INVASIVE SPECIES II

Food web changes associated with drought and invasive species in a tropical semiarid reservoir

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Abstract Fish and invertebrates are introduced in freshwaters around the world for commercial purposes, despite widely known impacts on food webs and biological invasions. As a proxy for artificial environments, we modeled a typical reservoir in a Brazilian semiarid region using an ecosystem approach. We compared the role of native and non-native invasive species (NIS) in the food web, between dry and wet periods, and under the influence of an extreme drought period (from 2011 to 2015), simulating the variation in fish biomasses due to decreasing consumption. Key ecosystem groups were fishes (mainly NIS), birds, and insects. Nutrient cycling was dependent on invaders, while the trophic structure was detritus based during the drought. Biomass of detritivores was almost two times higher than herbivores, and native fish species decreased abruptly in response to invaders and volume variation. The dominance of low-trophic levels (TLII) and tilapia—*Oreochromis niloticus* (Linnaeus, 1758) and other tilapiines—resulted from interactions among invaders, feeding behavior on benthos, and environmental seasonality, tending toward biotic homogenization ("benthification") at the ecosystem level. An increasing relevance of detritivores with cascading effects in ecosystems subject to drought, multiple

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introductions, and ubiquitous food sources has clear implications for the fisheries and the water quality.

Introduction

There is a growing consensus that economic and political strategies overestimate the social benefits of reservoirs and aquaculture (Vitule et al., 2009; Attayde et al., 2011; Pelicice et al., 2014; Winemiller et al., 2016). Reservoirs human populations with water, food, and rural irrigation (Barbosa et al., 2012; Letnic et al., 2014). However, they cause profound changes in the hydrological regime of hydrographic basins, altering the short- and long-term dynamics of aquatic communities (Rahel, 2007; Agostinho et al., 2016), affecting fishery productivity (Johnson et al., 2008), and facilitating invasive species introduction (Vitule et al., 2012; Daga et al., 2015; Ortega et al., 2015).

While the social benefits provided by the multiple uses of a reservoir vary regionally and locally, biotic homogenization scenarios are predictable (Radeloff et al., 2015), offsetting many of the potential benefits of non-native species introduction (Gozlan, 2008; Vitule et al., 2012). The inadequate management of the aquaculture held in the net cages increases the introduction of non-native species (Ortega et al., 2015; Padial et al., 2017), causing biotic homogenization, spread of invaders at a regional level, and an overall negative impact on fishing activities (Vitule et al., 2009; Naylor et al., 2009).

Reservoirs have an overall negative status as the prime sources of invasive propagules on freshwaters (Rahel, 2007; Johnson et al., 2008; Leprieur et al., 2008; Vitule et al., 2009, 2017). The presence or establishment of NIS creates opportunities for "novel interactions" (Sih et al., 2010) to take place,

facilitating other non-native species to enter, with multiplicative effects on the ecosystem (Gurevitch, 2006; Saul & Jeschke, 2015; Simberloff, 2015). Predation interactions between fish and other groups accounts in the process of invasion (Sih et al., 2010) and environmental influence, including water fluctuation (Pereira et al., 2017), contribute to the non-random aspect of biological invasions. For example, a water-level reduction or increase in temperature can influence fish diets and the abundance of their potential food sources (Chaparro et al., 2015; Pereira et al., 2017).

Inter annual dry periods and shallow human-made reservoirs are common in the Brazilian semiarid region. However, the wet period shortened abnormally from 2011 to 2015, thereby affecting aquatic communities' metabolism and biodiversity (Sena et al., 2014; Novaes et al., 2015; Rodrigues-Filho et al., 2016). This is important because these reservoirs are often subject to release of non-native propagules and to extreme climatic conditions, such as the persistent dry period represented here. Water-level variation and turbidity influence encounters and inter specific interactions (Lake, 2003), in which predation is directly related to prey and predator biomass and to the degree of the volume reduction (González-Bergonzoni et al., 2016). Indeed, both native and non-native species respond to environmental changes and lake morphometry under the effects of winds and periodic mixtures, independently of being introduced (Bezerra et al., 2014; Schwalb et al., 2014). The interaction between introduced prey and predator is central given the multiple effects of NIS on Neotropical reservoirs (Rahel, 2007; Agostinho et al., 2016), especially considering the "Enemy Release Hypothesis" (Keane & Crawley, 2002). It predicts the success of NIS because they are free from their natural enemies (e.g., Torchin et al., 2003) and could budge more energy on their fitness than the native fauna—a phenomenon known as "Evolution of Increased Competitive Ability" (Blossey & Notzold, 1995).

In this study, we evaluate the role of interactions, environmental variation, and fishery on the food web of a reservoir in the Brazilian semiarid region. Our models were built with the Ecopath with Ecosim (EwE) approach, commonly applied to marine environments (Coll & Libralato, 2012; Heymans et al., 2014), but also used in freshwater environments (e.g., Angelini et al., 2006, 2013; Feroz Khan & Panikkar,

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2009). We based our approach on local sampling (including birds, invertebrates, fishes, fish gut content, and landing data estimate) of a reservoir in wet and dry seasons and an annual model. We also simulated the impact of NIS and water-level reduction on the food web during a long-term drought (2011–2015), using four forcing functions (i.e., linear, exponential, inversely exponential, and observed water volume data). Finally, we disentangled the trophodynamics and environmental variation associated to benthification in altered environments.

Materials and methods

Study area and sampling

The Sítios Novos reservoir (S03°46.325′ W038° 57.822′) is close to the coastline (40 km) of Ceará State, Brazil (Fig. 1). The region is defined as a dry and semiarid tropical savanna (Peel et al., 2007). The reservoir has an overall hydrological capacity of 126 km^3 and a superficial area of 16.48 km^2, with annual salinity averaging 0.45 ppt (Bezerra et al., 2014).

We sampled three stretches of the reservoir (Fig. 1), standardized by effort in a model-oriented sampling design, sequentially capturing phytoplankton, zooplankton, benthic invertebrates, and fish, such as detailed in "Sampling effort" in the Electronic Supplementary Material (ESM). We covered dry and wet periods, bimonthly, in seven campaigns (Fig. 2).

Ecopath with Ecosim modeling

We used the Ecopath with Ecosim (EwE) to build the three models in dry and wet periods, and annually (Christensen & Walters, 2004). The EwE model is based on the mass-balance assumption, in which the consumption by a predator (or group) leads to the mortality of its prey (or group). This is mathematically described by linear equations:

$$B_i \times PB_i \times EE_i - \sum B_j \times QB_j \times DC_{ji} - EX_i = 0,$$
(1)

where Bi is the biomass of group i; PB_i is the production/biomass rate or mortality of i; EE_i is the ecotrophic efficiency of i, which varies from 0 to 1 and represents the fraction of the production transferred to higher TLs or exported from the system; B_j is the biomass of predator j; QB_j is the food consumption per unit of biomass for predator j; DC_{ji} is the fraction of i in the diet of j; and EX_i is the export of i (fishing mortality). The biomasses were calculated in ton $\times$ km^{-2}, and the flows expressed in ton $\times$ km^{-2} $\times$ year^{-1}.

Dataset

The dataset was also model oriented in phytoplankton, zooplankton, benthic invertebrates, fish, and fish gut content. The food web compartments, laboratorial procedures, and preliminary inputs to the food web were provided in the ESM, along with model parameterization and mass balancing processes.

We included three multi-cohort groups in our models: *Cichla* spp., *O. niloticus*, and Atherinidae. This last group was the only cohort in which adults and juveniles were captured in sufficient numbers to approach the real comparison between biomass and production in dry and wet periods (more details in the ESM).

Food web modeling analyses (Ecopath, Ecosim, and Ecotroph)

Ecopath outputs provide ecosystem attribute estimates (sensu Odum, 1969) to compare models of the dry and wet periods. The sum of the energy of all ecosystem flows (production, consumption, exports, respiration, and flow to detritus) is TST (total system throughput), directly related to the total primary production (PP), which, divided by total respiration (PP/TR), represents the ecosystem stability. The total activity (TA) is represented by TR/TB (total respiration/total biomass). The net production (NP) and cycling forms the Finn Index (Finn, 1976), related to resilience and energy cycling, highlights the energy attributed to detritus cycling (DC). The emergent properties Ascendancy and Overhead also indicate ecosystem stability (Ulanowicz et al., 2009).

Fig. 1 Sítios Novos reservoir in the Brazilian semiarid region and sampling stations (A, B e C)
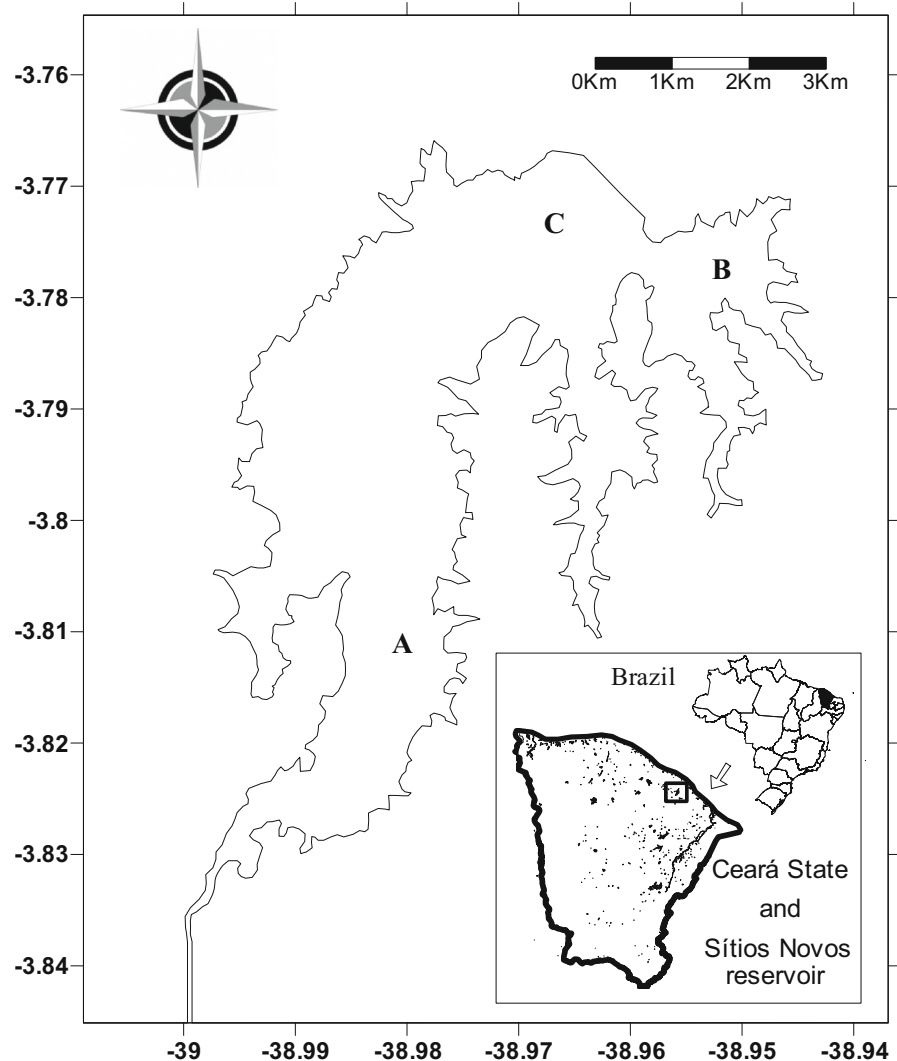
We used the network parameter ratios in dry/wet as well as detritivory/herbivory to understand the difference between periods. The mixed trophic impact (MTI) matrix represents the relative impact (positive or negative) of a single component over all others; this matrix was used by Libralato et al. (2006) to calculate the Keystoneness Index (KSi), which indicates the key species in a system. We analyzed the biomass distribution under fishery yields in dry and wet periods using the EcoTroph plug-in (Gascuel & Pauly, 2009).

Time dynamic model (Ecosim)

The dry and wet models were then joined deliberately in a new model (annual), by averaging the overall biomass sampling (in dry and wet periods) to obtain each group's biomass. The other input parameters were the same since they refer more to the life history than to the seasonal changes. This last model was used to perform simulations using the time dynamic module Ecosim. The EwE temporal module is derived from Eq. 1 (see Walters et al., 1997):
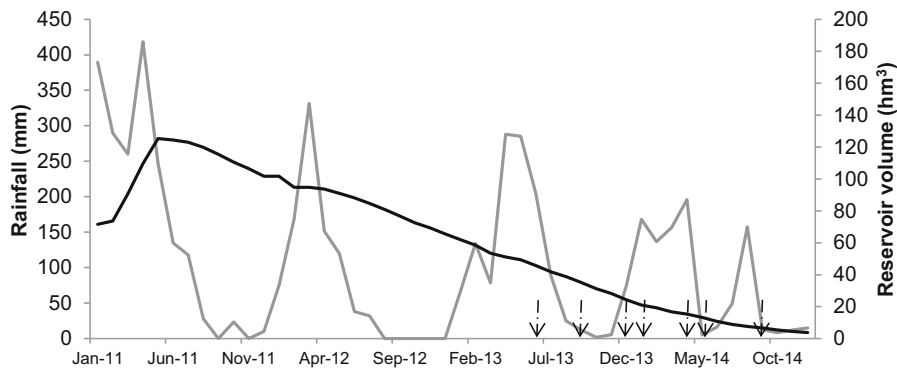
Fig. 2 Rainfall (gray line, mm), reservoir volume (black line, h × m³) in Sítios Novos reservoir, Brazil. Dashed arrows indicate sampling of biotic components. We used reservoir volume variation as a forcing function in the simulation (see text). Data sources for rainfall and volume: Companhia de Gestão dos Recursos Hídricos do Estado do Ceará—COGERH e Fundação Cearense de Meteorologia e Recursos Hídricos—FUNCEME, Brazil

$$\frac{dB_i}{d_t} = g_i \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i,$$

$$(2)$$

where dB_i/d_t is the change in the biomass of functional group i (B_i) over time t, g_i is the net growth efficiency (production/consumption ratio), Q_{ij} is the consumption of group i by group j, I_i is the immigration of functional group i, MO_i is the non-predation rate of natural mortality, F_i fishing mortality, and e_i emigration of functional group i.

The consumption rates, Q_{ij}, are based on the foraging arena concept, where the biomasses are divided into vulnerable and invulnerable states (v_{ij}):

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times P_j}{2v_{ij} + a_{ij} \times P_j},$$

$$(3)$$

where a_{ij} is the effective search rate of predator j feeding on prey i, B_i is the biomass of the prey, P_j is the biomass of predator, and v_{ij} is the vulnerability of prey i to predator j. The values that the vulnerabilities assume indicate the type of flow control, with $v_{ij} = 2$, $v_{ij} = 1$, and $v_{ij} > 2$ representing a mixed flow control, a bottom-up control, and a top-down control, respectively (Walters & Martell, 2004).

We simulated the temporal variation of relative biomass (end/initial Biomass) for fish groups over the 4 years of drought (2011–2015) using the annual model, and the default values of EwE ($v_{ij} = 2.0$), according to the theory of the foraging arena (Ahrens et al., 2012). The Ecosim module contains a routine to allow a 'forcing function,' which may represent a physical driver influencing trophic interactions by varying the search rate values (a_{ij}).

Because we do not know exactly how the years of drought affected the predator–prey interactions, four types of forecast forcing functions (FFF) were explored (see Fig. ESM 1): linear (I), exponential (II), inversely exponential (III), and volumetric (IV, i.e., the observed volume dynamic in the period—Fig. 2, black line). Each FFF was deterministic, but together added to a non-deterministic influence of decreasing water level on predation interactions and biomasses, that could be either bottom-up or top-down influenced: in I, a continuous decrease in predation was expected over time; in II, there was a fast impact on prey–predator interactions, then relaxed with the time; in III, there was a time lag in which predation is not influenced by the water reduction, then suffering a sudden impact; in IV, prey–predator interactions were influenced by observed data of the volume (Fig. 2).

These curves were used as FFF over predator–prey interactions by providing the magnitude in which a fish species interacts with all its prospective prey as their availability decreases. Such hypotheses were related to the biota's life history and habitat reduction (Chaparro et al., 2015; González-Bergonzoni et al., 2016; Pereira et al., 2017), when the severe dry period affected the reservoir volume. Thus, the annual model was used to develop four types of simulations, one for each FFF, and the final biomasses relative to the respective initial biomasses were selected monthly as output (end biomass/initial biomass).
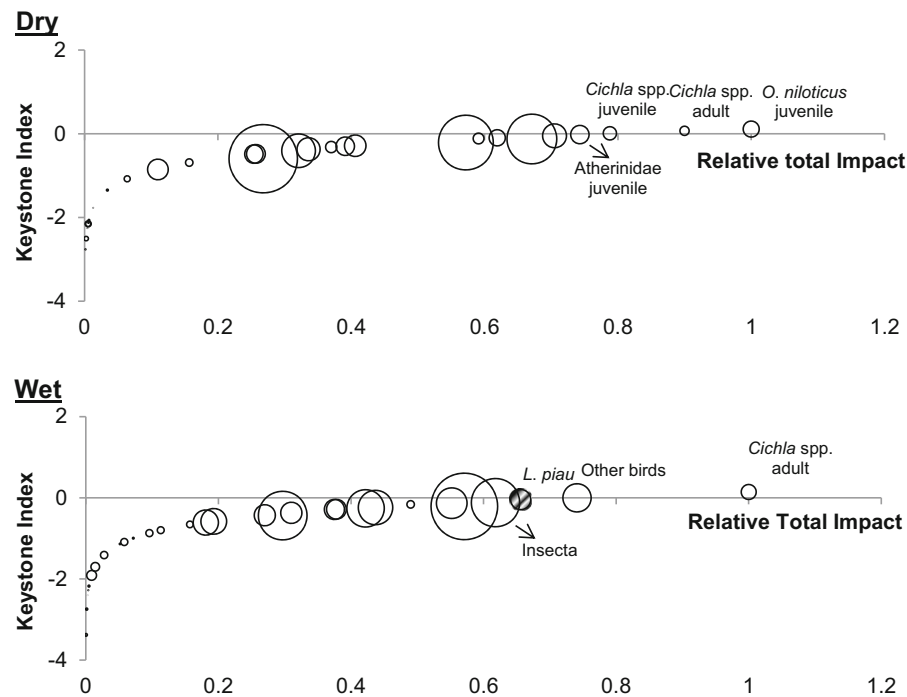
Fig. 3 Keystone Index *vs*. Relative Total Impact for dry and wet Ecopath models at an artificial reservoir (based on Sítios Novos reservoir, Brazil). Circle sizes are relative to group biomass. Circle fill is showing native fish species. Main four keystone species names are emphasized

Simulation statistical analysis

After Ecosim simulations, we applied general least square (GLS) models (Zuur et al., 2009), using the time-series outputs (relative biomasses) as the dependent variables and their respective Forecast Forcing Function (Fig. 2 and ESM 1) as the explanatory variable in four GLS models, separately. The aim of these models was to determine which FFF was the best explanation of the respective forced predator–prey interactions and, consequently, the outputs. The best GLS model was chosen with the lowest AIC (Akaike Information Criterion) value using the package "nlme" in R (Pinheiro et al., 2013).

In the best model chosen, we separated key compartments (relative biomasses of native fish species) from the relative biomasses of key NIS and joined the last with abiotic variables in a model, with the aim of segregating and identifying the main drivers of native species from 2011 to 2015 (invaders, abiotic factors, or both):

$$B_{lp} \times B_{pb} = B_0 + B_{cs} + B_{on} + FFFc + T_m \qquad (4)$$

Thus, relative biomass of native species B_{lp} (*Leporinus piau* Fowler, 1941) and B_{pb} (*Prochilodus brevis* Steindachner, 1875) were explained by: B_0 (intercept), B_{cs} (*Cichla* spp. relative biomass), B_{on} (O. *niloticus* relative biomass), FFF_C (most parsimonious FFF), and T_m (time, 1–48 months), again using the GLS method with temporal autocorrelation controlled in an autoregressive pattern ("corCAR1" function).

Results

Food web in the dry and wet periods

The annual Ecopath model had 12 fish species, nine macroinvertebrate groups, six bird groups, three zooplankton groups, three primary producers, along with detritus, in a food web of 34 groups, while in dry and wet periods, resulted in 30 and 31 groups, respectively (Table 1). The diet composition matrix (DC) in the dry, wet, and annual models (Tables ESM 1, ESM 2,

Table 1 Biomass (B, $t \times km^{-2}$), Production (P/B, $t \times km^{-2} \times year^{-1}$), Consumption (Q/B, $t \times km^{-2} \times year^{-1}$), and Catch (C, $t \times km^{-2} \times year^{-1}$) in the Ecopath models (dry and wet, see the main text) for an artificial lake in a semiarid area (Sítios Novos reservoir, Brazil)

Group	Dry					Wet					C
	TL	B	P/B	Q/B	EE	TL	B	P/B	Q/B	EE	
Birds											
Ardea alba	**3.64**	1.46	0.11	0.73	**0**	**2.84**	1.46	0.11	0.73	**0**	
Butorides striata	**3.78**	0.02	0.2	1.31	**0**	**2.71**	0.02	0.2	1.31	**0**	
Caracara plancus	**3.11**	0.15	0.09	0.59	**0**	**3.19**	0.15	0.09	0.59	**0**	
Egretta thula	**3.65**	0.2	0.15	0.98	**0**	**2.92**	0.2	0.15	0.98	**0**	
Phalacrocorax brasilianus	**3.85**	0.04	0.11	0.77	**0**	**2.25**	0.04	0.11	0.77	**0**	
Other birds	**2.54**	1.73	0.19	1.28	**0.01**	**2.82**	1.73	0.19	1.28	**0.01**	
Fish											
Arapaima gigas	**3.5**	0.01	0.44	3.83	**0**	**3.16**	0.01	0.44	3.83	**0**	
Cichla spp. juvenile	**3.13**	0.78	1.13	26.63	**0.56**	**2.75**	1.01	1.13	26.63	**0.86**	0.1
Cichla spp. adult	**3.4**	0.41	0.73	11.42	**0.93**	**3.04**	0.54	0.73	11.42	**0.7**	0.58
O. niloticus juvenile	**2.42**	1.09	1.2	14.89	**0.54**	**2.29**	0.92	1.2	15.2	**0.77**	0.1
O. niloticus adult	**2.62**	1.11	1.29	7.94	**0.99**	**2.59**	1	1.3	7.94	**0.99**	1.41
Atherinidae juvenile	**2.59**	1.4	3.15	32.9	**0.68**	**2.49**	0.88	1.74	30.4	**0.21**	0.24
Atherinidae adult	**2.88**	2.28	1.86	15.43	**0.55**	**2.45**	2.02	1.92	15.43	**0.32**	0.47
Plagioscion magdalenae	**2.91**	**1.87**	1.58	12.97	0.6	**2.51**	**2.53**	1.58	12.97	0.6	1.17
*Prochilodus brevis***						**2.14**	**2.96**	1.14	11.22	0.6	1.41
*Leporinus piau***						**2.5**	**0.92**	1.28	10.34	0.6	0.71
Poecilia sp.	**2.71**	**2.14**	2.74	28.4	0.6						
Astyanax aff. *bimaculatus*	**2.97**	**0.29**	4.26	16.84	0.6						0.24
Macroinvertebrates											
Turbellaria	**2**	0.01	20.99	83.97	**0.7**	**2**	0.01	20.99	83.97	**0.41**	
Clitellata	**2**	0.01	18.63	74.53	**0.84**	**2**	0.02	18.63	74.53	**0.86**	
Other Gastropoda	**2**	0.04	11.49	45.97	**0.97**	**2**	0.15	11.49	45.97	**0.95**	
Oligochaeta						**2**	0.02	20.47	81.9	**0.95**	
Bivalvia						**2**	0.14	3.75	15.01	**0.99**	
Ostracoda	**2.01**	1.4	8.4	33.61	**0.98**	**2**	1.4	8.4	33.61	**0.8**	
Shrimp	**2**	1.41	22.5	90	**0.82**						
Insecta	**2.09**	**9.25**	10.09	40.35	0.9	**2**	**4.84**	10.09	40.35	0.9	
Melanoides tuberculata	**2**	17.18	4.81	13.43	**0.04**	**2**	4.91	4.81	13.43	**0.55**	
Zooplankton											
Cladocera	**2**	0.54	12	48	**0.51**	**2**	0.13	12	48	**0.97**	
Rotifera	**2**	0.58	6	24	**0.6**	**2**	0.15	6	24	**0.72**	
Copepoda	**2.11**	4.36	24	96	**0.72**	**2**	0.16	24	96	**0.99**	
Phytoplankton											
Bacillariophyta	**1**	0.13	1.08		**0.6**	**1**	0.03	1.08		**0.96**	
Chlorophyta	**1**	0.21	1.09		**0.85**	**1**	0.25	1.09		**0.99**	
Cyanophyta	**1**	11.15	73.16		**0.48**	**1**	9.05	73.16		**0.23**	
Detritus	**1**	12			**0.68**	**1**	12			**0.4**	

Values in bold were estimated by the EwE. Blank cells represent the lack of a compartment in each period. **Endemic to Brazil

Table 2 Network Analysis in two Ecopath models for dry and wet periods at an artificial lake in a semiarid area (based on Sítios Novos reservoir, Brazil)

Parameter	Dry	Wet	Unit	Dry/wet
Total consumption (TC)	1464.72	537.92	t km^{-2} year^{-1}	2.72
Total respiration (TR)	675.83	253.37	t km^{-2} year^{-1}	2.67
Flow to detritus	991.28	706.86	t km^{-2} year^{-1}	1.40
Total flow	3448.56	1927.70	t km^{-2} year^{-1}	1.79
Total biomass (TB)	61.23	37.66	Ton	1.63
Primary production (PP)	815.79	662.53	Ton	1.23
TR/TB	13.32	17.59	t km^{-2} year^{-1}	0.76
PP/TR	1.21	2.61		0.46
Net system production (NP)	139.96	409.16	t km^{-2} year^{-1}	0.34
PP/TB	13.32	17.59		0.76
Detritus cycling (DC)	479.60	146.65	t km^{-2} year^{-1}	3.27
Finn index (cycling)	13.91	7.61	% Total throughput	1.83
Ascendency	20.60	24.50	%	0.84
Overhead	79.40	75.50	%	1.05
Detritivory/Herbivory ratio	1.72	1.82		0.94
Total catch	4.26	5.81	t km^{-2} year^{-1}	0.73

Fig. 4 Total Log biomass (LogB—black lines) and Catch (LogCatch—gray lines) of the trophic levels in dry and wet Ecotroph models for Brazilian semiarid—based on Sítios Novos reservoir
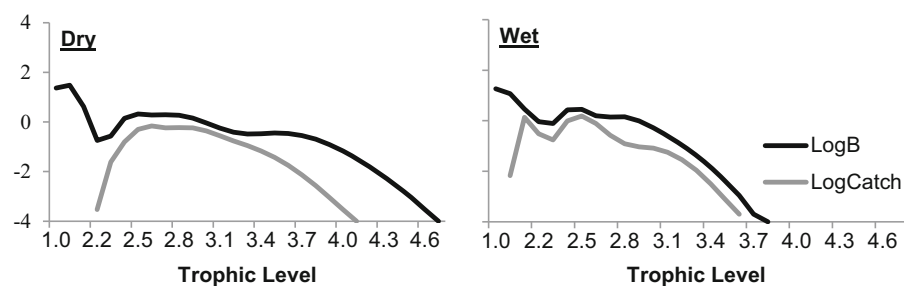
ESM 3) could be summarized in the trophic level value.

Non-native species dominated the fish community almost exclusively, with only *L. piau* and *P. brevis* being endemic and not occurring in the dry period. We highlighted Atherinidae fishes (a multi-cohort group), most commonly found in marine environments, but the higher biomass in the food web was the invasive invertebrate *Melanoides tuberculata* (Müller, 1774). Birds were common from tropical ecosystems, but only one species found was endemic to Brazil, the band-tailed hornero *Furnarius figulus* (Lichtenstein, 1823) (included in Other birds, see "*Sampling of Birds*" in the ESM).

Food web model (Ecopath)

In general, matter exchange and availability (biomass, flows, and cycling) were greater in the dry period

(Table 2). Higher dry/wet ratio indicated that dry period showed higher detritus cycling and consequently higher food web stability and diversity (of flows) on the network, while wet period showed higher homogenization of flows. In contrast, net production and catches were higher in the wet period, given the presence of locally exploited endemic fish species (*L. piau* and *P. brevis*). However, the detritivory/herbivory ratio was constant in both periods with prevalence of detritivory.

The main key groups were non-native predatory *Cichla* spp. adults and *Cichla* spp. juveniles, in the dry period. In the wet period, adult *Cichla* spp. and *O. niloticus* juveniles (Fig. 3). The other key groups were carnivorous or omnivorous in the dry period (Atherinidae juvenile), and piscivorous, omnivorous, and detritivorous in the wet (Other Birds, *L. piau* and Insecta, respectively).
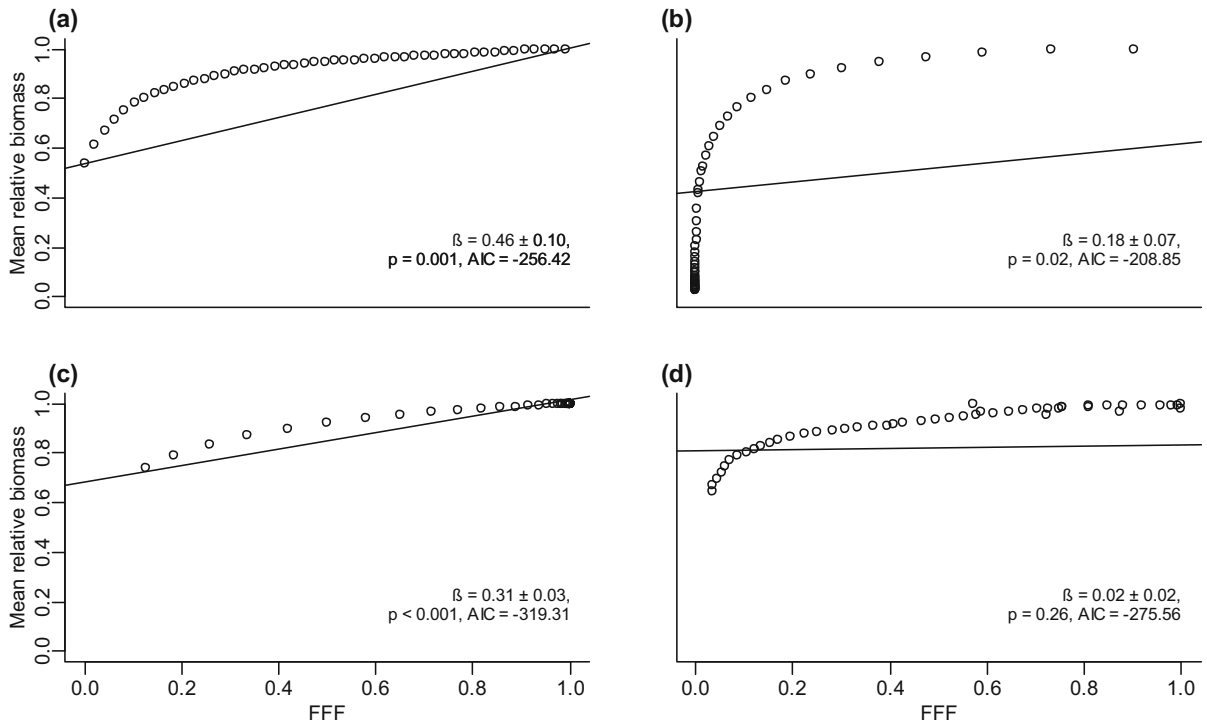
Fig. 5 Coefficient of regression (β) and Akaike Information Criteria (AIC) of mean relative fish biomass (2011–2015) in GLS models, using Forecast Forcing Functions (FFF): **(a)** linear, **(b)** exponential, **(c)** inversely exponential, and **(d)** volume variation. Simulations on monthly basis from 2011 to 2015 in the Ecosim model (see text for more details)

Table 3 Explanation of the relative biomass of native species in relation to non-natives, abiotic factors, and their interactions (monthly from 2011 to 2015) in a general least squares (GLS) model

Explanatory variables	β_{GLS}	Std-error	T-value	P value	ρ
					1
β_0	0.42	0.21	2.03	0.05	
Cichla spp	− 0.57	0.07	− 8.47	< 0.001	
O. niloticus	− 0.77	0.14	− 5.68	< 0.001	
FFF3	4.64	0.36	12.77	< 0.001	
Cichla spp.: *O.niloticus*	1.87	0.10	18.54	< 0.001	
Cichla spp.: FFF3	− 3.24	0.43	− 7.58	< 0.001	
O. niloticus: FFF3	− 5.85	0.45	− 13.09	< 0.001	
***Cichla* spp.: *O. niloticus*: FFF3**	**4.50**	**0.36**	**12.34**	**< 0.001**	

Dependent variables: relative biomasses of *L. piau* and *P. brevis* (native fish species). Explanatory variables: relative biomasses of *Cichla* spp. and *O. niloticus* (non-native species) and FFF3, the inversely exponential forcing function. Autocorrelation structure is corAR1(form = ∼ time). In bold: the most comprehensive explanatory variables (complete model) and the structural correlation (ρ)

Trophic spectra (Ecotroph)

Total biomass (LogB) was distributed over 4.7 trophic levels (TL) in the dry period, while it made up 3.8 TL in the wet (Fig. 4). The total catch (LogCatch) decreased 0.6 *TL* from the dry to the wet period with a higher catch on lower TL, mainly on *P. brevis* (TL = 2.1) and *L. piau* (TL = 2.5). Due to a decrease in TL during the wet period, there was indeed a higher fishing effort on large predators *Cichla* spp. juveniles (TL = 3.1) and adults (TL = 3.3), reaching values close to their biomass. The trophic network had low relative biomass at intermediate trophic levels, analogous to wasp-waist systems (Cury, 2000).

Time dynamic simulations (Ecosim)

All the four forecast forcing functions (FFF) returned outputs (relative biomass) like their respective FFF trends (Fig. ESM 2), but the exponential inverse function (III) was the most parsimonious ($\beta = 0.31 \pm 0.03$, $P < 0.001$, AIC = − 319.31, Fig. 5). The exceptions were some specialist groups, such as an insectivorous fish *Poecilia* sp. (Fig. ESM 2, continuous gray lines), differing from the overall dynamics of the other components, and the FFF IV (volume variation), not effective over predation interactions and on relative fish biomass during the period of simulation ($\beta = 0.02 \pm 0.02$, $P = 0.26$, AIC = − 275.56, Figs. ESM 2, 5d). Using relative biomass of endemic fish species as dependent variable, the structural correlation (ρ) of *L. piau* and *P. brevis* over the months was 1 (Table 3), indeed, both NIS (*Cichla* spp., *O. niloticus*) and abiotic variables (FFF III) influenced endemic fish relative biomasses.

Discussion

Our food web had a higher energy flow during the dry period, but lower consumption and a higher degree detritivory in the wet, nutrient cycling was twice as large in dry than in wet, a proxy of stability sensu Odum (1969). Apart from the annual seasonality, detritivory was more relevant than herbivory as a support for predators in higher TL's, and the inversely exponential function represented drought effects. Groups are then expected to respond with constant biomass with a time lag (∼ 32 months), after which

they vary differentially and exponentially. Otherwise, both drought and NIS determines the long-term pressure over native species. In a scenario of resource limitation and apparent competition, the inverse exponential curve was the most parsimonious for representing an abrupt biomass decrease of native species during the years of drought, differing from other theoretical curves and from the volumetric variation in the period. The enemy release hypothesis (ERH) and the evolution of increased competitive ability (EICA) presume direct and indirect effects (Sih et al., 2010) that could confirm this type of regulation.

A growing body of evidence argues for the relevance of detritivory in food webs globally (Mayer et al., 2014; Paterson et al., 2014), especially in eutrophic lakes and reservoirs (Cai et al., 2017), in which plankton consumers cannot control phytoplankton growth (Frau et al., 2017). Apart from the differences between pelagic and benthic food webs, it is common to associate wet periods with increasing inputs of organic matter, as well as the upwelling organic matter to eutrophication (Molisani et al., 2010; Bezerra et al., 2014; Brasil et al., 2016), which could lead to blooms of toxin-producing microalgae (e.g., *Microcystis* spp., *Aphanizomenon* spp., or *Anabaena* spp.) and force detritivory during the wet period. Such algae can dominate the phytoplankton community during eutrophication (Higgins & Zanden, 2010). Thus, blue-green algae could limit the pelagic trophic network, creating a blue-green state (Conley et al., 2009; Elliott, 2012; Paerl & Paul, 2012). Under these circumstances, resources are available to benthic invaders, such as the non-native *M. tuberculata* and other generalist species in our study, that could drive the omnivorous fishes to benthivory. Such alternative state has an increased energy dissipation in the upper trophic levels in the blue-green state (D'Alelio et al., 2016), which is also linked to omnivory (Meerhoff et al., 2007; González-Bergonzoni et al., 2016) and the consumption on benthos, as shown by our study. This phenomenon has once called "benthification" in oligotrophic waters (Mills et al., 2003; Mayer et al., 2014), representing a sudden change from turbidity to clarity caused by invertebrate filter feeders consuming phytoplankton, a change which benefits generalist fish (Karatayev et al., 2007).

We are shown that detritus flows are the preferred pathway for the natives *L. piau* and *P. brevis*, as well as for NIS fish species, highlighting detritivory by *O.*
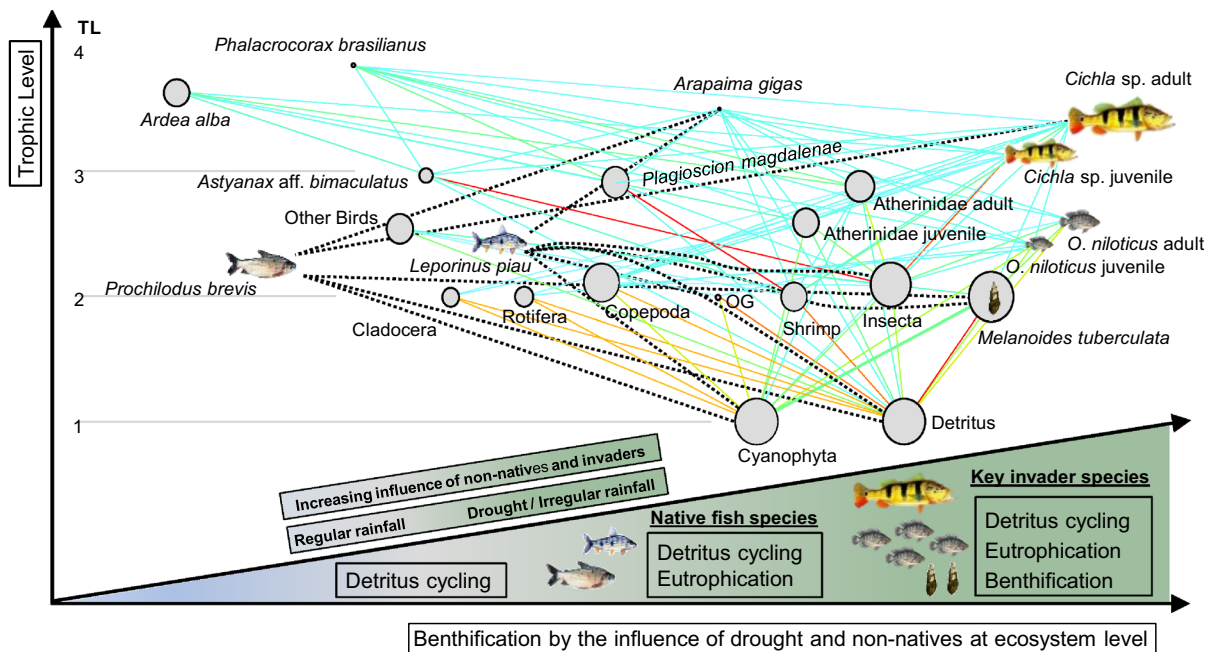
Fig. 6 "Benthification" by the increasing influence of invaders and drought at ecosystem level (based on Sítios Novos reservoir, Brazil). The x-axis could indicate benthification either in long-term droughts or in short wet seasons with sparse rainfalls. Less representative groups: Bacillariophyta, *Butorides striata*, *Caracara plancus*, Chlorophyta, Clitellata, *Egretta thula*, Ostracoda, *Poecilia* sp., and Turbellaria were omitted. Warming colors indicate interaction strengthening. Black linkages indicate interactions with natives. *OG* other gastropoda

niloticus (juvenile and adult), despite the preference of other non-natives such as Atherinidae for pelagic and insectivorous paths. During the long-term drought, key NIS species *O. niloticus* (omnivorous) and *Poecilia* sp. (insectivorous) were widely favored, while the biomasses of other fishes decreased. The exponential decrease in the biomass of native species under drought conditions corresponds to the success of invaders. The ability to feed on benthos and insects, as well as the consumption of *M. tuberculata*, expanded the niche of *O. niloticus*. The consumption on *M. tuberculata* is uncommon since Gastropoda is sometimes treated as a "*cul-de-sac*" in ecosystems (Twardochleb & Olden, 2016). However, niche expansions are a common opportunistic behavior of *O. niloticus* (Njiru et al., 2004; Weyl, 2008; Attayde et al., 2011), regardless of the non-palatability of this prey.

Juvenile *O. niloticus* were the main keystone group during the dry period, followed by *Cichla* spp. adults, the main keystone group in the wet period. The interacting groups *O. niloticus,* non-native insects, and *M. tuberculata* are among the main food sources for the top-predator NIS *Cichla* spp., directly or

indirectly. The top-down effect of *Cichla* spp. creates conditions for intermediate consumers in a feedback loop. The homogenization perspective resulting from deterministic interaction among these NIS leads us to extend the concept of benthification as a "new" forcing towards biotic homogenization at ecosystem level (Fig. 6).

Thus, the dominance of *M. tuberculata* and *O. niloticus* and its indirect effects on native species in the short term (dry–wet periods) provided a greater understanding of the long-term dynamics of invaders, where it hindered top-down or bottom-up patterns. It has global implications because the genera *Oreochromis* and bass fish analogous to *Cichla* spp. are among the eight most introduced fishes in the world (Toussaint et al., 2016), and due to the artificial eutrophication in aquatic environments, already considered in the "blue-green future" perspective (Conley et al., 2009; Elliott, 2012; Paerl & Paul, 2012). Their generalist features with high adaptive potential are essential checkpoints in the system's functioning (Kovalenko et al., 2012; Thomaz et al., 2015; Yu et al., 2016), given a potential state of invasion

meltdown (Gurevitch, 2006; Simberloff, 2006). Conversely, we could not dig further on benthification effects associated to the ubiquitous presence of the pelagic Atherinidae. Such brackish individuals were probably *Atherinella brasiliensis* (Quoy & Gaimard, 1825), but we lacked the deep taxonomy needed to get into the species level (see Electronic Supplementary Material for further explanation).

Reservoirs are sources of invasive species at rates between 2.4 and 300 times faster than natural lentic ecosystems (Johnson et al., 2008), especially in complex systems of channel integration (Letnic et al., 2014). Therefore, stakeholders cannot be passive when it comes to the control of the intentional and unintentional spread of NIS, particularly *O. niloticus* and *M. tuberculata* in the Brazilian semiarid region. Some negative effects of NIS are obvious. However, the population-level consequences and the mechanisms that NIS propagate across multiple ecological levels and ecosystem dimensions, which should inspire caution (e.g., Gurevitch, 2006; Gurevitch et al., 2011; Simberloff, 2011; Simberloff & Vitule, 2014). Researchers and government authorities need to pay greater attention to benthification as a pattern, considering the overall expansion of aquaculture (Pelicice et al., 2014; Daga et al., 2015), especially if it comes from artificial ecosystems near underexplored areas (Padial et al., 2017). From 2017 onwards, the expansion of water channels through the Brazilian semiarid will link Sítios Novos reservoir in the "Integration Channel" of Ceará State (sizing 225 km) to the São Francisco River, with more than 500 km of artificial channels and at least 20 other reservoirs of equal or larger size (Cirilo et al., 2017). The spread of NIS into protected areas of the Brazilian semiarid is, therefore, in line (Lima et al., 2013; Rodrigues-Filho et al., 2016).

In conclusion, our model-oriented research design showed that Sítios Novos reservoir is a system "in development" based on detritivory, with greater stability and flows during the dry period. Interannually, the variation in fish relative biomass correlates with the dry periods, detritivory, and the dominance of NIS, which are the main drivers of the food web. The non-native *O. niloticus* is clearly expanding its niche and driving the food web to benthification. Ongoing with the drought, there is a current hatchery policy that can intensify the effects of *O. niloticus* on native and non-native species, destabilizing the ecosystem and

probably intensifying biotic homogenization, with "benthification at ecosystem level". Other invaders such as mosquitoes and snails are indeed influenced by trophic interactions and water-level decrease in long term; another question with public health implications. Overall, the effects of invaders were conspicuous and representative of other food webs under similar circumstances. Reservoirs in the Brazilian semiarid region incorporates five of the six pathways for invasion (release, escape, contamination, corridors, and natural dispersion) that favor biotic homogenization and the extinction of native species (Hulme, 2015). Taken together damming policies, river channelization, fish introductions, and NIS fish breeding in net cages (keeping the potential for escapes in mind) can spread non-native species and their homogenizing effects along the highly connected freshwaters (Spencer et al., 1991; Johnson et al., 2009; Estes et al., 2011; Preston et al., 2012), such as we speculated for benthification.

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