneous among all the groups (F = 1.14, p = 0.35). Although not statistically significant,

FIGURE 3 Polar plot depicting taxonomic shifts (Δ) in benthic macroinvertebrate assemblages between the least-impacted upstream site and the dam-affected sites under influence of the 12 SHPs (a-c). The length and angle of each coloured bar represent (respectively) the magnitude (i.e., Euclidian distance) and direction of a taxonomic shift for a given SHP in the ordination space (PC1 and PC2). (d) The resultant directionality of taxonomic shifts (i.e., mean resultant length of Rayleigh's test) is represented by a coloured circle: Δ -Reservoir (red), Δ -Dewatering (orange), and Δ -Downstream (dark blue).



TABLE 2 Directional statistics of shifts (Δ) in taxonomic composition between the least-impacted upstream site and the three types of dam-affected sites (i.e., reservoir, dewatering and downstream) for macroinvertebrate and fish assemblages.

Assemblage	Site-comparison	Resultant direction (°)	ρ	p-value
Macroinvertebrates	Δ -Reservoir	-5.73	0.78	<0.001
	Δ -Dewatering	6.43	0.50	0.05
	Δ -Downstream	4.11	0.35	0.36
Fish	Δ -Reservoir	129.56	0.67	0.03
	Δ -Dewatering	81.02	0.14	0.80
	Δ -Downstream	60.23	0.06	0.96

Note: Resultant directions in degrees, resultant lengths (ρ) and *p*-values are provided. Significant relationships are highlighted in bold (*p* < 0.05).

most reservoir sites were grouped within the top-left quadrant of the ordination space, corresponding to higher relative abundances of the cichlid *Geophagus brasiliensis* (Quoy & Gaimard, 1824), the erythrinid *Hoplias malabaricus* (Bloch, 1794) and the characin *Astyanax* cf. *lacustris* (Lütken, 1875)—three species often associated with low-flow habitats or even standing waters in southern Brazil (Borba et al., 2019; Frehse et al., 2021; Hirschmann et al., 2008). Most upstream, dewatering and downstream sites were grouped outside this quadrant, where species associated with fluvial habitats were more abundant. For instance, the heptapterid *Rhamdia quelen* (Quoy & Gaimard, 1824), the cichlid *Chrenicichla igara* Lucena & Kullander (1992) and most loricariids loaded to the lower right in ordination space, although the last two were not significantly correlated with PC1 nor PC2. We did not collect any non-native fishes during our surveys, but local anglers and dam operators reported the presence in low densities of the common carp *Cyprinus carpio* Linnaeus (1758), grass carp *Ctenopharyngodon idella* (Valenciennes, 1844) and largemouth bass *Micropterus salmoides* (Lacepède, 1802).

Directional departures from upstream assemblage structure also occurred for fishes, but overall changes were more variable than A

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in macroinvertebrate assemblages (Figure 5; Table 2). We only detected significant directional changes in fish assemblage composition for Δ -Reservoir, generally moving towards the top-left panel of the ordination space (Figure 5a; Rayleigh's test, $\rho = 0.67$, p = 0.003). This direction corresponds to higher abundances of species associated with low-flow habitats such as *G. brasiliensis*, *H. malabaricus* and *A. lacustris* (Figure 2b for reference). The distribution of angles for Δ -Dewatering and Δ -Downstream did not differ from uniform distributions (Figure 5; Table 2), and directionality of change for all dam-affected sites were not significantly different (Watson's test statistic, $U_{\text{reservoir-dewatering}} = 0.11$, p > 0.10; $U_{\text{reservoir-downstream}} = 0.13$, p > 0.10; $U_{\text{dewatering-downstream}} = 0.03$, p > 0.10).

SHP attributes also explained shifts in fish assemblage composition for the upstream-reservoir and upstream-downstream site comparisons. The most supportive model for the magnitude of upstream-reservoir assemblage changes included reservoir area as the sole predictor (Table 3); this model was five times more likely given the data than the next most competitive model (AICc = -3.96, $w_i = 0.49$). Larger reservoirs were found to have greater effects on the magnitude of Δ -Reservoir (Figure 4g; $R^2 = 0.30$, F = 5.67, p = 0.04). Similar to macroinvertebrate assemblages, none of the candidate models outperformed the null models for Δ -Dewatering (Table 3), indicating that the attributes tested are not good predictors of fish composition shifts or that there is little variability in the shifts among SHPs. Dam height was the most supportive predictor of assemblage shift directionality in the sites located downstream of dams (AICc = 5.72, $w_i = 0.30$), with taller dams producing larger negative changes along PC1 in Δ -Downstream (Figure 4h; $R^2 = 0.32$, F = 6.22, p = 0.03). As observed for macroinvertebrates, the magnitude and direction of taxonomic composition shifts in

TABLE 3 Model selection process for the relationships between magnitude and direction of taxonomic shifts (Δ) and SHP attributes based on AIC.

ssemblage	Site-comparison	Dependent variable	Candidate model	Rank	AIC _c	ΔAIC	w _i	ER
lacroinvertebrates	Δ -Reservoir	Magnitude	Height(+)	1	0.1	0.0	0.31	-
			River + Height(+)	2	1.6	1.5	0.15	2.1
			Null	3	1.8	1.7	0.13	2.4
			Area(+)	3	1.8	1.7	0.13	2.4
		Direction PC1	Distance(+)	1	11.2	0.0	0.36	-
			Area(+) + Distance(+)	2	13.0	1.8	0.15	2.4
			Height(+)+ Distance(+)	3	13.2	1.9	0.14	2.6
		Direction PC2	River + Height(-) + Distance(+)	1	2.3	0.0	0.17	-
			River + Height(-)	2	2.3	0.0	0.17	1.0
			River + Area(-)	3	3.2	0.9	0.11	1.6
	Δ -Dewatering	Magnitude	Null	1	5.2	0.0	0.43	-
			Age(+)	2	7.1	1.9	0.17	2.6
			Height(-)	3	8.6	3.4	0.08	5.4
		Direction PC1	Distance(-)	1	16.9	0.0	0.31	-
			Null	2	17.2	0.3	0.26	1.2
			River	3	19.5	2.6	0.08	3.6
		Direction PC2	Area(-)	1	-6.9	0.0	0.35	-
			River + Area(-)	2	-6.8	0.1	0.33	1.1
			River + Height(-)	3	-3.3	3.5	0.06	5.9
	Δ -Downstream	Magnitude	Distance(+)	1	6.4	0.0	0.31	-
			Null	2	7.8	1.4	0.15	2.0
			River + Distance(+)	3	8.8	2.4	0.10	3.2
		Direction PC1	Distance(+)	1	10.3	0.0	0.36	-
			Null	2	11.7	1.5	0.17	2.1
			Distance(+)+Age(+)	3	13.4	3.1	0.08	4.8
		Direction PC2	Null	1	-6.5	0.0	0.22	-
			Distance(+)	2	-5.9	0.6	0.16	1.4
			River + Distance(+)	3	-5.8	0.7	0.15	1.4

TABLE 3 (Continued)

Assemblage	Site-comparison	Dependent variable	Candidate model	Rank	AIC _c	ΔAIC	w _i	ER
Fish	Δ -Reservoir	Magnitude	Area(+)	1	-4.0	0.0	0.49	-
			Area(+) +Age(+)	2	-0.8	3.2	0.10	4.8
			Null	3	-0.1	3.8	0.07	6.8
		Direction PC1	Null	1	9.4	0.0	0.24	-
			River	2	10.1	0.7	0.17	1.4
			Area(-)	3	10.3	0.9	0.16	1.5
		Direction PC2	Null	1	0.4	0.0	0.30	-
			Distance(-)	2	2.3	1.9	0.12	2.6
			River	3	2.3	1.9	0.12	2.6
	Δ -Dewatering	Magnitude	Null	1	-11.2	0.0	0.32	-
			Area(+)	2	-9.8	1.4	0.16	2.0
			Height(+)	3	-8.9	2.3	0.10	3.1
		Direction PC1	Null	1	7.6	0.0	0.39	-
			Age(+)	2	9.3	1.7	0.17	2.4
			Area(-)	3	10.4	2.8	0.10	4.0
		Direction PC2	Null	1	2.2	0.0	0.34	-
			Age(+)	2	2.9	0.7	0.24	1.4
			Height(-)	3	5.3	3.2	0.07	4.9
	Δ -Downstream	Magnitude	Null	1	1.5	0.0	0.24	-
			Age(+)	2	2.5	1.0	0.14	1.6
			River	3	3.0	1.5	0.11	2.1
		Direction PC1	Height(–)	1	5.7	0.0	0.30	-
			Area(-)	2	5.9	0.2	0.27	1.1
			Null	3	7.9	2.1	0.10	2.9
		Direction PC2	Null	1	15.2	0.0	0.38	-
			Height(-)	2	17.2	2.1	0.14	2.8
			Distance(-)	3	17.9	2.7	0.10	3.9

Note: Global models include the river sub-basin (River), dam height (Height), reservoir area (Area), distance to upstream headwater (Distance) and dam age (Age). All of the possible combinations of variables from the global models were ranked according to AICc, and the three most supportive models for each site-comparison are shown. The sign of coefficients of the most supportive models are inside parenthesis and significant relationships are in bold (p < 0.05). Values of AICc, Δ AIC, weights (w_i) and evidence ratio (ER) of each model are provided.

different site-comparisons are not predictable by the same SHP attributes (Table 3).

4 | DISCUSSION

Despite the growing ubiquity of SHPs in different parts of the world, our understanding of their ecological implications remains largely incomplete. In the Chapecó River Basin, Brazil, we found that habitat lentification and flow alteration caused by SHPs modifies the taxonomic composition of macroinvertebrate and fish assemblages, but these changes vary in both magnitude and directionality. We revealed strong evidence for directional shifts in taxonomic composition, reflecting a gradual replacement of taxa associated with fast-flowing habitats (i.e., fluvial specialists) by habitat generalists and taxa with affinity to standing waters. We also found that

the magnitude of these shifts is predictable, albeit not consistently, by structural and spatial attributes of the dams, particularly those related to dam height, reservoir area and the longitudinal position of the SHP. Although our sampling design does not allow us to estimate potential biases introduced by habitat-selectivity of the sampling methods and by spatial autocorrelations associated with the sequential order of sampling sites, these results are consistent with general expectations from the literature that also report changes in community composition caused by water storage, diversion and flow regulation (e.g., Anderson, Freeman, & Pringle, 2006; Jumani et al., 2018; Linares et al., 2019). Overall, our results demonstrate that SHPs cause measurable impacts on riverine biota and that the magnitude of these impacts can be directly linked to the wide range of structural attributes found in SHPs, suggesting the need for more effective environmental policies and regulations for the SHP sector.

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FIGURE 4 Relationships between the magnitude and direction of shifts in site-comparison taxonomic composition (Δ) and SHP attributes for (a-f) macroinvertebrate and (g-h) fish assemblages. Results are based on the most supportive candidate models from Table 3, and only significant relationships are presented (p < 0.05). Plots (c) and (d) are partial regressions based on the same model and depict the residuals of the relationships controlled by all of the other variables in the candidate model (i.e., river, distance to headwater and dam height). Circles and diamond symbols differentiate site-comparisons in Chapecó and Chapecozinho rivers, respectively.

Water storage in reservoirs had the strongest influence on changes in taxonomic composition of both macroinvertebrate and fish assemblages. Storage and backwater effects by small dams modify the hydrology and geomorphology of rivers upstream from the impoundment, resulting in overall reductions of water velocity and the deposition of fine sediments (Csiki & Rhoads, 2010; Fantin-Cruz et al., 2020). Such physical changes on basic habitat characteristics have important implications for freshwater biodiversity, particularly for guilds of macroinvertebrates that rely on fastflowing, oxygenated waters and consolidated substrates (Linares et al., 2019; Ruocco et al., 2019; Stanley et al., 2002). We detected decreases in relative abundances of some families of mayflies (e.g., Baetidae and Leptophlebiidae), stoneflies (e.g., Perlidae) and caddisflies (e.g., Philopotamidae), which are considered fluvial specialists and indicators of ecosystem integrity (Bispo & Oliveira, 2007; Hart & Finelli, 1999). Conversely, generalist species (e.g., Chironomidae, Hirundinidae, Caenidae) tend to be dominant in reservoirs with higher storage capacity and poor water quality (Freeman & Marcinek, 2006; Stanley et al., 2002). Likewise, the pearl cichlid G. brasiliensis is common in reservoirs, with juveniles being strikingly abundant in SHPs with larger storage capacity. This species has omnivorous habits, sedentary behaviour and an equilibrium life-history strategy (Bastos et al., 2011), which explain its success in colonising habitats with more stable flows. Other studies in southern Brazil also have reported major increases in abundances of G. brasiliensis after dam closures (Borba et al., 2019; Frehse et al., 2021; Hirschmann et al., 2008), reinforcing its high affinity with artificial lentic habitats.

Habitat effects of dewatering and artificial downstream releases by SHPs also were associated with shifts in taxonomic composition of macroinvertebrates, but were not as clear for fishes. Other studies examining the effects of SHPs on macroinvertebrates also reported extirpations of fluvial specialists, dominance of generalists and even the facilitation of invasions by non-native molluscs downstream of the impoundment (Anderson et al., 2017; Jesus et al., 2004; Linares et al., 2019). Aquatic forms of macroinvertebrates are, in general, susceptible to fine-scale changes in habitat characteristics associated with dam operations such as sedimentation and reduced water velocity, making them highly suitable bioindicators (Hart & Finelli, 1999; Haxton & Findlay, 2008; Mbaka & Mwaniki, 2015). Other factors affecting shifts in macroinvertebrate composition below small dams include warm-water releases (Lessard & Hayes, 2003), movement constraints (Benstead et al., 1999), and changes in primary productivity and nutrient cycling (Arroita et al., 2017; Haxton & Findlay, 2008). By contrast, we did not detect significant shifts in fish assemblages downstream or in dewatering sites, contradicting studies that reported dewatering to be the most relevant impact of SHPs on fish assemblages (Anderson, Freeman, & Pringle, 2006; Jumani et al., 2018; Kubecka et al., 1997). These studies reported reductions in fish size and declines in abundance of species with more complex life cycles (e.g., species that perform seasonal migrations) in dewatering sections and immediately below SHPs. The mismatch between these findings and our results can be explained, at least in part, by the lack of long-distance migratory species in our study, which are historically absent in the Upper Chapecó

FIGURE 5 Polar plot depicting taxonomic shifts (Δ) in fish assemblages between the least-impacted upstream site and the dam-affected sites under the influence of the 12 SHPs (a-c). The length and angle of each coloured bar represent (respectively) the magnitude (i.e., Euclidian distance) and direction of a shift for a given SHP in the ordination space (PC1 and PC2). (d) The resultant directionality of taxonomic shifts (i.e., mean resultant length of Rayleigh's test) is represented by a coloured circle: Δ -Reservoir (red), Δ -Dewatering (orange) and Δ -Downstream (dark blue).



(Barradas et al., 2012). Another study in a similar system in southern Brazil examined the effects of dewatering on fish assemblages in a much larger dam (130 MW and dewatering section of 22 km) and also did not report major shifts in fish composition or losses of fluvial specialists—although the relative abundance of some species such as G. brasiliensis increased four-fold (Borba et al., 2019). Their findings suggest that the patterns we observed are consistent with other studies on larger diversion dams in the region.

The magnitude and direction of shifts in taxonomic composition were quite variable among SHPs in our study, which in some instances were explained by structural dam attributes. Dam height is a simple surrogate of biophysical impacts associated with water storage, such as water residence time, sediment transport and thermal modification (Poff & Hart, 2002). Although this approximation has limitations on describing the hydrological effects of small dams by focusing on the impacts of storage and not of diversion (Kibler, 2017), the magnitude and direction of shifts in macroinvertebrate composition were fairly well-predicted by dam height in reservoir assemblages in our study. Dam height also was a good predictor of the direction of shifts in fish composition below the dam, indicating that more regulated flows favour generalist species such as G. brasiliensis downstream of the SHPs. Alternatively, the magnitude of shifts in the composition of fish species in reservoir sites were best predicted by reservoir area, probably reflecting the

increased availability and stability of spawning and rearing habitats in littoral zones for some species. For instance, more stable water bodies favour recruitments of the species G. brasiliensis and H. malabaricus that spawn in nests, conditions that are more likely to be supported in larger reservoirs (de Lima et al., 2017). The longitudinal position was the only predictor of taxonomic shifts below the SHPs for macroinvertebrates, indicating that the magnitude of changes in assemblages and the replacement of fast-flowing taxa is larger for dams located further downstream in a river network. River ecologists have theorised that the spatial position of dams along the longitudinal gradient may result in distinct ecological effects, and that some of these effects can even accumulate downstream (Ward & Stanford, 1983). These ideas are now gaining traction as a greater body of empirical evidence has accumulated (dos Santos et al., 2017; Loures & Pompeu, 2018; Miranda & Dembkowski, 2016; Ticiani et al., 2023). The degree of flow regulation and water residence time accumulate in the downstream direction in dam cascades (Lehner et al., 2011; Swanson et al., 2021), with observed patterns in macroinvertebrate assemblages being a potential response to serial disturbances in flow regimes by the SHP cascades of the Chapecó Basin.

One of the primary environmental concerns regarding the proliferation of SHPs is their potential for causing ecological changes that can manifest cumulatively across the riverscape (Couto et al., 2021; WILEY- Freshwater Biology

Couto & Olden, 2018; Kibler & Tullos, 2013). Direct lentification through reservoir storage and dewatering has already affected over a third (36%) of the 390km of the Chapecó and Chapecozinho mainstems (estimated here from their confluence to the headwaters based on images from Google Earth). An additional part of the remaining 64% is subjected to flow regulation and backwater effects. Therefore, it is reasonable to expect that the shifts in taxonomic composition which we observed also are occurring throughout much of the Basin. For instance, cumulative habitat lentification can facilitate the establishment of generalist and invasive species throughout the riverscape (Freeman & Marcinek, 2006; Johnson et al., 2008; Loures & Pompeu, 2019). Anecdotally, anglers from different locations across the Chapecó Basin have reported that G. brasiliensis was rare and not as widespread just a few decades ago, when few SHPs were built (Couto, personal communication). Our results indicate that G. brasiliensis has high affinity for SHP reservoirs, representing possible sources for its spread basinwide. In addition, cumulative lentification of fast-flowing habitats such as rapids and riffles may result in local or even global extinctions of endemic species that depend on these habitats, such as the pike cichlids of the genus Crenicichla (De Lucena, 2007; Ruocco et al., 2019). Investigating the cumulative basinwide effects of habitat lentification and flow regulation in the Chapecó Basin remains a pressing need, but these effects have been largely underestimated in environmental assessments for new SHP construction (Desenvolver, 2016).

The proliferation of SHPs is posing threats to freshwater biodiversity globally, yet many countries require just a simplified version of environmental impact assessments (EIAs) as part of SHP licensing procedures (Couto & Olden, 2018; Erlewein, 2013; Lange et al., 2019). Our research demonstrates that SHPs produce measurable changes in the taxonomic composition of macroinvertebrate and fish assemblages, adding new evidence to a mounting body of literature that is reporting similar patterns in other parts of the world (Anderson, Freeman, & Pringle, 2006; Jumani et al., 2018; Linares et al., 2019). Furthermore, our results reveal that macroinvertebrate and fish assemblages follow directional shifts in taxonomic composition in the presence of SHPs (i.e., replacement of fluvial specialists by taxa associated with standing waters), but with variable degrees of severity. This indicates that the "small" modifier alone is not an accurate representation of the potential ecological effects of SHPs, which is concerning considering that differentiating "large" and "small" is a primary decision node to determine whether a full or simplified EIA is required during hydropower licensing (Couto & Olden, 2018). Although some dam attributes emerged as potential proxies of impacts on biodiversity (e.g., dam height, reservoir area, longitudinal position), we did not find a consistent predictor of the magnitude of shifts in assemblage composition in the Chapecó Basin. This suggests that it is unlikely that a priori classifications of dams based on their structural attributes can replace site-specific and cumulative impact assessments. Managers and policymakers should look beyond hydropower-size classifications to design and implement effective policies, regulations and mitigation actions targeting the conservation of freshwater biodiversity.

AUTHOR CONTRIBUTIONS

Conceptualization and developing methods: TBAC and JDO. Conducting the research: TBAC, RSR, PPUA, RCP, GLC, TVTO, HMVES, YFFS and JDO. Data analysis: TBAC and JDO. Data interpretation: TBAC, RSR, JRSV and JDO. Preparation of figures & tables: TBAC, YFFS and JDO. Writing the first draft: TBAC and JDO. Revising critically and editing subsequent drafts: TBAC, RSR, PPUA, RCP, GLC, TVTO, JRSV, HMVES, YFFS and JDO. All authors approved the final version and have agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

ACKNOWLEDGMENTS

We thank Camila Cipriani, Anderson Kassner, Fernanda Pessoa and Rebeka Lehner for assistance during fieldwork activities, and Parque Nacional das Araucárias, ADAMI and Usina Rio do Mato for the logistic support. This study was conducted under approval of the Institutional Animal Care and Use Committee (IACUC) of the University of Washington and permits from ICMBio (61355-1/2018). JDO was supported by H Mason Keeler Endowed Professorship from the School of Aquatic and Fishery Sciences, University of Washington, also supporting TBAC. Grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPg) support RSR (421288/2017-5; 405290/2018-7) and JRSV (310850/2012-6; 303776/2015-3). RCP is supported by the Serrapilheira Institute (grant no. Serra-R-2011-37572) and grant no. 2020/11953-2, São Paulo Research Foundation (FAPESP). TBAC was supported by CNPq/Science Without Borders Fellowship (203991/2014-1) and fieldwork activities were funded by Rufford Foundation, Society for Conservation Biology (LACA section), and National Geographic Society.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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How to cite this article: Couto, T. B. A., Rezende, R. S., de Aquino, P. P. U., Costa-Pereira, R., de Campos, G. L., Occhi, T. V. T., Vitule, J. R. S., Espírito-Santo, H. M. V., Soares, Y. F. F., & Olden, J. D. (2023). Effects of small hydropower dams on macroinvertebrate and fish assemblages in southern Brazil. *Freshwater Biology*, 68, 956–971. <u>https://doi.org/10.1111/</u> fwb.14078 971