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Damming interacts with the flood pulse to alter zooplankton communities in an Amazonian river

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Abstract

1. Flow modification of lotic ecosystems is one of the main threats to global freshwater biodiversity. Commonly, and in the river studied here, modification results from hydroelectric dam installation.
2. We evaluated the impacts of damming on zooplankton communities in the Amazonian floodplain of the Madeira River (Porto Velho, Rondônia, Brazil) following construction in 2012 of the run-of-river dam of Jirau Hydroelectric Power Plant. Using data sampled between 2009 and 2015, we tested for discontinuities in zooplankton community composition attributable to damming and the naturally occurring flood pulse.
3. The flood pulse remained the main predictor explaining variation in zooplankton community structure even with the installation of the dam on the Madeira River. Despite this, discontinuities for the entire zooplankton community and for the main compositional groups (testate amoebae, rotifers, cladocerans, and copepods) were detected in relation to the dam (pre-/post-dam periods), mainly in ebb and low water, and with weaker evidence of dam effects during flood and highwater hydrological periods.
4. A multivariate regression tree explained 9.6% of the variation in zooplankton communities and identified four groups: (1) flood and high-water periods; (2) low water post-dam; (3) low water pre-dam; and (4) ebb hydrological periods. The deviance in each multivariate regression tree node was attributable to variation in eight rotifer, three testate amoeba, and three copepod taxa.
5. Our study demonstrates that the flood pulse, dam construction, and interaction between both of these factors affect zooplankton community structure in the Madeira River. While for many zooplankton community variables, effects occurred mainly during ebb and low-water periods, some effects were also observed during high water and flood periods. We thus recommend the establishment of a permanent environmental monitoring programme during all hydrological periods in tropical floodplain rivers and the addition of sampling sites downstream from dams.

6. Many rivers in the world are increasingly disrupted by multiple dams, yet little is known of their effects, especially for run-of-river dams. Our study identified short-term impacts of only one run-of-river dam on zooplankton communities. More research is needed on the effects of multiple run-of-river dams on zooplankton and other biota, especially in tropical floodplain rivers, so that negative effects can be understood and ameliorated.

KEYWORDS
hydrological period, Jirau Hydroelectric Power Plant, Madeira River, run-of-river dam, zooplankton community structure

1 | INTRODUCTION

Anthropogenic modification of river hydrology has been identified as one of the five main threats to global freshwater biodiversity (Dudgeon et al., 2006). This should particularly affect environments with a naturally marked variation in flow regime such as floodplains (Bunn & Arthington, 2002). The damming of floodplains disrupts hydrological dynamics, changing the magnitude, frequency, duration, time, and rate of flows with potential effects on the dynamics, structure, and functioning of the entire ecosystem (Braghin et al., 2015; Castello & Macedo, 2015; Poff et al., 1997; Timpe & Kaplan, 2017). Thus, the relative importance of disturbance and the ecosystem processes altered by damming may vary over time (Bortolini, Pineda, Rodrigues, Jati, & Velho, 2017), especially where a strong flood pulse is present (Simões et al., 2013).

Planktonic communities are often structured spatially and temporally by environmental and biological gradients. The physical and chemical effects of damming can affect plankton community composition in altered water channels and floodplains (Fan, He, & Wang, 2015; Gascón et al., 2016; Heino, Melo, et al., 2015; Heino, Soininen, Alahuhta, Lappalainen, & Virtanen, 2015; Zhao et al., 2017). For plankton, critical habitat alterations imposed by damming include modified quantity and quality of sediment transport (Castello & Macedo, 2015; Fearnside, 2013) as well as changes in natural seasonality in river flows that reduces the habitat diversity and favours high levels of endemism (Junk, Bayley, & Sparks, 1989; Salo et al., 1986). In addition, the mobility and dispersal of planktonic organisms along the river itself are reduced by the physical barrier of the dam (Zhao et al., 2017).

In the Amazon, approximately 140 hydroelectric power plants are in operation or under construction, and 288 more are planned to be built (Latrubesse et al., 2017). Given that natural flood pulse dynamics can be strongly influenced by dams (Conceição, Higuti, Campos, & Martens, 2018; Souza-Filho, 2009), we evaluated the impacts of damming on zooplankton communities in the floodplain of the tropical Madeira River (Rondônia state, Brazil) following the construction of Jirau Hydroelectric Power Plant. We tested for spatial and temporal discontinuities in zooplankton composition between 2009 and 2015, encompassing pre- and post-dam periods. We hypothesised that temporal discontinuities in zooplankton community structure in the floodplain would be related to the natural seasonality of flows prior to dam construction, with a different pattern occurring post-construction, induced by damming. Also, we hypothesised that zooplankton richness would increase during low water and decrease during the high-water hydrological periods, with increases in both hydrological periods in the post-dam phase because of decreases in water flow.

2 | METHODS

2.1 | Study area

The Madeira River is one of the world's 10 largest rivers in terms of discharge, being the widest and most important tributary of the Amazon River (Latrubesse, Stevaux, & Sinha, 2005; Molina-Carpio, 2008). It is about 1,450 km in length (Bastos et al., 2006) and is formed by the confluence of Beni (Bolivia) and Mamoré (Bolivian–Brazilian border) rivers at Villa Bella, Bolivia. In Brazil, it runs along the northwest of Rondônia state and enters the state of Amazonas, where it joins with the Amazon River downstream of the city of Manaus (Leite et al., 2011). The climate is humid tropical, with mean annual precipitation of 1,900–2,200 mm (Bastos, Almeida, Dorea, & Barbosa, 2007; Leite et al., 2011; Moreira-Turcq, Seyler, Guyot, & Etcheber, 2003), average annual air temperature of 25.2°C (20.9–31.1°C) and relative air humidity around 85% (81%–89%; Torrente-Vilara, Zuanon, Amadio, & Doria, 2008).

Discharge in the Madeira River occurs as an annual unimodal cycle defined by four hydrological periods: low water, flood, high water, and ebb. At low water, discharge is minimal and river beaches are exposed (August to November). Discharge is greatest during the high-water period when marginal areas become flooded (February to May; Barthem, Costa, Cassemiro, Leite, & Silva, 2014). Transitional periods occur at the onset of the rainy season as discharge increases (flood—December to January) and as the flood retreats (ebb—June to July; Barthem et al., 2014). The flood pulse produces marked effects, with large changes in water level (ranging from 15.4 at low water

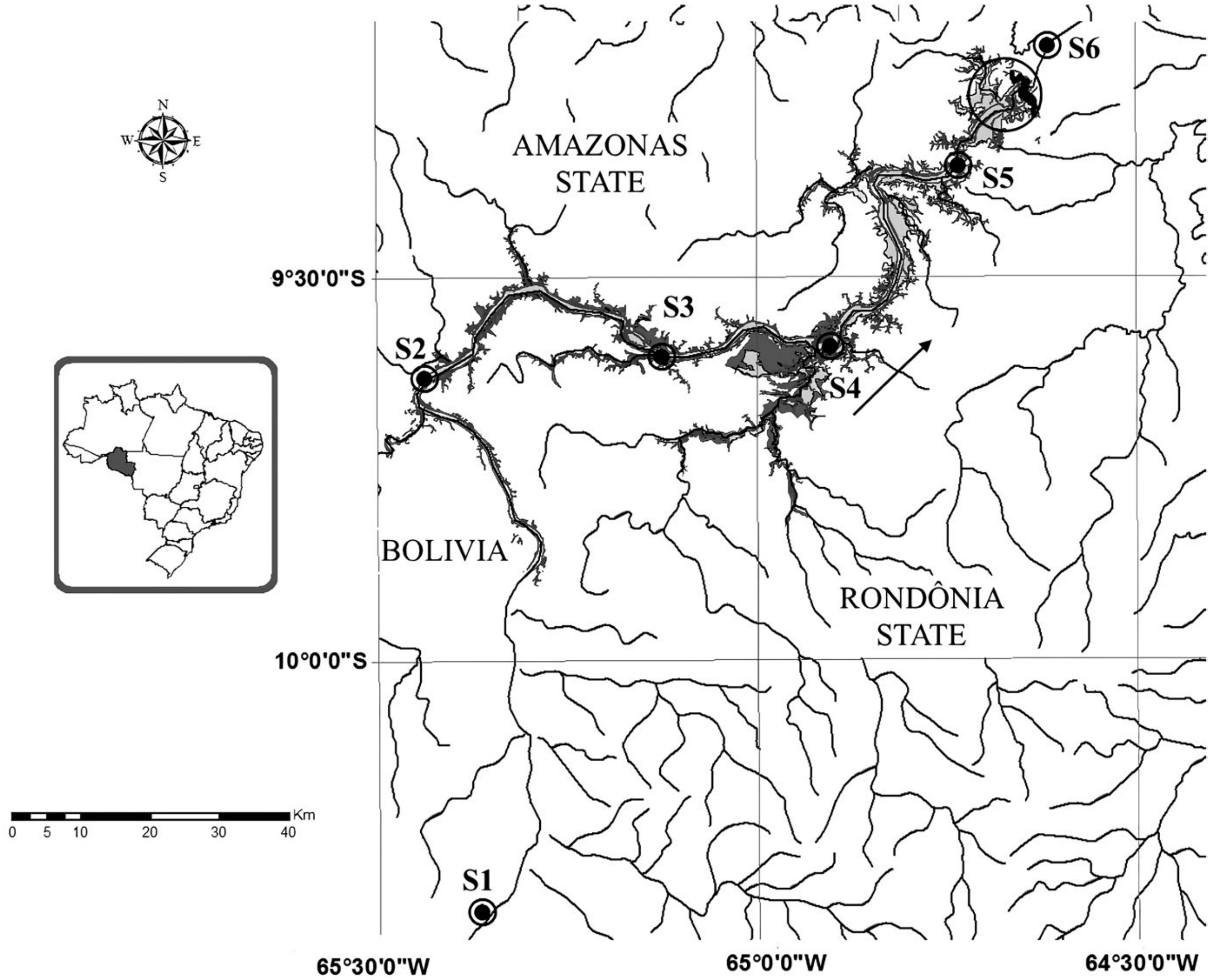

FIGURE 1 Location of sampling sites in the Madeira River. The open circle between sites S5 and S6 indicates the location of Jirau Hydroelectric Power Plant. The arrow indicates the direction of water flow

to 21.8 m at high water—Molina-Carpio et al., 2017; Torrente-Vilara et al., 2008). Mean annual discharge (1967–2013) at the Porto Velho station is 18,500 m^3/s with discharge varying between 2,322 and 47,236 m^3/s, comprising nearly 10% of the discharge of the Amazon River into the Atlantic Ocean (Molina-Carpio et al., 2017; Torrente-Vilara et al., 2008).

The Jirau Hydroelectric Power Plant is located in the Madeira River, at 136 km upstream from Porto Velho city, Rondônia state, Brazil (Figure 1). The construction of the dam was finished in July 2012. This facility is considered a mega dam in terms of power generation (3,750 MW of installed capacity; Latrubesse et al., 2017). Jirau is also a run-of-river dam, operating via the natural river flow, without the need for the formation of a large reservoir with strongly lentic conditions (Pracheil, DeRolph, Schramm, & Bevelhimer, 2016). Horizontal axis turbines occur in run-of-river dams (Wang, Chen, Liu, & Zhu, 2016), and it is possible to maintain up to 70% of the original river flow (Cella-Ribeiro, Doria, Dutka-Gianelli, Alves, & Torrente-Vilara, 2017). The required electrical capacity was achieved at lower stored volumes of water, and the residence time of the water in the reservoir is shorter than is normally the case for mega dams (Fearnside, 2014). The reservoir area attains a maximum of 361.6 km^2 and varies seasonally from 21 km^2 at low water to 207.7 km^2 at high water (Energia Sustentável do Brasil, 2018). From 2013 to 2015, average annual discharge was 22.066 m^3/s, ranging from 5.215 m^3/s in the 2015 low-water period to 54.021 m^3/s in the 2014 high-water period (ANA, 2018).

2.2 | Sampling

A monitoring programme of the Madeira River was carried out by Life Consultoria Ambiental (LCA), and the data included in this current study were collected by them as part of their Environmental Impact Study. A total of 22 sampling campaigns were carried out by LCA from 2009 to 2015 at six sites in the mainstem of the Madeira River, five of which were located upstream (S1, S2, S3, S4 and S5) and one downstream from the dam (S6; Figure 1). The sampling campaigns consisted of 12 visits in the pre-dam phase, between September 2009 and July 2012 (three sampling campaigns in each hydrological period—low water, flood, high water and ebb) and 10 visits in the post-dam phase, between October 2012 and April 2015 (three sampling campaigns in low water and flood, and two in high water and ebb period).

To assess zooplankton communities at each site, 1,000 L of pumped water was filtered through a 68-µm mesh plankton net. Collected organisms were fixed in 4% formalin buffered with calcium carbonate. For quantitative analysis, the samples were concentrated to 75 ml, and about 10% of that volume was sub-sampled with a Hensen–Stempel pipette. At least 250 individuals from each zooplankton group were counted per sample using a Sedgwick–Rafter chamber and a light microscope. Samples with only a few individuals (<250 individuals from each zooplankton group) were fully counted. To enable qualitative analyses, further aliquots of 2 ml were removed from the concentrated samples after decantation, and examined until no new species were found. Zooplankton were identified to the lowest possible taxonomic level, and total density was expressed in individuals per cubic metre (ind/m^3). In the case of copepods, only adults could be identified to species; larval and juvenile forms were identified to family (Diaptomidae or Cyclopidae).

2.3 | Data analyses

Prior to the analyses, density values of all zooplankton taxa, including the rare taxa, were log-chord-transformed (Legendre & Borcard, 2018). The chord transformation, applied to log-transformed abundances, removes the effect of double-zeros from the analysis, enabling the calculation of Euclidean distances (Borcard, Gillet, & Legendre, 2018; Legendre & Borcard, 2018). We performed a permutational multivariate analysis of variance using distance matrices (PERMANOVA; Anderson, 2001) to detect compositional differences across all zooplankton, as well as in the major taxonomic groups (testate amoebae, rotifers, cladocerans, and copepods) attributable to the influence of damming, hydrological periods and/or between sampling sites, and to their interactions. Three factors were created for the PERMANOVA: damming (pre- and post-dam construction, abbreviated DAM), hydrological periods (1 = low water, 2 = flood, 3 = high water and 4 = ebb, abbreviated HYDR), and site (sampling sites from S1 to S6, abbreviated SITE). We carried out the analyses including all hydrological periods as well as for each hydrologic period separately to detect effects of damming and site by period interactions. We conducted additional analyses that were spatially restricted to the sampling sites farthest upstream (S1) and nearest downstream (S6) from the dam, the end-point comparison. PERMANOVA was performed using Euclidean distance and *p*-values were estimated from 999 permutations using the function *adonis2*, package *vegan* (Oksanen et al., 2018) in R (R Core Team, 2018). Two redundancy analyses (Legendre & Legendre, 2012) were performed: one using the DAM factor and the other with the HYDR factor, using the function *rda*, package *vegan*. To visualise the similarities of zooplankton community between all sites grouped by damming and hydrological periods, we plotted the position of the sites through time using the R function *plot*.

Similarly, we tested the influence of damming, the flood pulse, sampling sites and their interactions on total zooplankton richness and richness within major taxonomic groups. For this, we performed a factorial ANOVA using the same three factors as in the PERMANOVA analysis: DAM, HYDR and SITE, using the *aov* function of the *stats* package in R (R Core Team, 2018).

We also used multivariate regression tree (MRT; De'ath, 2002) for modelling relationships between species and the factors (pre- and post-dam and hydrological periods). This analysis tested the hypothesis that discontinuities in zooplankton community would be related to the natural seasonality of the floodplain prior to dam construction, but that a different post-dam pattern would occur, probably because of changes to the environmental gradients resulting from the impoundment. In MRT, the total sums-of-squares of the zooplankton density values represent the dissimilarity among the zooplankton densities, and the least-squares criterion is used to split data into two groups several times, based on one of the two factors (damming or hydrological periods; De'ath, 2002; Ge et al., 2008). The split chosen each time has the least dissimilarity within groups and more dissimilarity between groups related to a factor, after comparing all the possible splits. Following the first split, new splits are formed independently and hierarchically (Bachraty, Legendre, & Desbruyères, 2009; Borcard et al., 2018; Davidson, Sayer, Perrow, Bramm, & Jeppesen, 2010; De'ath, 2002; Ge et al., 2008). Zooplankton species density is shown as bar plots for each MRT group, along with the number of samples included in that group and the sum-of-square errors (Borcard et al., 2018).

To verify the MRT, a cross-validation test was performed by splitting the data. Then, a new model from one data subset was estimated and its predictive accuracy was then tested on the other data subset (not included in its construction; Davidson et al., 2010). This process was repeated until each sample had been left out in turn and the cross-validated relative error stabilised (CVRE; Breiman, Friedman, Olshen, & Stone, 1984; Davidson et al., 2010). The model with the minimum CVRE was selected as the best predictive tree (Davidson et al., 2010, 2012; De'ath & Fabricus, 2000), where values closer to one represent poor predictors for the tree splits and closer to zero represent perfect predictors (Borcard et al., 2018; Legendre & Legendre, 2012). For the MRT analysis, we used the *mvpart* function in R-package *mvpart* (De'ath, 2014). Discriminant species (those that contribute the most to the deviance in MRT) were identified by computing *summary* of the function *MRT* in R-package *mvpartWRAP* (Ouellette & Legendre, 2012).

3 | RESULTS

A total of 190,622 individuals from 228 zooplankton taxa were identified across the six mainstem Madeira River sampling sites from 2009 to 2015. Across all communities, 93 taxa were rotifers, 81 testate amoebae, 33 cladocerans and 21 copepods (Supporting

TABLE 1 Focusing on the sites farthest upstream and closest downstream to the dam, R^2 and PERMANOVA significance between zooplankton community groups and factors: DAM (pre- and post-dam construction); HYDR (hydrological periods) and SITE (sampling sites S1 and S6)

	DAM		HYDR		SITE		DAM: HYDR		DAM: SITE		HYDR: SITE		DAM: HYDR: SITE		Residual
Hydrological period	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2
All zooplankton															
All	**0.038**	0.005	**0.098**	0.002	0.022	0.424	**0.107**	0.001	0.018	0.762	0.053	0.941	0.058	0.796	0.605
Flood	**0.163**	0.003	–	–	0.074	0.693	–	–	0.065	0.863	–	–	–	–	0.698
High water	**0.143**	0.001	–	–	**0.107**	0.043	–	–	0.096	0.176	–	–	–	–	0.654
Ebb	**0.203**	0.032	–	–	0.112	0.760	–	–	0.147	0.339	–	–	–	–	0.538
Low water	0.216	0.140	–	–	0.077	0.988	–	–	0.094	0.934	–	–	–	–	0.612
Testate amoebae															
All	**0.069**	0.002	0.064	0.552	**0.038**	0.049	0.060	0.645	0.011	0.970	0.051	0.851	0.078	0.217	0.628
Flood	**0.199**	0.011	–	–	0.068	0.581	–	–	0.075	0.483	–	–	–	–	0.657
High water	0.104	0.184	–	–	**0.142**	0.025	–	–	**0.133**	0.050	–	–	–	–	0.621
Ebb	0.150	0.484	–	–	0.194	0.155	–	–	0.065	0.972	–	–	–	–	0.591
Low water	**0.246**	0.032	–	–	0.122	0.531	–	–	0.116	0.596	–	–	–	–	0.516
Rotifers															
All	0.028	0.151	**0.108**	0.002	0.014	0.935	**0.118**	0.001	0.018	0.693	0.050	0.953	0.042	0.998	0.621
Flood	0.135	0.106	–	–	0.076	0.662	–	–	0.041	0.991	–	–	–	–	0.748
High water	**0.131**	0.028	–	–	0.060	0.965	–	–	0.073	0.835	–	–	–	–	0.736
Ebb	**0.250**	0.013	–	–	0.107	0.667	–	–	0.128	0.459	–	–	–	–	0.515
Low water	0.246	0.122	–	–	0.089	0.837	–	–	0.090	0.830	–	–	–	–	0.574
Cladocerans															
All	0.018	0.536	**0.125**	0.003	0.034	0.089	**0.090**	0.049	**0.040**	0.034	0.044	0.876	0.066	0.404	0.581
Flood	**0.143**	0.003	–	–	**0.136**	0.010	–	–	0.113	0.086	–	–	–	–	0.607
High water	0.115	0.193	–	–	0.066	0.711	–	–	0.108	0.265	–	–	–	–	0.710
Ebb	0.137	0.487	–	–	0.089	0.719	–	–	0.196	0.273	–	–	–	–	0.576
Low water	0.165	0.293	–	–	0.121	0.592	–	–	0.098	0.856	–	–	–	–	0.616
Copepods															
All	**0.084**	0.001	0.067	0.461	0.009	0.933	**0.118**	0.023	0.006	0.985	0.041	0.912	0.050	0.763	0.624
Flood	**0.235**	0.026	–	–	0.033	0.820	–	–	0.029	0.870	–	–	–	–	0.703
High water	**0.211**	0.018	–	–	0.100	0.270	–	–	0.069	0.498	–	–	–	–	0.619
Ebb	0.122	0.558	–	–	0.147	0.973	–	–	0.236	0.189	–	–	–	–	0.595
Low water	0.327	0.126	–	–	0.019	0.960	–	–	0.040	0.877	–	–	–	–	0.614

Numbers in bold are significant at $p \le 0.05$.

TABLE 2 Across all river sites, R^2 and PERMANOVA significance for zooplankton community groups and three factors: DAM (pre- and post-dam construction); HYDR (hydrological periods) and SITE (sampling sites from S1 to S6)

	DAM		HYDR		SITE		DAM: HYDR		DAM: SITE		HYDR: SITE		DAM: HYDR: SITE		Residual
Hydrological period	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2
All zooplankton															
All	**0.025**	0.001	**0.092**	0.001	0.030	0.964	**0.036**	0.001	0.032	0.874	0.089	0.997	0.088	0.999	0.608
Flood	**0.046**	0.015	–	–	0.115	0.988	–	–	0.128	0.929	–	–	–	–	0.710
High water	**0.062**	0.025	–	–	0.231	0.187	–	–	0.196	0.756	–	–	–	–	0.510
Ebb	**0.086**	0.012	–	–	0.159	0.999	–	–	0.171	0.999	–	–	–	–	0.583
Low water	**0.075**	0.003	–	–	0.116	0.951	–	–	0.102	0.997	–	–	–	–	0.706
Testate amoebae															
All	**0.022**	0.001	**0.041**	0.001	0.034	0.689	0.026	0.124	0.037	0.440	0.116	0.246	0.103	0.767	0.619
Flood	**0.045**	0.032	–	–	0.122	0.928	–	–	0.131	0.779	–	–	–	–	0.701
High water	0.034	0.684	–	–	**0.282**	0.012	–	–	0.193	0.629	–	–	–	–	0.490
Ebb	**0.071**	0.012	–	–	0.214	0.297	–	–	0.238	0.096	–	–	–	–	0.476
Low water	**0.056**	0.022	–	–	0.133	0.635	–	–	0.117	0.883	–	–	–	–	0.693
Rotifers															
All	**0.019**	0.001	**0.102**	0.001	0.026	0.994	**0.040**	0.001	0.032	0.783	0.084	0.999	0.087	0.996	0.609
Flood	0.036	0.164	–	–	0.117	0.924	–	–	0.160	0.222	–	–	–	–	0.686
High water	**0.071**	0.044	–	–	0.200	0.792	–	–	0.181	0.925	–	–	–	–	0.547
Ebb	**0.100**	0.008	–	–	0.153	0.996	–	–	0.181	0.950	–	–	–	–	0.566
Low water	**0.096**	0.005	–	–	0.103	0.961	–	–	0.088	0.996	–	–	–	–	0.712
Cladocerans															
All	**0.014**	0.049	**0.075**	0.001	0.037	0.431	**0.034**	0.036	0.047	0.098	0.095	0.800	0.097	0.769	0.601
Flood	0.037	0.197	–	–	0.156	0.287	–	–	0.119	0.850	–	–	–	–	0.688
High water	0.058	0.229	–	–	0.217	0.412	–	–	0.227	0.357	–	–	–	–	0.498
Ebb	0.079	0.156	–	–	0.140	0.975	–	–	0.184	0.831	–	–	–	–	0.596
Low water	**0.064**	0.046	–	–	0.117	0.704	–	–	0.141	0.454	–	–	–	–	0.677
Copepods															
All	**0.057**	0.001	**0.115**	0.001	0.037	0.303	**0.034**	0.025	0.026	0.810	0.082	0.910	0.086	0.828	0.562
Flood	0.052	0.102	–	–	0.155	0.334	–	–	0.109	0.785	–	–	–	–	0.683
High water	**0.139**	0.002	–	–	**0.248**	0.036	–	–	**0.272**	0.020	–	–	–	–	0.341
Ebb	**0.127**	0.002	–	–	0.173	0.527	–	–	0.267	0.071	–	–	–	–	0.433
Low water	**0.104**	0.002	–	–	0.102	0.930	–	–	0.083	0.984	–	–	–	–	0.710

Numbers in bold are significant at $p \leq 0.05$.

Information Table S1). The most abundant group was rotifers, making up 45.3% of all organisms, followed by copepods (30.4%), testate amoebae (16.1%), and cladocerans (8.2%). Copepod populations consisted mainly of larval and juvenile forms (nauplii and copepodite, respectively) that, together, accounted for more than 83% of the total copepod abundance, with only 16.64% being adults. Because adults are required for full species-level identification, the dominance of juvenile forms may have contributed to the reduced copepod richness relative to all other groups. A few density peaks were detected pre-dam in low-water hydrological periods mainly comprising rotifers and copepods, but also occasionally cladocerans (Supporting Information Figure S2a). Density peaks continued to occur in the low-water period post-dam, but they were less pronounced than in the pre-dam phase.

With respect to richness, almost all pre-dam phase samples were dominated by rotifer taxa (Supporting Information Figure S2b). In post-dam phase samples, both rotifers and testate amoebae had high richness, except during the ebb hydrologic period in 2014, where there was a richness peak in all zooplankton groups, especially rotifers. In general, zooplankton richness decreased post-dam. The factorial ANOVA analyses revealed that richness of the all zooplankton together, as well as richness of the major taxonomic groups (testate amoebae, rotifers, copepods), was influenced by both damming and the flood pulse (Supporting Information Table S2). Cladoceran richness was affected only by damming.

3.1 | The end-point comparison

Damming and hydrological periods together explained 13.6% of the zooplankton community variation at sites S1 and S6 (Table 1). However, the significant interaction DAM:HYDR indicated that the effect attributable to dam construction differed between hydrological periods. This was also observed when analysing the effect of the dam by each hydrological period separately: damming was associated with changes in zooplankton community structure during flood ($R^2 = 0.163$), high water ($R^2 = 0.143$), and ebb ($R^2 = 0.203$) periods, but had no significant effect in low water. The structure of the overall zooplankton community and its main taxonomic groups only differed spatially (SITE) during high water (Table 1).

Considering zooplankton groups separately across all hydrological periods, differences in community structure were detected between pre- and post-dam periods (DAM, hydrological period All; Table 1) only for testate amoebae ($R^2 = 0.069$) and copepods ($R^2 = 0.084$). Considering the hydrological periods separately for factor DAM, testate amoebae, cladocerans, and copepods responded during the flood hydrological period; rotifers and copepods responded during high water and ebb hydrological periods; and testate amoebae responded during low-water hydrological period. Hydrological period alone (HYDR; Table 1) induced changes in the community structure only in rotifers and cladocerans. Also, community structure only differed spatially during high water for testate amoebae and during the flood period for cladocerans.

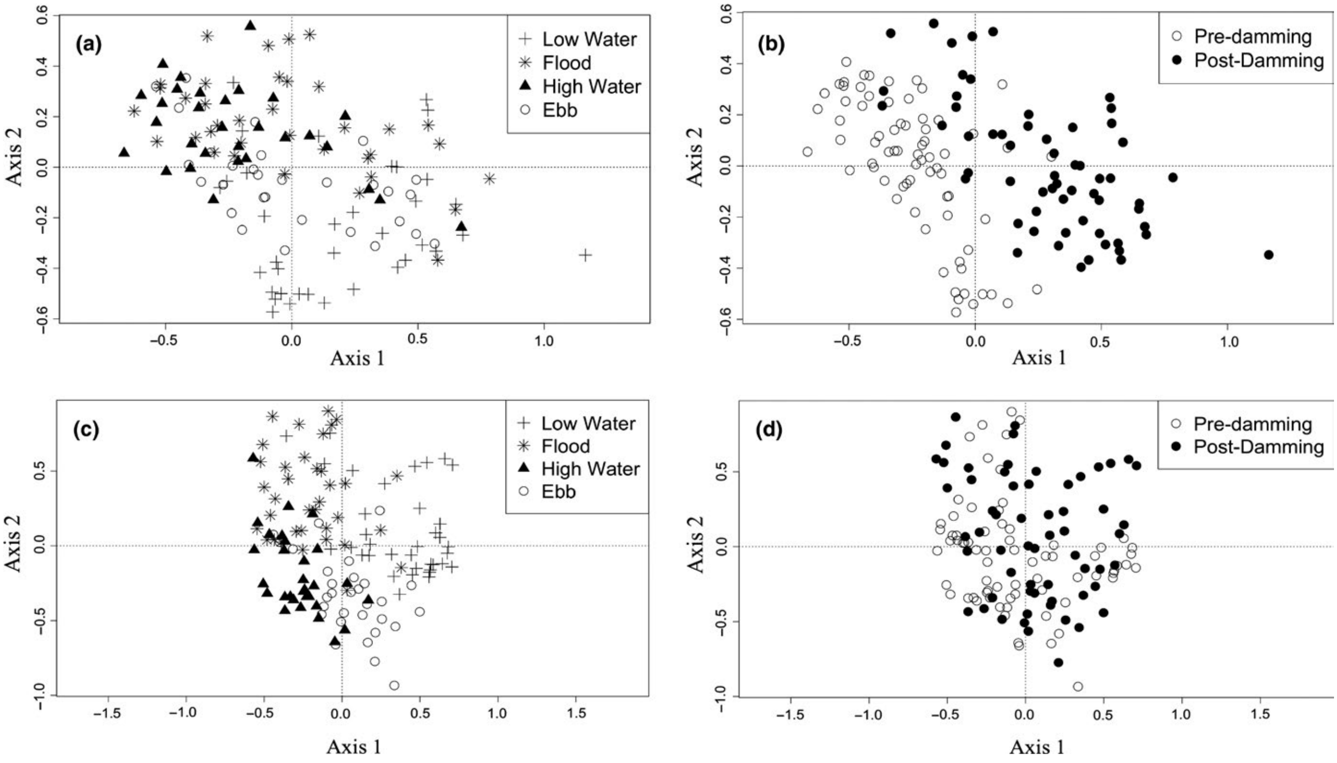

FIGURE 2 Redundancy analyses plots for sites according to zooplankton community composition related to the dam (DAM) factor (plots a and b; $R^2_{adj} = 0.018$) and to the hydrological period (HYDR) factor (plots c and d; $R^2_{adj} = 0.072$) in the Madeira River between 2009 and 2015 with marker indications corresponding to the following: (a, c) the hydrological periods and (b, d) pre- and post-dam construction

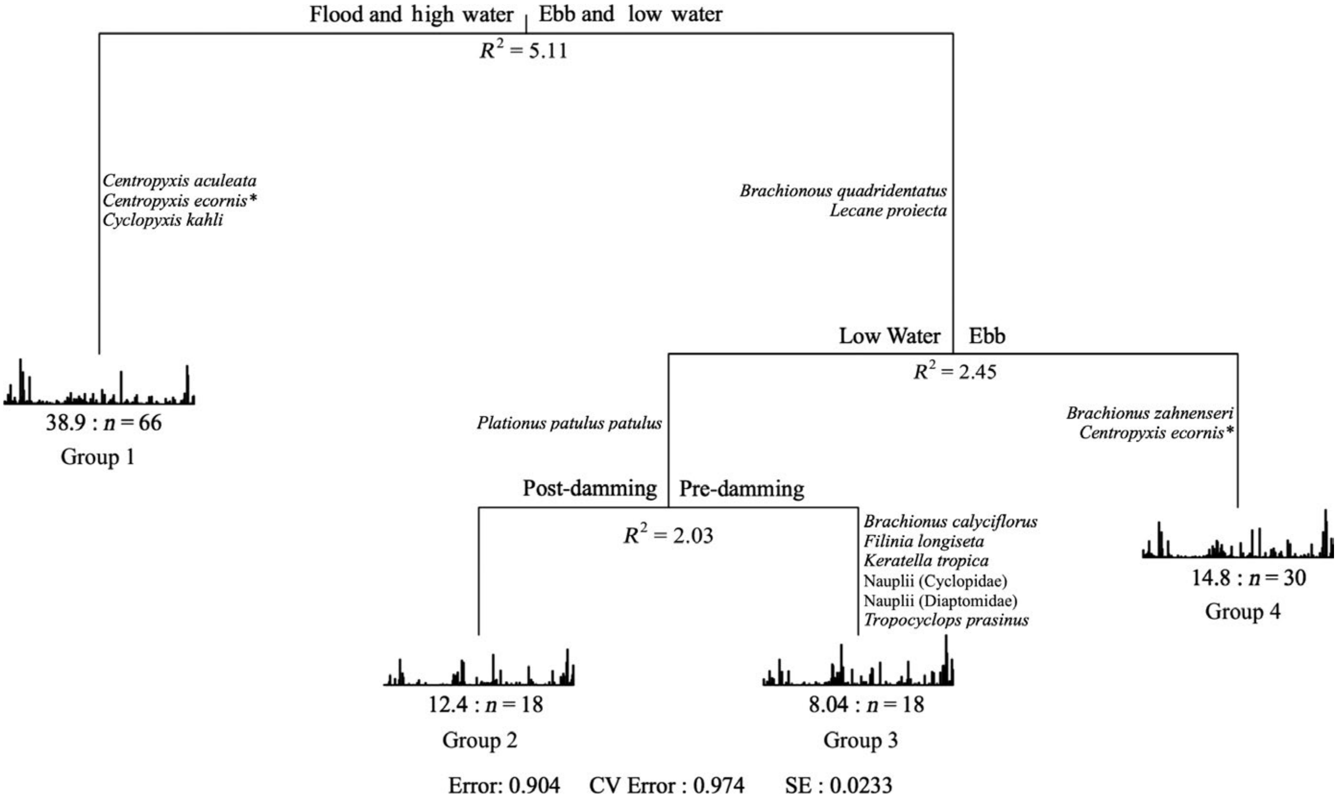

FIGURE 3 Multivariate regression tree (MRT) analysis of the interaction between zooplankton densities in all six study sites and two factors: hydrological periods and dam construction on the Madeira River (R^2 = 0.096). The small bar plots in each leaf of the tree show the multivariate zooplankton density averages within each MRT group; *n* indicates the number of samples; the other number is the sum of the squared errors within each group. The names indicated refer to the most important species explaining the deviance in each node in the MRT. *This taxon was important to explain the deviance in two nodes

3.2 | All sites

Considering all six sites (S1–S6) along the Madeira River, significant differences in zooplankton community structure were attributable to the flood pulse (HYDR; Table 2) and also to dam construction in all hydrological periods (DAM; Table 2). Considering the effect of damming by hydrological period, the percentage of variation in zooplankton composition significantly explained by damming ranged from 4.6% in flood to 8.6% in ebb hydrological periods. In the low-water period, community variation in all zooplankton groups attributable to damming was significant; in the ebb period, damming induced variation in testate amoebae, rotifers and copepods; in the flood period for testate amoebae; and in the high-water period for rotifers. Damming was also responsible for the largest variation in community structure, occurring during the ebb period for testate amoebae (R^2 = 0.071) and rotifers (R^2 = 0.100) but during high water for copepods (R^2 = 0.139). The hydrological period alone (HYDR; Table 2) also affected the zooplankton community, explaining 9.2% of overall zooplankton community variation, 4.1% of testate amoebae, 10.2% of rotifers, 1.4% of cladocerans, and 5.7% of copepods. The only variation in communities between sampling sites (SITE; Table 2) occurred for testate amoebae (R^2 = 0.282) and copepods (R^2 = 0.248) during the high-water period.

The redundancy analysis plots clearly showed differences in zooplankton community structure related to damming (Figure 2b) and hydrological period (Figure 2c). It was also possible to detect the interaction between these two variables (Figure 2a,d) as revealed by the PERMANOVA (Table 2). Mainly in low water and ebb hydrological periods, it was possible to detect greater differences in zooplankton community structure pre- and post-dam.

The MRT model computed for the six study sites indicated three interpretable splits, based on the CVRE (Supporting Information Figure S1), and explained 9.6% of the variation in zooplankton community structure (Figure 3). The first and strongest discontinuity divided the data at the first node according to hydrological period, separating flood and high water (Group 1) from ebb and low-water periods. This node explained 5.11% of variation in the data, with six taxa considered the most important to explain its deviance: three testate amoebae that were more related to sites in flood and high-water hydrological periods—*Centropyxis aculeata*, *Centropyxis ecornis* and *Cyclopyxis kahli*; three rotifers that were more related to sites in ebb and low-water hydrological periods—*Brachionous quadridentatus*, *Lecane proiecta*, and *Keratella tropica*, a rotifer taxon that was more related to sites in low-water pre-dam phase. The second node also divided the communities according to hydrological periods, separating ebb (Group 4) from the low-water hydrological periods and explaining 2.45% of zooplankton community variation. Five taxa were considered the most important to its deviance: *Plationus patulus patulus* was more related to sites in low water; *Brachionus zahnenseri* and *Centropyxis ecornis* were more related to sites in ebb hydrological period; and the last two species important to this deviance were *Keratella tropica* and *Brachionus calyciflorus*, both more related to sites in low-water pre-dam phase. Finally, the third node of the MRT revealed a discontinuity related to damming, explaining 2.03% of the zooplankton community variation and separating the low-water period communities into post-dam (Group 2) and pre-dam (Group 3) based predominantly on six zooplankton taxa, all related to low water-pre-dam phase—*Brachionus calyciflorus*, *Filinia longiseta*, *Keratella tropica*; the nauplii copepod forms of cyclopidae and diaptomidae, and the copepod *Tropocyclops prasinus*.

4 | DISCUSSION

As also observed in other studies of tropical and temperate rivers (Frutos, Neiff, & Neiff, 2006; Jose de Paggi & Paggi, 2014; Lair, 2006; Matsumura-Tundisi, Tundisi, Souza-Soares, & Tundisi, 2015), the zooplankton community of the Madeira River was dominated by rotifers and copepods (mainly larval and juvenile forms), especially pre-dam. In terms of richness, rotifers had greatest taxon richness both pre- and post-dam. Even at their highest densities, the number of copepod taxa was the lowest of all zooplanktonic groups. This occurs commonly in rivers because larval and juvenile copepod forms predominate, while the adults, necessary for species-level taxonomic determination, are scarce (Jose de Paggi & Paggi, 2014).

Floodplains are highly complex including lotic and lentic systems that are intermittently connected (Fantin-Cruz, Loverde-Oliveira, Bonecker, Girad, & Motta-Marque, 2011; Thomaz, Pagioro, Bini, Roberto, & Rocha, 2004) by the hydrologic variability of the flood pulse substantially altering the physical, chemical and biological characteristics of the water (Junk et al., 1989; Padial et al., 2012). The flood pulse is the major force controlling biota in river floodplains, maintaining a dynamic equilibrium (Bino, Wassens, Kingsford, Thomas, & Spencer, 2018; Conceição et al., 2018; Junk et al., 1989). Anthropogenic changes to hydrology usually alter or completely eliminate the flood pulse from downstream floodplains, and also sometimes permanently inundate upstream floodplains (Junk et al., 1989), modifying community structure (Agostinho, Thomaz, & Gomes, 2004; Braghin et al., 2015). The present study shows that the flood pulse is the main predictor of variation in zooplankton community structure in the Madeira River. Moreover, although a perturbation introduced by impoundment was detected, the analyses all demonstrated that the magnitude of the effect depended on the flood pulse that was still evident post-dam. The continued presence of the flood pulse effect post-dam is unusual but was probably a function of relatively short reservoir water residence times and a high continuous flow (22.066 m^3/s; ANA, 2018), characteristic of run-of-river dams, coupled with the very marked flood pulse of Madeira River.

4.1 | Interaction of damming with hydrological period

Interestingly, the effect of damming on zooplankton communities on the end-point comparison was minimal compared to most other observations in tropical impoundments. The introduction of a dam normally results in the creation of three distinct longitudinal zones: a riverine (lotic) zone, a transition zone and a lacustrine (lentic) zone (Wetzel, 2001), which has been shown previously to influence zooplankton communities (Bunn & Arthington, 2002; Portinho, Perbiche-Neves, & Nogueira, 2016). However, in our study, the Madeira River retained high flows and short water residence time because it has a run-of-river dam. Also, spatial differences in zooplankton community structure were not observed across all taxa or hydrological periods.

Generally, strong effects of the dam on zooplankton communities were not observed during flood and high-water hydrological periods across the six sites in the Madeira River. Effects that were detected in these periods were always the smallest relative to the other hydrological periods for the affected taxa. Furthermore, the MRT showed similarities in zooplankton community structure (labelled Group 1) between flood and high-water hydrological periods. The lack of effect of the dam during the higher discharge periods is probably because, during floods, a large amount of water, with particular environmental conditions and organisms (Bozelli, Thomaz, Padial, Lopes, & Bini, 2015), is delivered from upstream, as well as terrestrial allocthonous matter delivered from the flooded regions into the river (Jardine et al., 2012). These inflows increase habitat similarity along rivers by minimising resource variation (Thomaz, Bini, & Bozelli, 2007) and by dilution, thereby homogenising environments and biota regionally, potentially also facilitating the dispersal and recruitment of rare or new species (Bonecker, Aoyagui, & Santos, 2009; Bozelli et al., 2015; Braghin et al., 2015; Havel & Shurin, 2004; Thomaz et al., 2007). In this way, the magnitude of flooding in the Madeira River, via its homogenising effects, could have resulted in a common zooplankton community response even post-dam in both flood and high-water periods.

Differences in zooplankton community structure and in its main compositional groups pre- and post-dam were mainly evident in the ebb (entire zooplankton community, testate amoebae and rotifers) and low-water hydrological periods (cladocerans). Other floodplain river studies have also detected the most pronounced differences in zooplankton community structure at ebb or low water (Frutos et al., 2006; Jose de Paggi & Paggi, 2014; Thomaz et al., 2007; Zhao et al., 2017). In the MRT analysis, the zooplankton communities in low-water periods pre- and post-dam were different enough to be classified into two groups. As water recedes, local processes operating at the habitat scale again become the major determinants of biological communities (Rodriguez & Lewis, 1997): both biotic interactions (e.g. competition and predation) and environmental conditions (e.g. physical and chemical water properties; Braghin et al., 2015; Simões, Lansac-Tôha, Velho, & Bonecker, 2012). Also, during the low-water period, isolated communities in each local habitat may diverge during succession, the sequence of which depends on organismal responses to the dominant local environmental characteristics and on the identity of the propagules transported (with some stochasticity) into the local water body during the last flood (Thomaz et al., 2007). These processes would explain the greater variation in zooplankton community structure detected during the ebb and low-water periods.

Rotifers and testate amoebae were the most important in distinguishing the ebb and low water from the flood and high-water hydrological periods. Rotifers usually reached their greatest density and richness values in the low-water period. Rotifers respond more quickly relative to larger zooplankton owing to their short generation times (Gillooly, 2000), better colonising abilities (Gabaldón et al., 2017), and their adaptability to short-term environmental variability (Balkić, Ternjej, & Špoljar, 2018). Water-level fluctuations affect rotifers (Frutos et al., 2006); they are expected to dominate after a high-water period, recolonising the water column, reaching peak densities and reproducing rapidly at the expense of other species (Dickman, 1969; Frutos et al., 2006; Gabaldón et al., 2017). Three testate amoebae species had their density peaks coinciding mainly with the flood period pre-dam when, in general, the other zooplankton groups were at their lowest densities. Diversity of testate amoebae is generally greater in the sediment or in association with macrophytes than in the water column (Alves, Velho, Simões, & Lansac-Tôha, 2010). However, the continuous water flow of rivers appears to facilitate their daily integration into the water column habitat from the substrate and associated vegetation (Alves et al., 2010; Lansac-Tôha, Velho, & Bonecker, 2003; Velho, Lansac-Tôha, & Bini, 1999, 2003). The annual flooding process that occurs naturally in the Madeira River may further promote this phenomenon by aiding the dispersal of littoral organisms into the river (Torres, 1996). These factors associated with river flow may explain the high density of testate amoebae recorded during the flooding hydrological period, especially prior to damming.

Rotifers were also important in distinguishing low water from ebb, and rotifers and (mainly) larval copepod stages were important for distinguishing pre- and post-dam in low-water hydrological periods (both were mainly related to low water pre-dam). Copepods have different reproductive strategies to rotifers. They can invest heavily in offspring, such that densities of nauplii and juveniles increase rapidly, whereas adult densities may be limited by predation (Hairston & Bohonak, 1998), potentially explaining the greatest densities of especially larval copepod stages in low-water periods. In sum, the reproductive characteristics of copepods and rotifers combined with organismal responses mainly related to local environmental characteristics during low water may explain the greater degree of variation in zooplankton community structure between ebb and low water.

Ultimately, we found no strong evidence of negative effects of the dam on zooplankton communities. The possibility remains that an unidentified factor (e.g. a climatic shift or other stochastic factor) that also changed over the dam construction period could have altered zooplankton communities in the post-dam phase compared to the pre-dam phase in a way that masked any effect of damming. This is impossible to verify without an undammed, control or reference river. Secondly, a large part of the variation in zooplankton community composition remained unexplained. While not uncommon in observational studies of biological communities (Beisner, Peres-Neto, Lindström, Barnett, & Longhi, 2006; Bortolini et al., 2017). It may indicate that one or more influential factors were not measured by our study. For example, we did not evaluate the effect of environmental variables on zooplankton community structure, so the inclusion of environmental variables may have increased the amount of variation explained.

4.2 | Spatial and temporal community variation

We detected few spatial differences in zooplankton community structure along the mainstem of the Madeira River, despite the fact that there are >10 tributaries discharging water and associated organisms into it between sites S1 and S6. This may be explained by the hydrological similarity observed across all the sampling sites, even when distant from each other. Furthermore, adjacent tributaries may have weakened the dam effects on communities through the continuous input of biotic and abiotic matter into the mainstem Madeira River, as tributaries are known to assist in restructuring biotic and abiotic variables in impounded rivers (Braghin et al., 2015).

5 | CONCLUSION AND RECOMMENDATIONS FOR MONITORING PROGRAMMES IN TROPICAL FLOODPLAIN RIVERS

In unimpounded ecosystems, the natural water flow and hydrological periods of floodplains can positively influence the diversity of aquatic organisms through the interaction of several factors that act at different spatial and temporal scales (Bunn & Arthington, 2002). For example, the natural flooding process reduces the interaction between organisms through dilution (Angeler, Alvarez-Cobelas, Rojo, & Sánchez-Carrillo, 2000; Quintana et al., 2006), thereby reducing competition and consequently, increasing biodiversity (Gabaldón et al., 2017). Moreover, flooding of areas adjacent to the main river also provides periodic connectivity between habitats, promoting biotic and abiotic homogenisation and favouring species dispersal (Bunn & Arthington, 2002), which may also reduce the risk of local extinctions (Braghin et al., 2015; Thomaz et al., 2007; Ward, Tockner, & Schiemer, 1999). Thus, although our study demonstrated that run-of-river type dams probably have less impact than do conventional dams, there were still clear effects on zooplankton community structure during the ebb and low-water periods, and also some effects in the other hydrological periods. Because zooplankton are adapted to the natural variation brought by the flood pulse, but not to the modifications induced by the impoundment, undesirable effects such as declines in species richness and the establishment of invasive exotic organisms (with further deleterious effects on native organisms) are expected over the longer term (Bunn & Arthington, 2002; Serafim-Júnior, Lansac-Tôha, Lopes, & Perbiche-Neves, 2016).

Our study considered only the short-term effects of the dam on the zooplankton communities. As some effects of the dam were observed on zooplankton communities, the limnological monitoring programme in the Madeira River should be continued in order to identify the potential long-term consequences of run-of-river dams. Given the paucity of studies of such dams in tropical regions, we recommend similar monitoring studies be done in other regions of the world. While, for many zooplankton community variables, the greatest effect of damming occurred during ebb and low-water periods, some effects were also observed during the flood and high-water periods. We thus further recommend that continued monitoring includes all hydrological periods in floodplain rivers internationally.

Monitoring programmes of floodplain tropical rivers should include sampling sites upstream of dams, but also several sampling sites further downstream from dams, as more widespread effects on biological communities have been detected in some studies to date (Bonecker et al., 2009; Braghin et al., 2015; Palhiarini, Schwind, Arrieira, Velho, & Lansac-Tôha, 2017). In our study, the limited number of sites may have reduced our ability to detect the impacts of damming. Furthermore, we recommend the inclusion of at least one control site in such monitoring programmes. An ideal control would consist of a river of similar size and environmental characteristics, but unimpounded (for example, for our Madeira River study, the Abunã River in Bolivia or Amazonas River in Brazil would be good candidates), to ensure that any effects detected (or undetected) are related to damming and not to another unidentified factor changing through time. Another possibility is to use as a control, another portion of the same river studied, but far upstream from the dam.

Finally, many rivers in the world are increasingly disrupted by multiple dams, as is the case for our study river. Another run-of-river dam (Santo Antônio Hydroelectric Power Plant), approximately 100 km downstream of the one studied here, is already in place, and others are planned (Fearnside, 2014). Few long-term studies have evaluated the cascading effects of multiple dams on zooplankton communities (Timpe & Kaplan, 2017), most examined effects on fish communities (Cumming, 2004; Loures & Pompeu, 2018; Oliveira, Baumgartner, Gomes, Dias, & Agostinho, 2018). Even less is known about cumulative effects of run-of-river dams over multiple years. A short-term study evaluating the cumulative effects of the Jirau and Santo Antônio run-of-river dams demonstrated little change in fish communities (Cella-Ribeiro et al., 2017), but effects on other biota have not been studied. Furthermore, potential longer-term effects of multiple run-of-river dams on fish, zooplankton and other biota remain unknown. Consequently, the cumulative impact of multiple run-of-river dams on the biological communities should be the focus of longer-term study, particularly in tropical floodplain rivers, so that negative effects can be understood and ameliorated.

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