ORIGINAL ARTICLE

Assessment of changes in the ichthyofauna in a tropical reservoir in south-eastern Brazil: Consequences of global warming?

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Abstract

Increases in temperatures over the last century, more intensively after the eighties, were recorded in several databases for the south-eastern Brazil. These increases are likely to change fish communities in aquatic systems by decreasing abundances, biomass and sizes of some species more sensitive to climate change. Reservoirs may be particularly susceptible to the effects of climate change, as they isolate previously connected areas limiting fish dispersal and migration, as well as increasing water temperature and thermal stratification. We assessed temporal changes in the abundance and biomass of the ichthyofauna in an isolate reservoir (inflowing waters from small tributaries in a highland region) aiming to associate changes with climate effects over three decades (1990, 2000, 2010). Two abundant native species, a loricariid *Loricariichthys castaneus* (Castelnau, 1855) and a cichlid *Geophagus brasiliensis* (Quoy & Gaimard, 1824), were selected to assess eventual response to climate changes in their geographical distribution in the Southeast Atlantic Hydrographic Region, considering different carbon emission scenarios using ecological niche models. A decrease in the densities and biomass of the ichthyofauna and of the two selected species were observed in both summer and winter over the three decades, coinciding with increases in temperatures. These decreases were correlated with increases in positive anomalies of temperature, which may be an indicator of climatic changes, although with low explanation of the data variation. The mean size of *L. castaneus* decreased between the nineties and 2010, whereas no significant trend was found for the size of *G. brasiliensis*. Our predictions of new area for future adequacy indicated a loss in the distribution area for both species (mainly for *G. brasiliensis*), considering the most pessimistic scenario for 2050 and 2070, possibly due to climatic changes. Both hydroelectric dams and global warming pose threats to freshwater fish diversity, and both will interact. Changes observed in the fish assemblage over the last decades were essential for an assessment of the consequences of global warming in this type of reservoir combining larger scale studies with future projections.

1 | INTRODUCTION

Climate changes are one of the main threats to global biodiversity and the cause of many concerns to environmental managers. The fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2014) revealed changes in temperature, precipitation and climate extremes in various sectors of South America, indicating that the mean annual air temperature in southern Brazil between 1913 and 2006 increased from 0.5°C to 0.6°C per decade (Magrin et al., 2014). In addition, the future climate projections are not encouraging (Zaninelli et al., 2019) with the average annual rainfall, evaporation and runoff being far greater in South America than in all other continents. Consequently, the environmental vulnerability of this continent to changes in climatic variables is critical.

Continental aquatic ecosystems are more susceptible to the effects of climate changes as they are fragmented and isolated in the landscape and are extremely exploited by ecosystem services provided to the human population, such as water supply, irrigation and hydroelectricity generation. The dogma of hydropower as clean and nonpolluting sources of energy has been changing in recent decades, with indications that dams are also contributing to climate change. Greenhouse gases (GHG) emissions from reservoirs stem primarily from the decomposition of organic matter that is either flooded, transferred to the reservoir via runoff and river inputs, or produced within the reservoir by aquatic plants and algal biomass (Deemer et al., 2016). Some tropical dams, when poorly designed, can emit more GHG than coal-fired thermoelectric plants (see Almeida et al., 2019). Nowadays, more than half of the world's largest river systems are fragmented by dams (Grill et al., 2019; Nilsson et al., 2005), with severe implications for the global diversity of freshwater fish (Liermann et al., 2012). Both hydropower dams and global warming pose threats to freshwater fish diversity and can interact. Reservoirs create potential areas for population isolation in thermally unsuitable habitats, leading to physiological stress, species declines or possible extirpation (Kano et al., 2016; Pandit et al., 2017). The eventual effects of climate change in reservoirs will be associated with extreme weather events such as increasing of the range of variation of flow and water level, with cascading consequences for fish assemblages. Therefore, the fragmentation of rivers by dams is a double blow to conservation of freshwater fish, contributing to GHG emissions and hampering the ability of species to respond to climate change.

Fish, as ectothermic organisms, are closely related to local climatic conditions through physiological mechanisms that limit tolerance or resilience (Comte & Olden, 2017). Biological responses to global climate change can be summarised into three categories: extinction, change in distribution and adaptation (genetic or plastic). Limited physiological tolerance to high temperatures and changing

biotic interactions are the leading causes of extinction of species associated with climate change (Cahill et al., 2013). Although the geographical range limits of species are dynamic and fluctuate over time, climate changes are impelling a redistribution of species to stay within appropriate environmental conditions (Pecl et al., 2017). Organisms also respond to recent and ongoing climate change through phenotypic plasticity (Merilä & Hendry, 2014; Parmesan, 2006). In particular, the decrease in the fish body size associated with climate change has also received increasing interest in the context of climate warming. The body size reduction is considered to be the third universal response to global warming (in addition to changes in species distribution and phenology), having the ability to predict which species are sensitive to climate change, regardless of nonclimatic factors (Daufresne & Boet, 2007; Daufresne et al., 2009; Gardner et al., 2011). In addition, the habitat fragmentation caused by reservoir prevents many fish species to migrate and find their proper environment, so plasticity and adaptability *in situ* may be the main mechanism for preventing extinction.

Species can respond to climate change seeking suitable conditions in the geographical space, where the species expand and contract their areas of distribution until they reach a new equilibrium situation (Bellard et al., 2012). Predictive species distribution modelling consists of computational processing that combines data on the occurrence of one or more species with environmental variables, thus building a representation of the conditions required by the species and projecting how their distribution may change under different scenarios of climate change (Anderson et al., 2003). In this context, the modelling of the ecological niche of species has stood out as a tool for investigating the relationship between species and the climate, allowing analyses that can contribute to the anticipation of species' responses to the impacts of climate change (Bond et al., 2011; Oliveira et al., 2019; Ruaro et al., 2019).

The aim of this study was to evaluate possible changes in the ichthyofauna of an isolated reservoir (inflowing waters from small tributaries in a highland region), with low connectivity and low possibility for fish dispersal. Eventual changes were investigated using historical primary data of the ichthyofauna that were accumulated over the last decades (about 30 years), as well as historical secondary data of environmental variables (rainfall, air temperature, air temperature anomalies). Specifically, the ichthyofauna was compared over the three decades and related to historical series of the meteorological data. In addition, two abundant native fish species were selected to be tested as indicator of climate change by assessing their abundance, biomass and body size over time. We also assessed the effects of climate change on the geographical distribution of these two selected species in the Southeast Atlantic Hydrographic Region, considering different carbon emission scenarios. The objective was to find distribution patterns at hydrographic basin scale considering

the climatic suitability of the selected species. We hypothesise that the climatic changes observed in the last decades can affect the fish in the studied reservoir, decreasing the abundance, the biomass and the size of some species more sensitive to these changes. The following questions were asked: (1) Will the temperature increases recorded in various databases for south-eastern Brazil in the past decades related to changes in the fish assemblage in a reservoir? (2) Did the fish assemblage in the reservoir show changes in abundance and biomass? (3) Did some selected species show changes in abundance, biomass and decrease in the body size?

Another raised hypothesis is that climate changes may cause changes in the distribution ranges of the selected fish species in the hydrographic region of the Southeast Atlantic considering the more pessimistic future scenario of carbon emissions. The following questions were asked: are the selected species responding to climate change looking for suitable conditions in the geographical space, where the species expand and contract their areas of distribution?

How the selected species are distributed considering different future carbon emission scenarios?

2 | MATERIAL AND METHODS

2.1 | Study area

The Southeast Atlantic Hydrographic Region is one of the twelve hydrographic regions of the Brazilian territory and occupies 2.5% of the county area covering five states including the Rio de Janeiro, with an area of 229.972 km^2 (Figure 1). The hydrographic regions are supposed to have homogeneous or similar natural, social and economic characteristics, in order to guide the planning and management of water resources. This hydrographic region is formed by the river basins that flow into the south-eastern Brazilian coast and is divided into five hydrographic units, including the coastal hydrographic unit
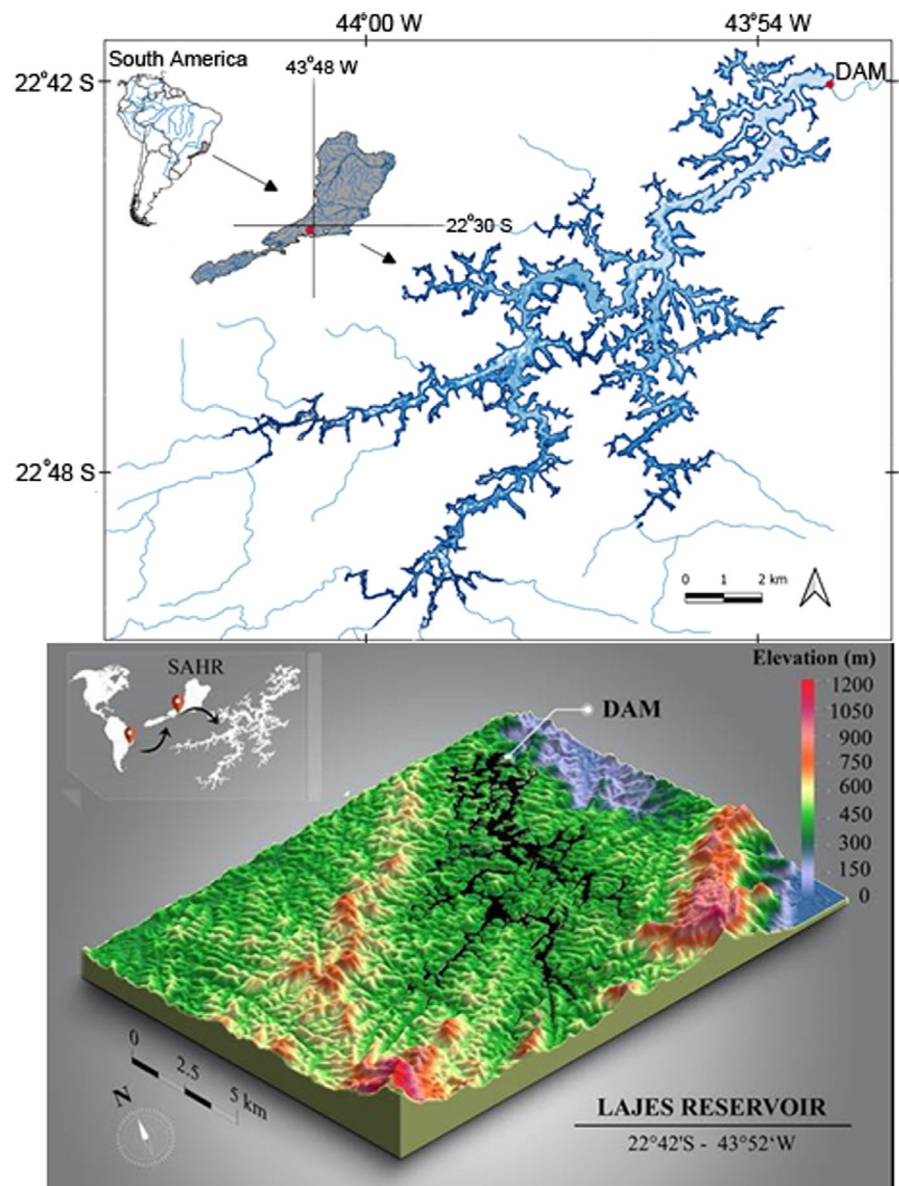

FIGURE 1 Map of the Lajes Reservoir and drainage basin in the Southeast Atlantic Hydrographic Region (SAHR), Brazil

where the Lajes Reservoir is located. The population of this region is predominantly urban (92% of its inhabitants) with a high population density, reaching 131.6 inhab/km^2, six times higher than the Brazilian average (22.4 inhab/km^2) (ANA, 2015).

The Lajes Reservoir (22°42′-22°50′S, 43°53′-44°05′W) has an area of 30 km^2 and is one of the oldest reservoirs designed for the primary purpose of generating electricity in Brazil and is located in the State of Rio de Janeiro (Figure 1). It was built between 1905 and 1908 by damming small streams in a highland region (ca. 415 m above the sea level). The reservoir today is also a strategic water supply for the municipality of Rio de Janeiro because of its good water quality. This oligotrophic reservoir has a poorly structured physical habitat, lacking routes for fish migration because its tributaries are small streams draining the slopes of the Serra do Mar mountains (Araújo & Santos, 2001; Guarino et al., 2005; Soares et al., 2008). Water levels oscillate between 3 and 5 m during the year (Araújo & Santos, 2001; Santos et al., 2004). This reservoir has low concentrations of nitrogen (< 10 μgL^{-1}), phosphate (< 120 μgL^{-1}) and chlorophyll (< 2.5 μgL^{-1}) with high water residence time (286 days) (Santos et al., 2004). The climate of region has two distinct seasons: a wet season, from late spring to early autumn, and a dry season, from late autumn to spring (Barbieri & Kronemberg, 1994; Guarino et al., 2005). Surface water temperature ranges from 21 to 31°C, pH between 6 and 8, dissolved oxygen is higher than 4.7 mgL^{-1} and Secchi transparency averages 2.3 m (Araújo & Santos, 2001). Fluctuation in rainfall combined with a regulated outflow results in peaks in water level (May–June) 3–4 months after the peak of rainfall season, with differences among extremes of flood and drawdown events reaching up to 9 m (Santos et al., 2004).

2.2 | **Fish** sampling

All fish samplings followed a standardised protocol on number of nets, mesh size and time of the net use, aiming at allow comparisons between time periods. Six gill nets (40 × 2.5 m; mesh of 15–110 mm between adjacent nodes) were set near the margins at dusk and retrieved the next morning, remaining in operation for 14 h. The sample unit was defined as the total number of fish or total biomass collected per of 600 m^2 of nets for 14 h. A total of 434 samples were collected in the summer (October–March) and 381 samples in the winter (April–September) (Table S1). The samples distributions were designed to cover the maximum reservoir area, namely the upper, middle and lower reservoir zones. Fish were caught alive, and their total length (TL) was measured; they were then returned alive to the water.

All collected fishes were identified to the lowest taxonomic level and measured to total length (in mm) and weighed (in g) and returned to the reservoir, except those who died while in the gill nets. Voucher specimens were fixed in 10% formalin for 48 h, then transferred to 70% ethanol and deposited in the Reference Collection of the Fish Ecology Laboratory of the of the Universidade Federal Rural do Rio de Janeiro.

2.3 | Database

Accumulated information consisted of primary database on the fish communities collected between 1994 and 2018. Information on the ichthyofauna and on the selected fish species included the following yearly temporal series: 1994; 1995–97; 1998–2001; 2003; 2004; 2008–09; 2011–12; 2015–18. As the sampling frequency varied among different years (monthly, bimonthly, quarterly), we tried to use balanced number of months between the dry (winter) and wet (summer) seasons for each year (Table S1) Two common and abundant native species, the loricarid *Loricariichthys castaneus* (Castelnau, 1855) and the cichlid *Geophagus brasiliensis* (Quoy & Gaimard, 1824), were evaluated as indicators of climate change, by comparing information on their abundance, biomass and body size over the time series (Table S2).

A secondary database with information on maximum temperature or the city of Rio de Janeiro in the period 1961–2017 obtained through the INMET—National Institute of Meteorology (2009a) (https://bdmep.inmet.gov.br) was used. The data that were used in this study refer to the periods 1931–1960, 1961–1990 and 1981–2010 for the monthly accumulated precipitation, average compensated temperature, maximum temperature and minimum temperature for the city of Rio de Janeiro (INMET, 2019b) (https://portal.inmet.gov.br/normais). Air temperature anomalies (annual averages) in period at 1910–2018 (108 samples) at geographical coordinate (22.6°S, 43.8°W) were obtained through the NOAA National Centers for Environmental Information (https://www.nd.noaa.gov/ag/).

2.4 | Data treatment

The information on fish fauna and meteorological variables was grouped over the annual time series. Seasonality was also considered, and samples from the dry season (winter, April–September) and the rainy season (summer, October–March) were analysed separately. A quadratic polynomial regression was used for the fish data to calculate the smallest square fit through the points and to fit the line to the data set using the *proj.lin* function in Microsoft Excel. The response variables used in this step were the abundance (numbers) and biomass (g) of the total number of fish, and the explanatory variable was time series from 1994 to 2018 during the winter and the summer. The similar analysis was performed for the abundance and biomass (g) of the two selected species. The temporal trend of the average fish body size for the two selected species was also evaluated by simple regression analysis with body size (cm) being the response variable and time series from 1994 to 2018 the explanatory variable (Raudenbush & Bryk, 2002).

A linear regression was also adjusted for the mean temperature, mean maximum temperature and mean minimum temperature over time (1961–2017) for the city of Rio de Janeiro, and for the temperature anomalies (annual) in the period 1911–2018 at reservoir geographical coordinates (22.6°S, 43.8°W).

A distance-based redundancy analysis (dbRDA, Legendre & Anderson, 1999; McArdle & Anderson, 2001) was used to detect patterns between the predictor variables (environmental variables that were not redundant—not collinearity between them) and the abundance of the two selected species, with samples coded by the three decades (1990, 2000 and 2010). To determine which environmental variable were better represented by the dbRDA axes, a Pearson correlation of each variable with each dbRDA axis was calculated. These analyses were performed using the software Primer 6.1.13 & PERMANOVA + 1.0.3 (Anderson et al., 2008).

2.5 | Ecological niche modelling

A maximum entropy approach (Maxent software for modelling species niches and distributions) was used to develop a predictive spatial model for the distribution of the two native fish species, the loricariid *Loricariichthys castaneus* and the cichlid *Geophagus brasiliensis*. From a set of climatic grids and georeferenced occurrence localities, the model expresses a probability distribution where each grid cell has a predicted climatic suitability of conditions for the species. Maxent builds models of species occurrence start with a uniform distribution of probability values over the entire grid and then conduct an optimisation routine that iteratively improves the model fit, measured as the gain. Gain is basically a likelihood (deviance) statistic that maximises the probability of the presences in relation to the background data, corrected for the case where the probabilities of all pixels are equal (uniform) (Phillips et al., 2006; Phillips & Dudik, 2008). We also quantified the future predictions from niche models using atmosphere–ocean general circulation models (AOGCM), and carbon emission scenarios. The data were divided into 70% for training and 30% for validation (test). The MaxEnt model was set to run with ten replicates, subsamples replicated run type, 10.000 random background points and a regularisation multiplier to control the intensity of regularisation at default value of 1. Model performance was assessed by the area under curve (AUC) value for the receiver operating characteristic (ROC) curve. That is, AUC measures the entire two-dimensional area underneath the entire ROC curve. ROC curve is based on sensitivity (omission rate) versus specificity (fractional predicted area) of the response between occurrence data and predictors, incorporating a binomial probability as a null model. Values close to 1 indicate that the model presented high performance; however, values close to 0.5 indicate that the performance was poor and that the rating is close to a random pattern (Elith et al., 2006).

A pixel was considered as either suitable or not for the species, based on a threshold probability indicative of species presence. This threshold probability was generated using the "maximum training sensitivity plus specificity" criteria. Sensitivity is the proportion of correctly predicted presences among all the presences, and specificity is the proportion of correctly predicted absences among all the absences. Maximum training sensitivity plus specificity optimises the trade-off between sensitivity and specificity using the training data. The selected limit to generate a distribution map that represents suitable climatic conditions for the species was in the format Cloglog, which is an estimate between 0 and 1 of probability of presence. The georeferenced data of species occurrence in the Southeast Atlantic Hydrographic Region were obtained through online databases SpeciesLink (http://splink.cria.org.br) filtering the records for the two species localised in the State of Rio de Janeiro.

2.6 | Bioclimatic variables

Present (average for the years 1970–2000) and future predictions for 2050 (average for 2041–2060) and for 2070 (average for 2061–2080) of bioclimatic variables, at 30 s spatial resolution (~ 1 km^2), were obtained from the Intergovernmental Panel on Climate Change model, 5th Assessment Report (IPCC–AR5) from the Worldclim Climate Database, Version 1 (http://www.worldclim.org/)—CCSM (Community Climate System Model, http://www.cesm.ucar.edu). The carbon emission scenarios for the atmosphere–ocean general circulation models (AOGCMs) were based on the two RCPs (Representative Concentration Pathway): optimistic (2.6) and pessimistic (8.5). Here, the term "optimistic" means a scenario of low accumulation of greenhouse gases in the earth's atmosphere in future, and the term "pessimistic" means a scenario of high accumulation of greenhouse gases.

Pearson's correlations (pairwise correlations) were applied between numeric biovariables climatic to identify the variables that are not correlated (<0.8) with any other variable to be inserted in the model. The logistic output of MaxEnt generates the relative ranking of variables used to generate model predictions and their importance in the models. Multicollinearity of variables may violate statistical assumptions and cause over-fitting in species distribution modelling; thus, we removed the highly correlated variables. The Jackknife test was applied for the two selected fish species aiming to show the variables with influences on the distribution of these species. The Jackknife shows the training gain of each variable if the model was run in isolation and compares it to the training gain with all the variables. This is useful to identify which variables have individually the most contribution to the model and that decreases the gain when it is omitted, which therefore appears to have the most information that is not present in the other variables. The training gain also reflects a model's ability to discriminate sites of known occurrence from random background sites, with larger values indicating greater discriminatory power (Elith et al., 2011; Merow et al., 2013). The model also provides a jackknife for test gain and AUC. From each map generated for climatic suitability, values were extracted from each pixel in the image that were used to calculate the percentage of the area. The areas lost, areas added and areas maintained in future predictions in different carbon emission scenarios were then estimated. The maps were performed using the software QGIS 3.10.0 with the reference system WGS84 EPGS4326.

3 | RESULTS

3.1 | Historical environmental data

The air temperature increased over the years (1911–2018) at the geographical coordinates (22.6°S, 43.8°W) in the Lajes Reservoir with positive anomaly in relation to the averaged period after the 80's (Figure 2, Table S3), confirming the trend line of the linear regression (R^2 = 0.77).

We compared the climatological normals from the three periods (1931 to 1960, 1961 to 1990 and 1981 to 2010 (INMET)) (Figure 3) for the city of Rio de Janeiro. While the rainfall regime remained stable, with a downward trend in the period 1981–2010, the average compensated temperature increased by approximately 1.5°C in the last period. The maximum temperature showed an increase of approximately 1.0°C in and the minimum temperature with an increase of approximately 0.5°C.

Comparison between the average compensated temperature, maximum temperature and minimum temperature for the city of Rio de Janeiro in the period 1961–2018 (Figure 4) showed a significant increase confirmed by the trend line and linear regression (R^2 = 0.71, p = 1.79047E^{-13}); R^2 = 0 73, p = 6.3081E^{-10}); R^2 = 0.58, p = 1.77131E^{-7}) respectively.

3.2 | Fish abundance and biomass data (1994–2018)

A decrease in abundance and biomass was observed for the total number (number/600 m^2 nets for 14 h) and biomass (grams/600 m^2 nets for 14 h) of fish and for the two selected species was more pronounced in the 1990 s, after which they presented a period of stability (2000 s and 2010 s), while the temperature showed a consistent linear increase (Figures 4 and 5).

A significant decrease in the average of the total number and biomass of fish species was observed in summer and winter and was detected by the polynomial regression (summer number:

R^2 = 0.38, p = 0.010); winter number: R^2 = 0.48 (p = 0.007); summer biomass: R^2 = 0.24 (p = 0.039); winter biomass: R^2 = 0.33 (p = 0.023) (Figure 5).

A decrease in the numerical abundance of *G. brasiliensis* was observed in summer and winter confirmed by the polynomial regression (summer number: R^2 = 0.32, p = 0.039; winter number: R^2 = 0.49, p = 0.005). However, a significant decrease in the biomass of this species was observed only in winter (R^2 = 0.29, p = 0.05), but not in summer (R^2 = 0.12, p = 0.117) (Figure 5).

In relation to *L. castaneus*, a significant decrease in the numerical abundance and biomass was observed in both summer and winter, confirmed by the polynomial regression (summer number: R^2 = 0.31, p = 0.025; winter number: R^2 = 0.31 (p = 0.036); summer biomass: R^2 = 0.30 (p = 0.022); winter biomass: R^2 = 0.33 (p = 0.033) (Figure 5).

The total length data of *L. castaneus* and *G. brasiliensis* individuals from 1994 to 2019 were analysed to observe eventual trends in size over time in the Lajes Reservoir. There was a tendency for *L. castaneus* to decrease in size with larger individuals in the 1990 s and smaller in 2010 (R^2 = 0.16, p = 0.0001). Regarding *G. brasiliensis*, no significant decrease pattern was observed over time (R^2 = 0.02, p = 0.288) (Figure 6).

3.3 | Relationships between the selected fish species and the predictor variables

The dbRDA analysis was used to assess the relationship between the abundances of the two selected species and the selected predictor variables temperature anomaly, maximum water temperature, rainfall, water level, transparency and dissolved oxygen. The first dbRDA axis accounted for 34.9% of the total variation in the fish data and distinguished a temporal trend according to the samples coded by decade (Figure 7). The first dbRDA axis was positively correlated with samples of the 1990 decade when the two selected species were more abundant and negatively correlated with the samples of the last decade (2010). More transparent waters, high
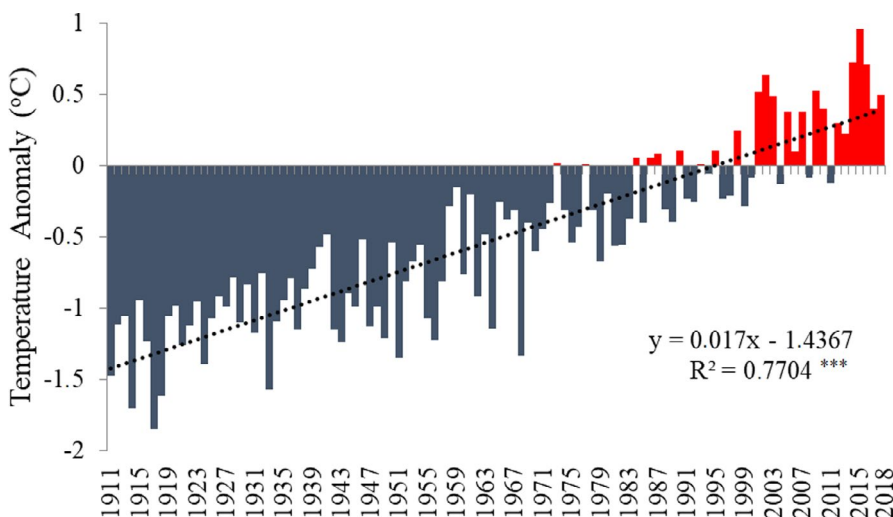

$$y = 0.017x - 1.4367$$
$$R^2 = 0.7704 ***$$

FIGURE 2 Annual temperature anomalies in the period 1911–2018 at geographical coordinate in the Lajes Reservoir (22.6°S, 43.8°W), with trend line and linear regression. Source: NOAA National Centers for Environmental Information, Climate at Glance: Global Time Series, published September 2019, retrieved on September 17, 2019 from https://www.ncdc.noaa.gov/cag/. *** p < 0.001
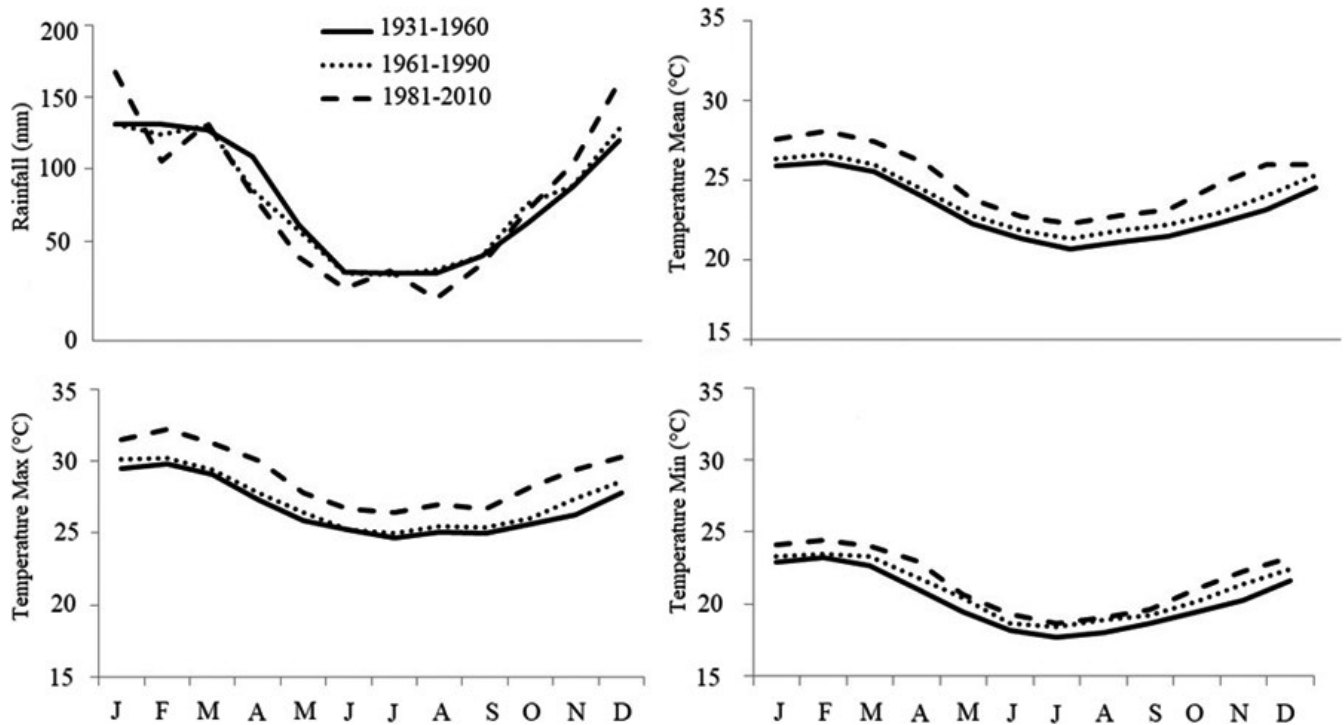
FIGURE 3 Comparison between the climatological normals of 1931–1960, 1961–1990 and 1981–2010 periods for the monthly accumulated precipitation, average compensated temperature, maximum temperature and minimum temperature in the city of Rio de Janeiro.
Source: INMET (2019b). https://portal.inmet.gov.br/normais

FIGURE 4 Trends in the mean temperature, mean maximum temperature and mean minimum temperature using linear regression, in the city of Rio de Janeiro in the period 1961–2017.
Source: INMET (2019a). http://www.inmet.gov.br/portal/index.php?r=clima/graficosClimaticos
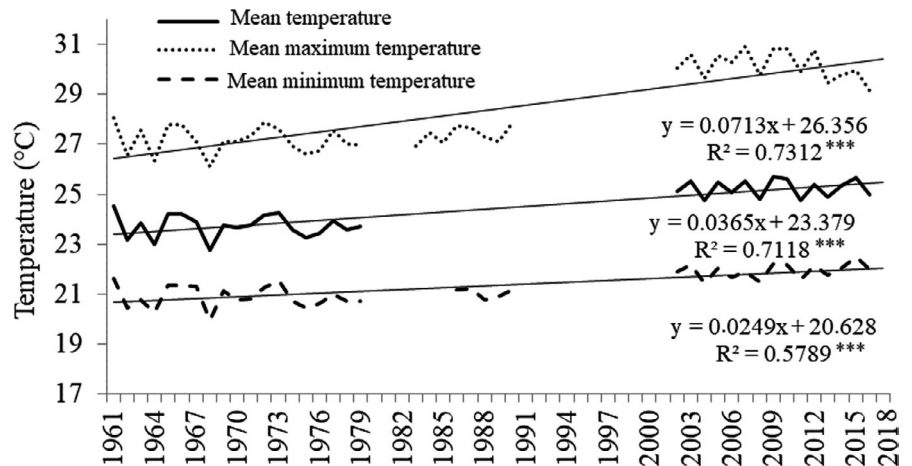
water level and positive temperature anomalies in the decade of 2010 coincided with the comparatively low density of the two selected species, which were positively related with rainfall. The second dbRDA axis accounted for 21.9% of the total variation in the fish data and was positively correlated with the temperature anomaly and maximum water temperature that were comparatively higher in the last decade. The temperature anomaly and water temperature were inversely correlated with the levels of dissolved oxygen. The dependent variables (*L. castaneus* and *G. brasiliensis*) were positively correlated with the first dbRDA axis.

3.4 | Climatic suitability of two native species—Southeast Atlantic Hydrographic Region

Six bioclimatic variables were selected as predictors of the two species distribution based on the initial Pearson correlations (pairwise correlations) to identify the variables that are not correlated (<0.8) with any other variable to be inserted in the model. The selected variables were isothermality, mean temperature of warmest quarter, temperature seasonality, precipitation of driest quarter, precipitation seasonality and precipitation of wettest quarter.
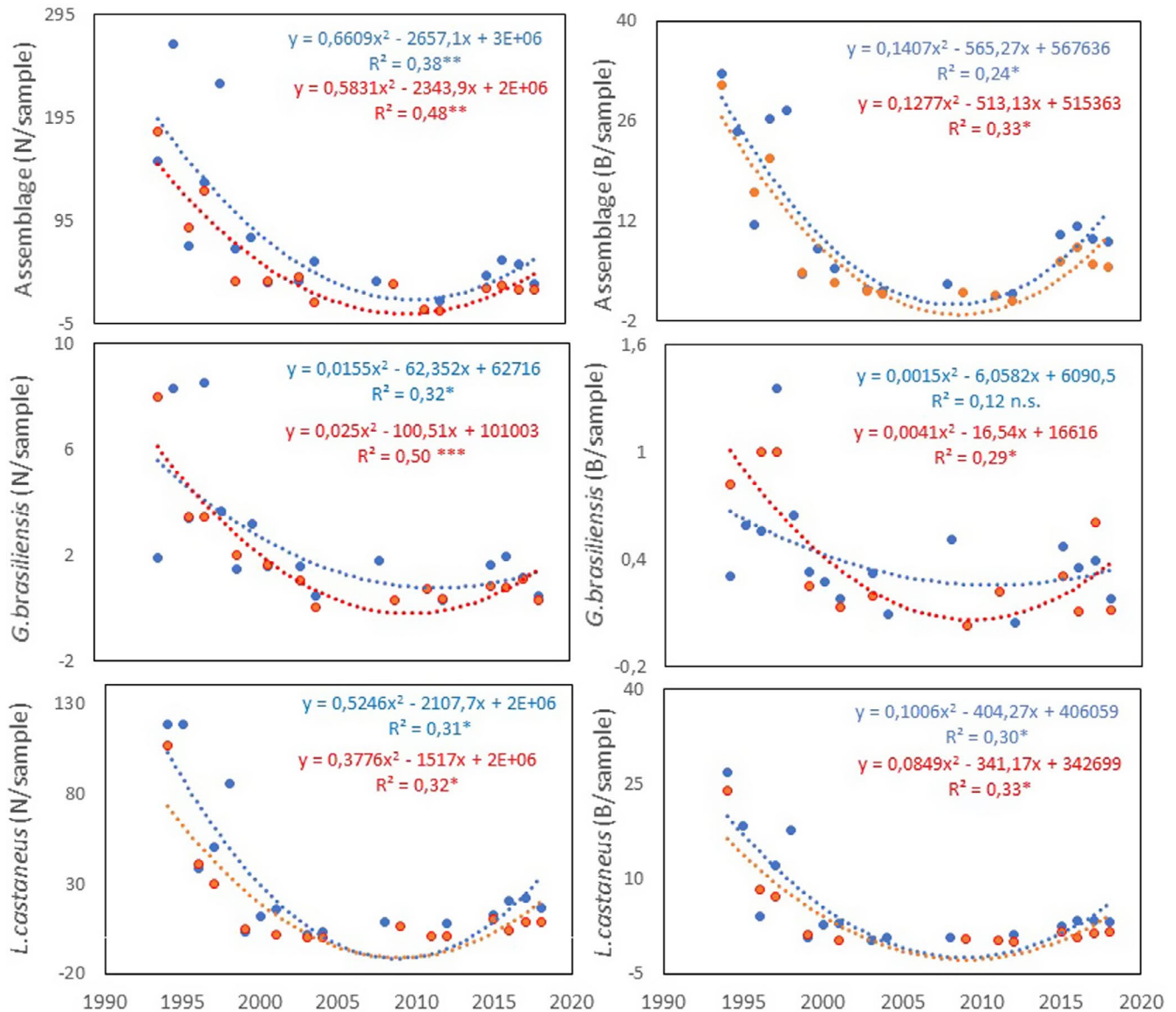
FIGURE 5 Total number/sample and biomass/sample of fish, number/sample and biomass/sample of individuals of *G. brasiliensis* and *L. castaneus* from 1994 to 2019 during winter and summer, with trend line and quadratic polynomial regression also shown. Legend: summer = blue; winter = Orange; *** $p < 0.001$; ** $p < 0.01$; *$p < 0.05$; ns=no significant.

After selecting the bioclimatic variables, the model was performed for each of the species. For *G. brasiliensis*, the results of the Jackknife test show that the variable with highest gain when used in isolation was isothermality, that is how large the day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillation, which therefore appears to have the most useful information by itself. The variable that decreases the most gain when it is omitted was Mean Temperature of Warmest Quarter, which therefore appears to have the most information that is not present in the other variables. For *L. castaneus*, the variable mean temperature of warmest quarter showed the highest gain when used in isolation and decreases significantly the gain when it is omitted. The variables with the highest percentage contribution were isothermality and mean temperature of warmest quarter and temperature seasonality, whereas the variables related to precipitation

presented less contribution for both species (Table 1; Figure S1 and Figure S2).

For *G. brasiliensis*, the presence of 77 records was used for training and 33 for testing. For *L. castaneus*, the presence of 21 records was used for training and 8 for testing. The Test AUC generated by the Maxent algorithm for the two species showed values above 0.9, which indicates good accuracy (Elith et al., 2006) (Figure S3 and Figure S4). The values of maximum training sensitivity plus specificity Cloglog threshold used for both species in the future predictions of 2050 and 2070 in the carbon emission scenarios (RCPs 2.6 and 8.5) are shown in Table S4 in the Supporting Information. This means that the probability of climatic suitability for the above species of the threshold value is adequate and the probabilities below this value would be classified as inadequate. The p-value associated with this limit is 0.001 indicating that we can reject the hypothesis that the

FIGURE 6 Total length of *L. castaneus*
and *G. brasiliensis* individuals from 1994 to
2019, with trend line and linear regression.
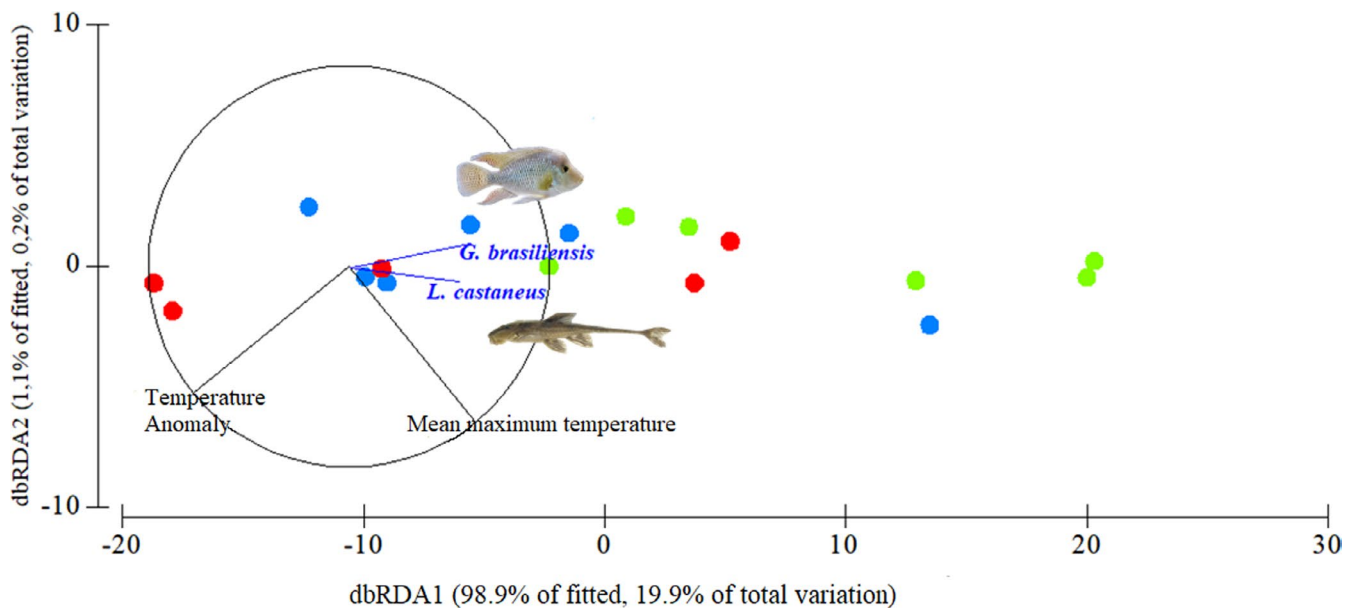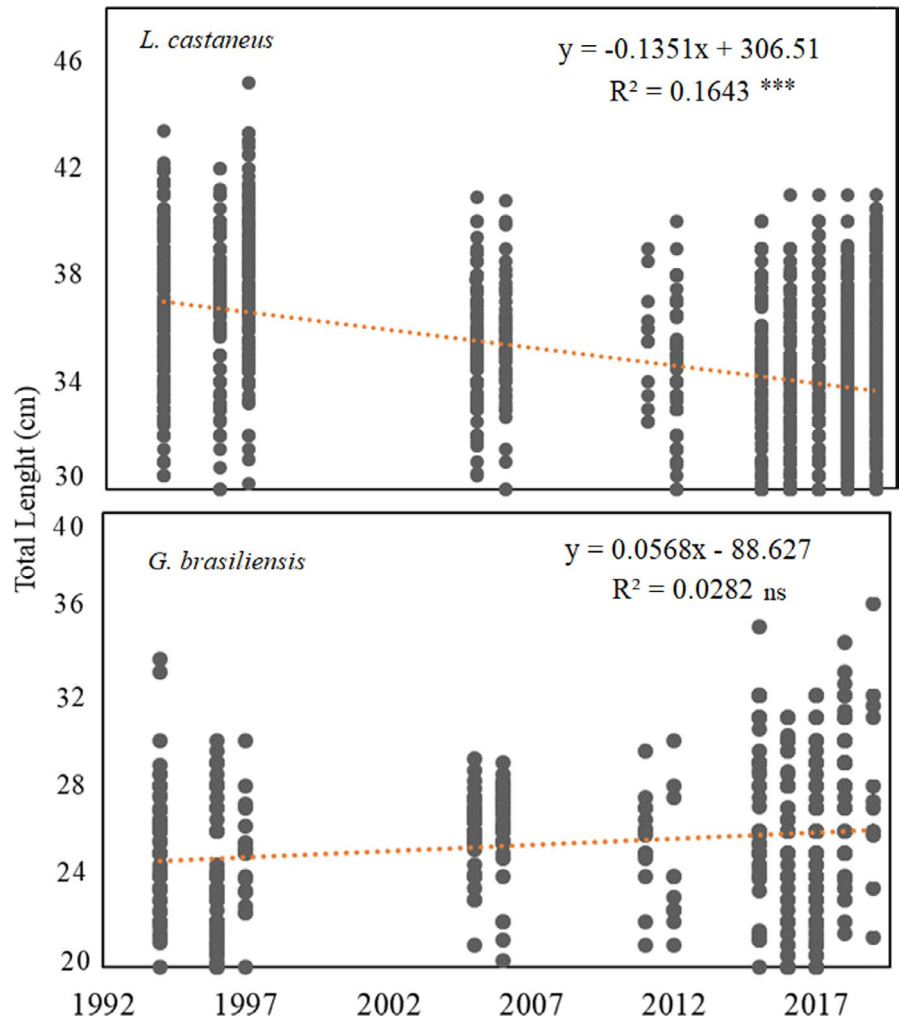*** p < 0.001; *** p < 0.01**; p < 0.05**; ns,
no significant

FIGURE 7 Plot of the first two axis of the distance-based redundancy analysis (dbRDA) for the two selected species (response variables) and the predictor variables (environmental variables), showing the percentage of variation explained by each dbRDA axis

TABLE 1 Bioclimatic variables used in the maximum entropy (MaxEnt) model and their percentage contribution (%) for *Geophagus brasiliensis* and *Loricariichthys castaneus*

|	G. brasiliensis				L._castaneus			
Future predictions	2050		2070		2050		2070	
Carbon emission scenarios	2.6	8.5	2.6	8.5	2.6	8.5	2.6	8.5
Isothermality	36.9	40.7	39.0	42.4	32.7	35.8	35.9	34.5
Mean Temperature of Warmest Quarter	36.6	35.6	33.3	34.9	52.6	51.9	51.6	52.5
Temperature Seasonality	14.6	14.5	15.4	14.6	8.4	5.2	7.5	7.6
Precipitation of Driest Quarter	6.7	5.5	6.5	6.0	3.0	3.1	1.8	2.3
Precipitation Seasonality	4.3	2.4	3.2	1.6	0.9	1.5	0.4	0.4
Precipitation of Wettest Quarter	0.5	1.1	2.3	0.3	2.2	2.2	2.5	2.4
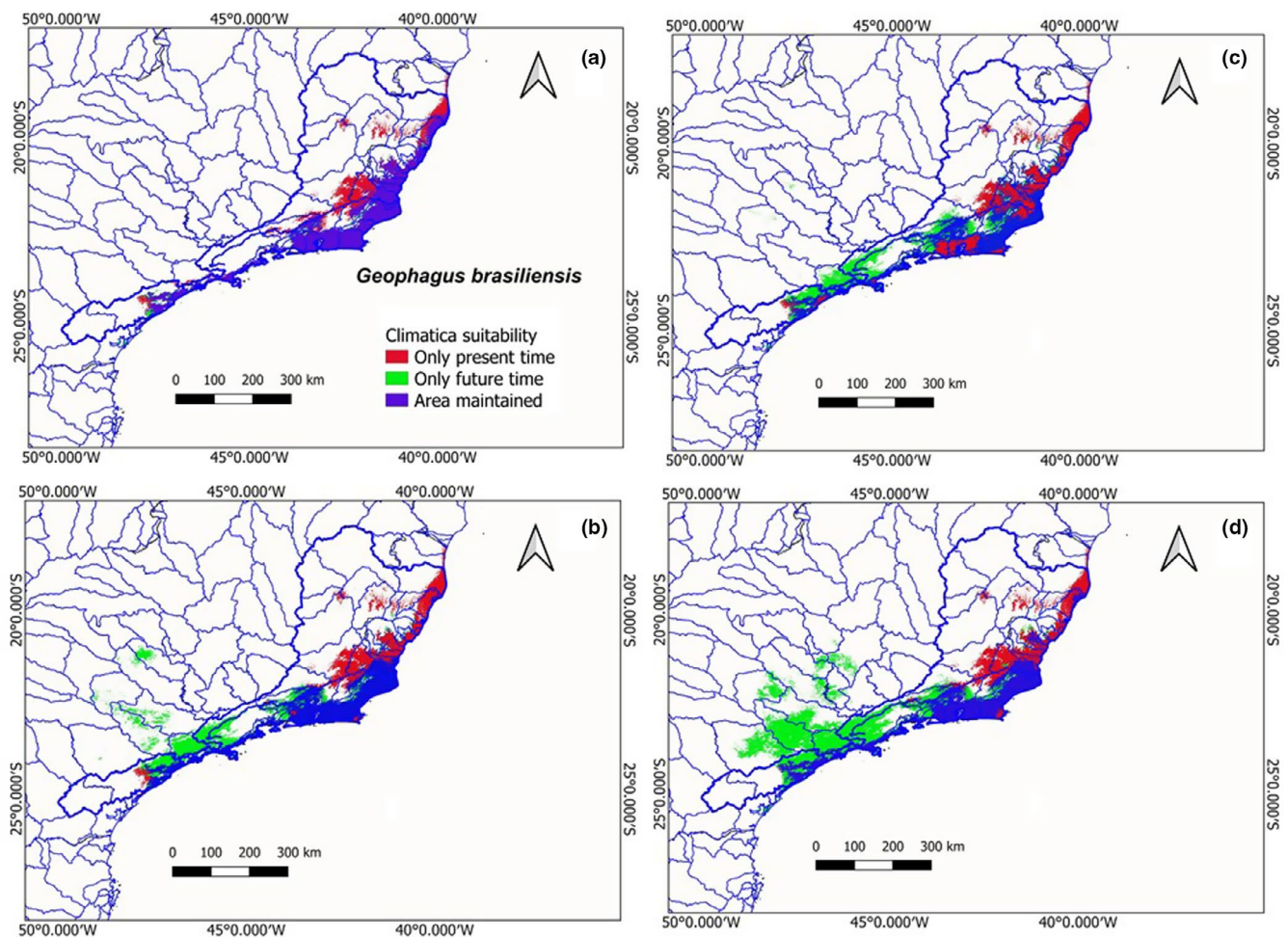
FIGURE 8 Climatic suitability of *Geophagus brasiliensis* in south-eastern basin (Brazil) for present time, future times e areas maintained (present and future) provided by the consensus model RCPs 2.6 and 8.5 for 2050 and 2070. a, 2050/RCPs 2.6; b, 2050/RCPs 8.5; c, 2070/RCPs 2.6; d, 2070/RCPs 8.5

model is at random and the hypothesis that the model can identify suitable and inappropriate areas for both species in the Southeast Atlantic Hydrographic Region must be accepted. MaxEnt generates the omission error rate for each cut-off limit. The omission error is when the model did not predict (omit) the existence of a location where the species truly occurs. Regarding maximum training sensitivity plus specificity test omission and training omission, *G. brasiliensis*

and *L. castaneus* present the low values of omission error for this threshold (<0.21) which is considerable acceptable. Maximum training presence binomial probability shows the model's p-value which was highly significant (p <0.0001), demonstrating that the model is better than chance (Table S4 in the Supporting Information).

Comparing the distribution model using the projections RCP 2.6 and RPC 8.5 for 2050 and 2070, changes were observed in the

distributions of climate suitability for *G. brasiliensis* and *L. castaneus*. For *G. brasiliensis*, the projections of RCP 2.6 and RCP 8.5 for 2050 and 2070 showed a greater loss of area (36.04%) in the RCP 8.5 projection for 2050 and lesser (21.85%) in the RCP 8.5 for 2070. Regarding the area gain, the lowest value (3.83%) was observed in the RCP 2.6 projections for 2050 and the highest value (47.19%) for the RCP 8.5 projections for 2070. The maintained areas showed the highest value (65.99%) in RCP 2.6 projections for 2050 and lower value (30.33%) for RCP 8.5 projections for 2070 (Figure 8, Table 2).

For *L. castaneus*, unlike *G. brasiliensis*, the RCP 2.6 projections for 2050 and 2070 showed irrelevant loss of area (0.29% and 0.16% respectively), whereas the RCP 8.5 projections for 2050 and 2070 showed loss of area of 17.45% and 36.72% respectively. In relation to the area gain, the highest value (30.29%) was observed in the RCP 2.6 projections for 2070 while the maintained areas showed the highest value (78.46%) in the RCP 2.6 projections for 2050 and the lowest value (47.19%) in the RCP 8.5 projection for 2070 (Figure 9, Table 2).

TABLE 2 Percentage of the area for each climate suitability map for the two selected species representing the lost areas (Present time), added areas (Future time) and maintained areas (Present and Future) in future predictions in different carbon emission scenarios

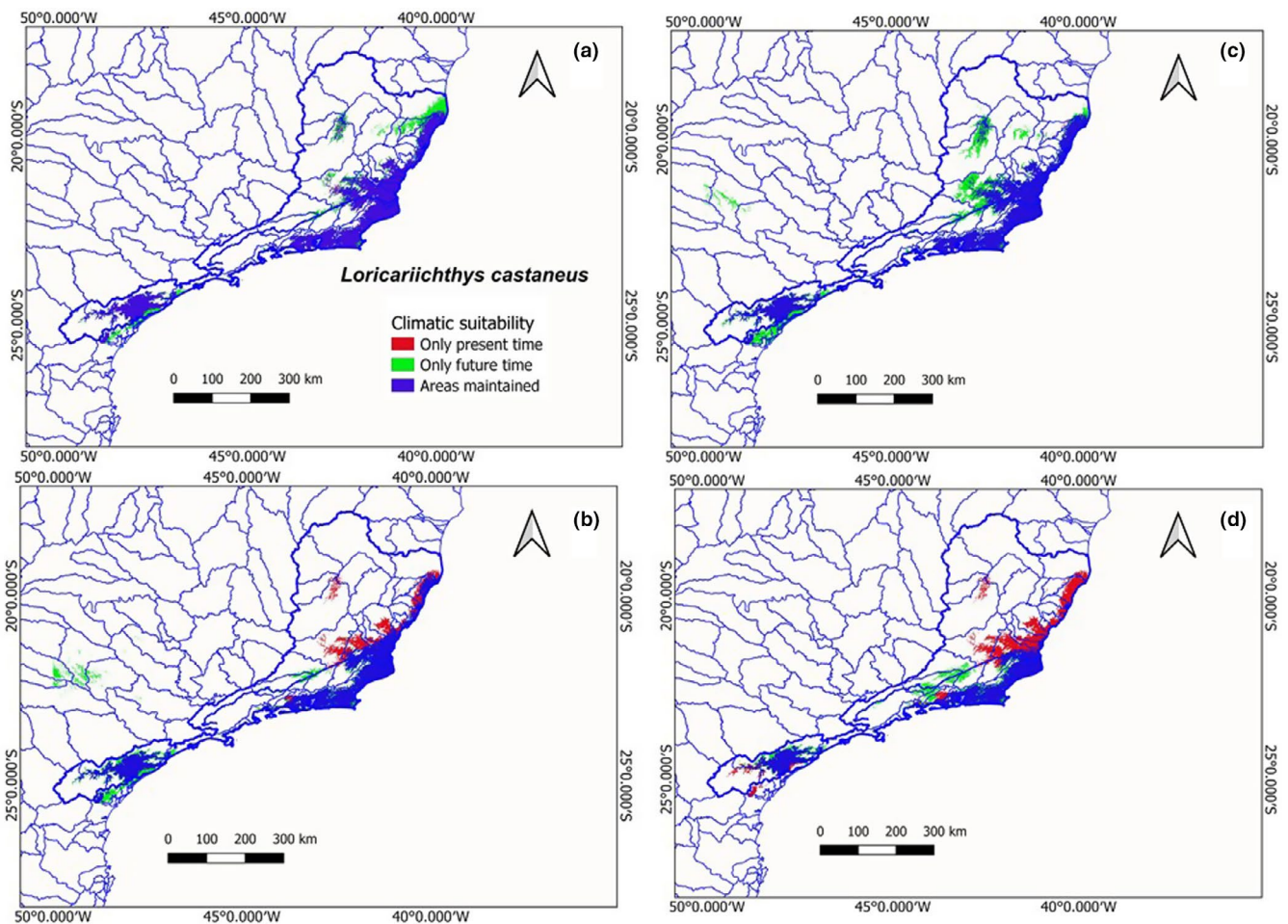| Species	Loricariichthys castaneus				Geophagus brasiliensis			
Future predictions	2050		2070		2050		2070	
Carbon emission scenarios	2.6	8.5	2.6	8.5	2.6	8.5	2.6	8.5
Present time (Area lost (%))	0.29	17.45	0.16	36.72	30.18	36.04	30.09	21.85
Future time (Area gain (%))	21.25	18.85	30.29	16.09	3.83	26.73	28.98	47.83
Maintained areas (%)	78.46	63.70	69.56	47.19	65.99	37.23	40.93	30.33

FIGURE 9 Climatic suitability of *Loricariichthys castaneus* in south-eastern basin (Brazil) for present time, future times e areas maintained (present and future) provided by the consensus model RCPs 2.6 and 8.5 for 2050 and 2070. a, 2050/RCPs 2.6; b, 2050/RCPs 8.5; c, 2070/RCPs 2.6; d, 2070/RCPs 8.5

Projections of RCP 2.6 for 2050 and 2070 for *G. brasiliensis* indicated a smaller reduction in the suitable areas currently observed and in the maintained areas when compared to RCP 8.5 projections for 2050 and 2070. A further large expansion of the area in the future was observed for the RCP 8.5 projections for 2050 and 2070 (Figure 8).

For *L. castaneus*, RCP 2.6 projections for 2050 and 2070 did not change in the suitable areas today and in the maintained areas, with expansion of the area in the future observed for 2070. However, for the RCP 8.5 projections for 2050 and 2070, the model indicated a reduction in the suitable areas currently observed in the areas maintained with an expansion of the area observed in the future observed for 2070 (Figure 9).

4 | DISCUSSION

A decreasing trend in the abundance and biomass of the ichthyofauna in the Lajes Reservoir are occurring over the three last decades, and it is likely that such changes, at least in part, are attributed to climate changes. An observed linear increase in air temperature does not seem to coincide with the nonlinear decrease in the abundance and biomass of the ichthyofauna, which at first is rapid and then stabilises. Biological responses are not necessarily proportional and, sometimes, as in the case of ecological systems, inherently nonlinear (Burkett et al., 2005; Rosenfeld, 2017). In this context, global warming affects mainly ectothermic organisms that respond more sharply to temperature variations than endothermic organisms, since their metabolism is directly dependent on the environment. Among the ectothermic organisms, aquatic species are especially sensitive to climate change and their ecosystems are among the most affected (Ohlberger, 2013; Paaijmans et al., 2013). Therefore, climate changes are expected to affect freshwater fish communities and to contribute to fish population declines or local extinctions (Almeida et al., 2019; Branco et al., 2009; Cahill et al., 2013; Frederico et al., 2016).

Temporal decreases abundances of *L. castaneus* and *G. brasiliensis* species from the 1990 s to the recent years (2010 s) were correlated with increases in temperature anomalies and in other variables (e.g. water level and transparency), with the highest abundances coinciding with high rainfall, according to dbRDA. This suggests that not only the temperature, but also other controlled or uncontrolled variables could be influencing the detected patterns. everal studies emphasise the warming trend in the city of Rio de Janeiro (Dereczynski et al., 2013; Silva & Dereczynski, 2014; Silva et al., 2014). The more importance of the temperature anomalies compared to the maximum temperature is probably due to the difference in efficiency of measurements in capturing signals of climate change. While temperature anomalies represent an efficient trend in the studied region from a long-term mean value, the mean maximum temperature is a local variable that suffers cyclical and seasonal variations and represents the present and punctual moment and may not be sufficiently refined to detect changes in the fish assemblage structure.

Declining body size has been suggested to be a universal response of organisms to rising temperatures (Sheridan & Bickford, 2011), and we found a downward trend in size for one of the selected species (*L. castaneus*). Aquatic ecosystems in tropical regions have a set of characteristics that increase their potential to be impacted by warming-induced size reductions due to less oxygen availability and greater effort required to increase oxygen uptake in water (Ilha et al., 2018; Ohlberger, 2013; Roze et al., 2013). This makes the effects of the temperature on hypoxia tolerance in fish an important subject to be investigate (He et al., 2015; Neubauer & Andersen, 2019). However, the hypothesis that oxygen supply is limiting growth and underlies size reductions driven by global warming has been disputed. Although some studies predict that some fish will become smaller in the future, the underlying mechanisms need a better understanding on this process (Lefevre Mckenzie et al., 2017; Lefevre McKenzie et al., 2017). *Loricariichthys castaneus* is a bottom-associated species and presents lower mobility, which may expose to great stress due to hypoxia condition in Lajes Reservoir. It could be related to the decrease in size found for this species; however, further studies are necessary to clarify this pattern. Our findings indicate that *L. castaneus* is a key species that is possibly suffering climate change effects and could be used as an indicator of these changes in other reservoirs of the south-eastern Brazil.

In reservoirs, the effects of climate change are associated with extreme weather events such as variations in rainfall, as well as increased water temperature and thermal stratification. When the river is dammed, it goes from a turbulent system, usually well-oxygenated and mixed, to a much more static system with a tendency to stratify. In the Lajes Reservoir, increases in rainfall were positively related with the abundance of the two studied species and the higher level of oxygen in the first decade that probably provided better conditions for the ichthyofauna. The Lajes Reservoir is a stratified system, with thermal stratification over most of the year and water column mixing only in winter. This is probably due to decreases in the water superficial temperature, low wind influence and long water retention time (Branco et al., 2009; Soares et al., 2008). Such conditions may lead to decreases in the concentrations of dissolved oxygen in the water column, which in turn may affect aquatic species, especially bottom-associated species (Branco et al., 2009). The impact of hypoxic conditions on the environment may reduce local biodiversity, influences fish physiological parameters, such as growth, reproduction and food intake, with hypoxia tolerance differing between fish species (Borowiec et al., 2016).

Both species analysed in this study are adapted to use environments with fluctuating and low oxygen concentration and are abundant in the Lajes Reservoir (Araújo & Santos, 2001; Duarte & Araújo, 2001; Guedes et al., 2020; Santos et al., 2004). According to Focesi Jr et al., (1979), air-breathing fishes from the Loricariidae family have anatomical and physiological adaptations to allow them to endure a variety of oxygen conditions. *Loricariichthys castaneus* is a bottom dwelling fish, occurring preferable in depths greater than 6 m, in low flow and predominantly muddy substrate (Costa et al., 2013; Guedes et al., 2020).

Geophagus brasiliensis occurs in a wide geographical area in South American, including tropical and subtropical regions and is an omnivorous-opportunist species that has successfully adapted to Lajes Reservoir (Santos et al., 2004). Mazzoni and Iglesias Rios (2002) found that populations of G. brasiliensis are exposed to different environmental conditions including variations in water temperature and oxygen concentrations. On the other hand, G. brasiliensis presents a comparatively greater mobility and it can disperse avoiding the stress caused by due to hypoxia conditions. In addition, G. brasiliensis use the anaerobic metabolism as the main strategy for optimising its strength in the absence of oxygen (Pereira et al., 2018).

Loss of climatic suitability was observed for G. brasiliensis and L. castaneus that will be affected considering the more pessimistic scenario for 2050 and 2070, projecting a new area of future adequacy, mainly for G. brasiliensis. In this analysis, we seek to search for climatically suitable areas for the two selected fish species in the watershed region, recognising that the fish face dispersion limitations due to the lack of hydrological connectivity, and may be prevented from reaching climatically suitable areas, which makes them vulnerable to climate change on a wide scale. Thus, in the face of climate change, dispersion restrictions are a complicating factor for species that cannot move freely, as is the case of most freshwater organisms in reservoirs (Comte & Olden, 2017; Strayer & Dudgeon, 2010).

Indication of loss of climatic suitability areas for the two selected fish species was found considering the most pessimistic future scenario on a larger scale. The Lajes Reservoir seems to be an appropriate study case and a suitable model to asses climate change, because it is one of the oldest reservoirs in Brazil, and is relatively isolated and with low connectivity. We observed that the ichthyofauna is decreasing in abundance and biomass, and this could be, at least in part, influenced by climate change. The abundant native species Loricariichthys castaneus tended to decrease in size, abundance and biomass and could be considered a species that should be further investigated for its sensitivity to climate change in this reservoir and in other aquatic environments. Changes observed in the fish assemblage over the last decades may be essential for an assessment of the consequences of global warming in this reservoir. However, future studies addressing biotic interactions and the influence of other environmental and habitat variables should be carried out to further investigate this issue. Both hydroelectric dams and global warming pose threats to freshwater fish diversity, and both will interact. This study is a step to contribute to improve the predictive capacity of responses to climate change, one of the requirements for outlining biodiversity conservation strategies.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

F.G.A. and M.C.C.A. conceived the study, M.C.C.A., G.H.S.G and W.U. analysed the data, and F.G.A. and M.C.C.A. wrote the manuscript, with contributions from the others authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.