
Water Level Rise Induced Limnological Changes Indirectly Influencing the Structure of Aquatic Macrophyte Communities in a Tropical Reservoir

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Abstract: This study aimed to evaluate the degree of contribution of limnological variables to explaining ecological processes involving aquatic macrophytes after an event of water level rise (WLR) of an artificial lake (Cursai Reservoir - CR), located in northeastern Brazil. Initially we tested the hypotheses that limnological characteristics, and species richness and composition of aquatic macrophytes, would change post-WLR. Once these hypotheses were confirmed, we evaluated the degree of influence (direct or indirect) of the variables to structuring the community of aquatic macrophytes in CR. We carried out four pre-WLR sampling expeditions and four post-WLR sampling expeditions to a permanent plot of 5 m x 40 m, wherein we assessed species richness, composition and cover, and measured 12 limnological variables. We used partial correlation analysis to evaluate the degree of contribution of the limnological changes to post-WLR structuring of the aquatic macrophyte community. The results pointed to an indirect correlation between the limnological changes and the structuring of the aquatic macrophyte community derived from the WLR, with interspecific interactions being the determining factors in structuring. The cover and species composition in the post-WLR period confirmed this inference. In this period, we found a reduction in cover of the weeds *Eichhornia crassipes*, *Paspalidium geminatum* and *Salvinia auriculata*, new records of *Egeria densa*, *Ludwigia leptocarpa* and *Ludwigia helminthorriza*, and an increase in cover of *Cyperus odoratus* and *Oxycaryum cubense*. We consider that fast WLRs in artificial lakes, such as occurred in CR, can be considered intermediate disturbances. In such cases, the ecological processes involving the aquatic macrophytes could be explained by the intermediate disturbance hypothesis (IDH), which reinforces interspecific interactions (moreover competition) as being the restructuring factor.

Keywords: Aquatic Plant, Community Ecology, IDH

1. Introduction

Contemporary understanding of the ecology of aquatic macrophytes does not allow patterns of species richness and composition to be conclusively determined, especially in ecosystems that are strongly influenced by water level rise

(WLR), such as artificial lakes [1-3]. WLR can alter ecological processes involving aquatic vascular flora, with the alterations being most evident in the aquatic/terrestrial transition zone (ATTZ), due to the complexity of

interspecific relationships [4]. Normal WLR alters the species richness and composition of aquatic vegetation, whereas prolonged absence of WLR leads to excessive growth of a few weedy species [5-7].

Although the influence of WLR on ecological processes involving aquatic macrophytes is recognized, there is no consensus upon the preponderant explanatory factor(s). Numerous studies have indicated that limnological variables can explain processes related to species richness and composition of aquatic macrophytes in natural [6, 8] or artificial environments [9-12]. According to some of these, the modification of limnological characteristics in the post-WLR period interferes directly with the morphophysiology of species, and alters the species composition by favoring those best adjusted to the new environmental condition [6, 12].

Other reports have pointed out that the interspecific interactions can also function as structuring factors of aquatic vegetation, although such interactions are dependent on environmental variables [5, 13-15]. In this case, altered limnological characteristics due to WLR favor species best adjusted to the new environmental conditions, and thus alter the interaction between species [14]. Thus, the relationship between limnological characteristics and species richness and/or composition of aquatic macrophytes after an event of WLR becomes indirect, with the processes being preponderantly due to interspecific interactions. Given the ambiguity about the degree of contribution of limnological variables to explaining post-WLR ecological processes involving aquatic macrophytes, further study evaluating the influence of these variables on the ecology of the aquatic vegetation is needed.

In this context, we proposed a study to test the hypotheses that changes in species richness and composition of aquatic macrophytes, as well as in the abiotic characteristics of the water, occur after an event of WLR of an artificial lake. After testing these hypotheses, we had the following objectives: (I) identify the set of limnological variables that are correlated with changes in species richness and composition of aquatic macrophytes after a WLR event; and (II) test if these limnological variables directly or indirectly influence the post-WLR structuring of the community of macrophytes.

2. Materials and Methods

2.1. Description of the Study Area and the WLR Event

The Cursai Reservoir (CR) (07°-52'-41.6" S, 035°010'-30.9" W) is located in the Capibaribe River watershed, in the state of Pernambuco, northeastern Brazil (Figure 1). The CR has a maximum depth of 95 m and a crest length of 137 m with a surface area of 58 km² and maximum volume of 24,000,000 m³ [16].

Rainfall is irregularly distributed from March to August, with a peak in June-July and a dry period in September-February [17]. The average monthly rainfall in the reservoir

watershed varies from 221 mm (in June-July) to less than 70 mm in the dry months [17]. However, in June 2010, the meteorological station at Tapacurá recorded 448 mm of precipitation, 203% above the average for this month, when 307 mm fell within only ten days. Such a phenomenal rainfall caused an extraordinary WLR in CR of 8 m [18], and an increase in volume of 76% [16].

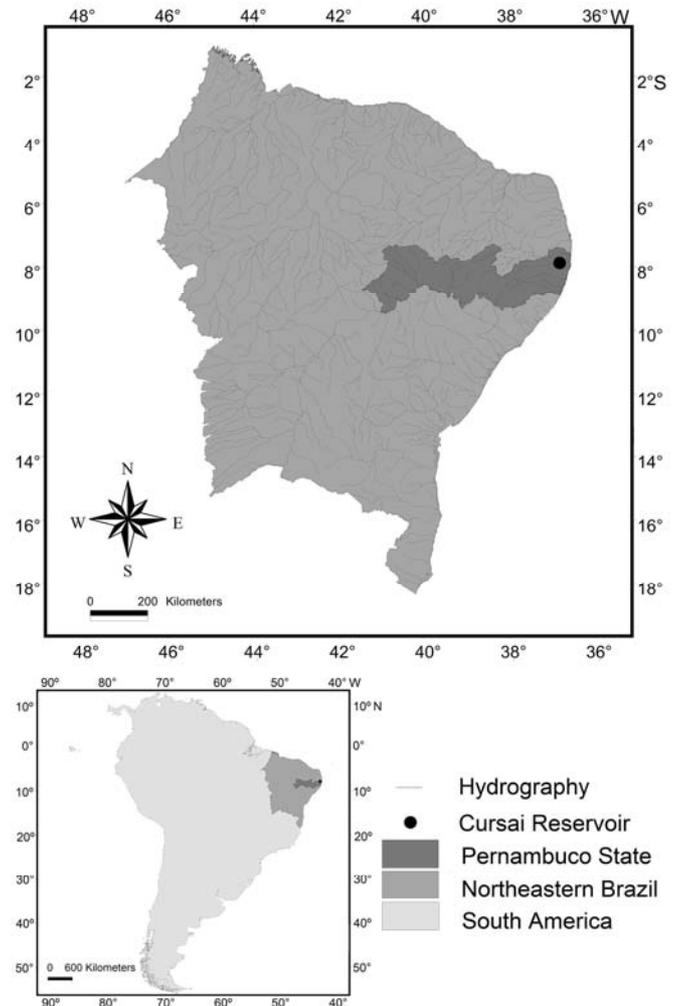


Figure 1. Map of Northeastern Brazil and the geographic location of the Cursai Reservoir (CR).

2.2. Sampling Periods and Data Collection

We made eight sampling expeditions to CR: four pre-WLR and four post-WLR. The expeditions in the pre-WLR period were in November 2008, and May, August and December 2009, whereas those in the post-WLR period occurred in August and November 2010, and February and June 2011. During the fourth sampling expedition in the post-WLR period, the CRreservoir had not yet decreased to 80% of its mean depth.

We established a permanent plot of 5 m X 40 m in the ATTZ of the reservoir, which was assessed during each sampling expedition for aquatic macrophyte species richness, composition, frequency of occurrence and cover. The frequency of occurrence and cover of the species were

obtained according to the methods of [19] and [20], respectively. For this study we adopted the concept of aquatic macrophytes proposed by [21], excluding species classified as amphibious to avoid mistaken records (stochastic) of species of strictly terrestrial habit. Species were identified using specialized literature, and collected specimens were incorporated into the Herbarium of the Universidade Federal Rural de Pernambuco (UFRPE). The taxonomic classification of the species followed [22] for ferns and allies and [23] for angiosperms.

The location of the study plot was established during the first sampling expedition, following two hierarchical criteria: 1st the plot should be located in an oxbow of the reservoir to reduce the effect of wind and drift displacement of free floating plants; 2nd the location should be maximally heterogeneous with regard to the aquatic vegetation, by avoiding patches of dominance of certain species. The initial edges of the plot stayed 0.5 m off the margin, towards the interior. The plot limits were marked with buoys. Based on the location of the buoys, we found that the plot experienced displacement of 0.4-1.8 m to the right or left (in relation to the initial position), resulting in a deviation of the plot area by $\pm 4.86 \text{ m}^2$ (only 2.4% of its total area).

During each sampling expedition we collected data on the following limnological variables: transparency (Secchi), conductivity (COND), temperature (TEMP), dissolved oxygen (DO), turbidity (TUR), pH, total phosphorous (TP), inorganic phosphate (PO_4), nitrate (NO_3) and nitrite (NO_2). These variables were chosen because they have been cited as predictors in studies evaluating the biological processes of aquatic macrophytes [9-11]. The limnological variables COND, DO, pH, TEMP and TUR were assessed in the field using a multiparameter device (YSI, model 556 MPS - *Multiprobe System*) and transparency was measured with a Secchi disc. Water samples were taken from the sub-surface (0.25 cm) in the plot edges and collected in duplicate. For laboratorial analyses, samples were cooled to avoid oxidizing the nitrogenate and phosphate compounds, and sent to the Limnology Laboratory of the Universidade Federal Rural de Pernambuco. The concentrations of NO_3 , NO_2 , PO_4 and TP were determined following accepted methodological protocols [24-26].

2.3. Analysis of Data

Species richness and composition and plant cover data were treated per period (pre- or post-WLR), with the sampling unit being the results for the permanent plot from a particular expedition. We assembled three matrices of data: A – biotic matrix of presence and absence of species recorded in the permanent plot for each period of water level; B - abiotic matrix of the limnological variables in each period of the water level; C - depth in the permanent plot.

From matrix “A” we estimated species richness for the pre- and post-WLR periods of CR, using the estimator CHAO 2. CHAO 2 was chosen because it is the most suitable

estimator for categorical data [27]. To determine if sampling effort influenced the richness estimate, we computed rarefaction curves for the data of the pre- and post-WLR periods separately [28], which occurred with 25 samples. The maximum and minimum confidence interval (95%) of the estimated richness or standard deviations of the rarefaction for the pre- and post-WLR periods were compared to determine similarity or difference in richness between periods. The estimates of richness and the procedures of rarefaction were performed in the software EstimateS version 9.1 [29].

To compare species composition of the permanent plot of CR in different periods of water level, we submitted matrix “A” to Non-Metric Multi-Dimensional Scaling (NMDS) analysis, with the Jaccard index and 1000 resamplings. To investigate if there were significant differences in floristic composition between pre- or post-WLR periods in CR, we performed a t-test with the scores of the plots on axes 1 and 2 of NMDS. The NMDS was performed in the software Past version 6.1 [30] and the t-test in software R [31].

To compare means of the limnological variables between pre- and post-WLR periods in CR, we performed t-tests, using the software R [31]. To identify the sets of limnological variables most correlated with the values of richness or the scores of NMDS, we performed linear multiple regression (forward stepwise), using the variation of the coefficient of error (QM error) as the criterion for selection of the sets of explanatory variables. Therefore, we correlated matrix “B” with the values of richness or the scores of the explanatory axes of NMDS. To investigate if the WLR of CR influenced the relationship between response variables (richness or the scores of NMDS) and the limnological variables selected by stepwise regressions, we made partial correlation analysis, using the depth of the permanent plot as a co-variable (matrix C).

We used the significance level (p) of the partial correlation analysis as the criterion to determine if the ecological attributes of richness or composition were explained by the limnological changes derived from WLR in CR. For the case of no-change or increase of the (p) of partial correlation we considered that the change of the post-WLR limnological characteristics in CR did not directly influence the ecological processes of the community. The analyses of multiple linear regression (forward stepwise) and the partial correlations were performed using the software R [31]. For the case of no functional relation between richness or composition with the post-WLR limnological characteristics, we evaluated the influence of competition on the relationship. Competition between plants is defined as the trend of neighbouring plants to utilize the same quantum of light, ions of mineral nutrient, water molecule or space [32]. Therefore, we used plant cover as an attribute for evaluating competition between species [32].

3. Results

3.1. Evaluation of Hypotheses

Ten species of aquatic macrophytes of nine genera and eight families were found in the permanent plot at CR (Table 1). Six species were recorded in the pre-WLR period and nine in the post-WLR period (Table 1).

Table 1. Cover (Cov) and list of the species of aquatic macrophytes identified in the permanent plot during four sampling expeditions (E1, E2, E3, E4) carried out in the pre- or post-water level rise (WLR) periods of the Cursai Reservoir. Legends: (+) Presence; (-) Absence.

Taxa	Pre-WLR				Cov (%)	Post-WLR				Cov (%)
	E1	E2	E3	E4		E1	E2	E3	E4	
ARALIACEAE										
<i>Hydrocotyle ranunculoides</i> L.f.	-	+	-	-	0.31	-	-	-	-	-
CYPERACEAE										
<i>Cyperus odoratus</i> L.	-	-	-	-	-	+	-	+	-	3.41
<i>Oxycaryum cubense</i> (Poepp. & Kunth) Palla	-	-	-	-	-	-	+	+	+	6.19
HYDROCHARITACEAE										
<i>Egeria densa</i> Planch.	-	-	-	-	-	+	+	+	+	3.37
ONAGRACEAE										
<i>Ludwigia leptocarpa</i> (Nutt.) H. Hara	-	-	-	-	-	-	-	-	+	2.53
<i>Ludwigia helminthoriza</i> (Mart.) H. Hara	-	+	-	+	3.37	+	+	+	+	18.94
POACEAE										
<i>Paspalidium geminatum</i> (Forsk.) Stapf	+	+	+	+	58.78	+	+	+	+	39.87
POLYGONACEAE										
<i>Polygonum ferrugineum</i> Wedd.	+	+	-	+	2.99	-	+	-	-	4.29
PONTEDERIACEAE										
<i>Eichhornia crassipes</i> (Mart.) Solms	+	+	+	+	4.64	+	+	+	+	0.97
SALVINIACEAE										
<i>Salvinia auriculata</i> Aubl.	+	+	+	+	29.92	+	-	+	+	20.43

The higher species richness in the post-WLR period was confirmed by the estimates of CHAO 2. There was no overlap by the confidence intervals of the estimated richnesses for the analyzed periods (Figure 2).

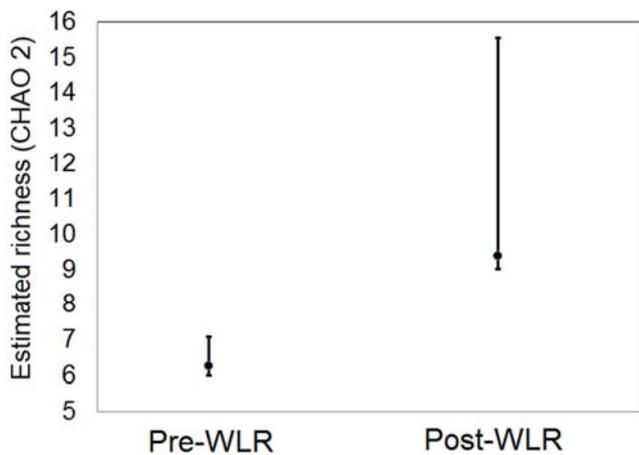


Figure 2. Confidence intervals and estimated richness of aquatic macrophytes (CHAO 2) for the periods of pre- and post-water level rise (WLR) in the Cursai Reservoir.

The rarefaction curves showed that the sampling effort did not interfere with the richness for the periods (Figure 3).

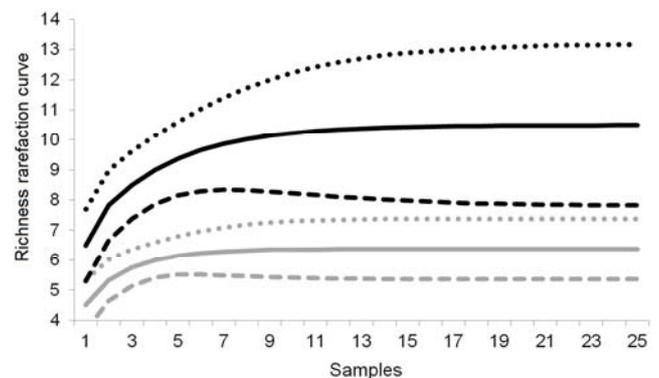


Figure 3. Rarefaction curve of species richness for the periods pre- (gray) and post- water level rise (black) in the Cursai Reservoir. Legend: full line represents the rarefaction of the number of species; dotted and dashed lines represent the standard deviations of the rarefaction for 25 sampling units.

The species *Eichhornia crassipes* and *Paspalidium geminatum* had a 100% frequency in CR (Table 1). *Hydrocotyle ranunculoides* and *Ludwigia leptocarpa* each had a single record for the pre- and post-WLR periods of the reservoir, respectively (Table 1). *Egeria densa*, *Cyperus odoratus* and *Oxycaryum cubense* were recorded only in the post-WLR period (Table 1). The t-test calculated using the scores extracted from the NMDS analysis confirmed the difference of the post-WLR species composition, this being

the variation observed by the gradient of the axis 1 ($p < 0.001$ / $t = 12.47$) (Figure 4).

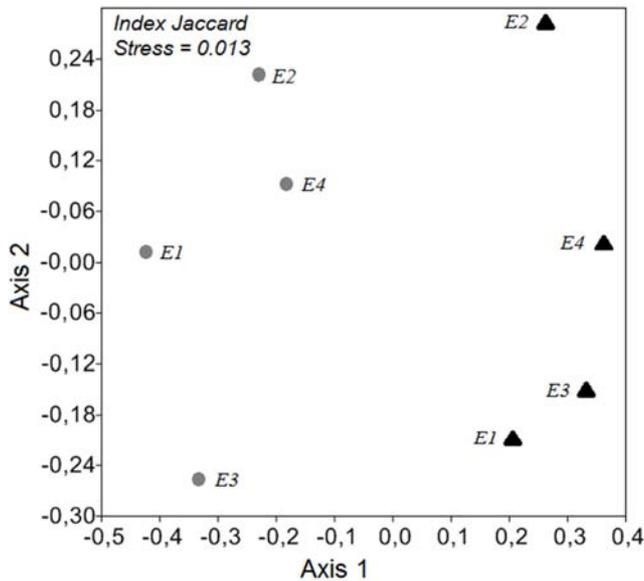


Figure 4. Non-Metric Multi-Dimensional Scale (NMDS) analysis representing the floristic gradient of aquatic macrophytes of the four sampling expeditions (E1, E2, E3, E4) carried out in the pre- (gray) or post-water level rise (black) periods in the Cursai Reservoir.

We found significant differences for COND, TUR, TP and PO_4 between pre- and post-WLR periods in CR (Table 2). The means for the variables NO_2 , TEMP, OD, Secchi, pH and NO_3 did not differ between periods (Table 2).

Table 2. Means and standard deviations (SD) of the limnological variables assessed in the permanent plot for pre- or post-water level rise (WLR) periods in the Cursai Reservoir. Results of t-test (t) between means of the limnological variables. Legends: (*) $p < 0.05$; (**) $p < 0.001$; ns – non significant.

Variables (unit of measurement)	Pre- WLR	Post- WLR	t test (t)
	Mean \pm SD	Mean \pm SD	
Dissolved oxygen ($mg.L^{-1}$)	5.55 \pm 0.92	5.88 \pm 0.45	ns
Nitrate ($mg.L^{-1}$)	1.07 \pm 0.33	1.67 \pm 0.18	ns
Nitrite ($mg.L^{-1}$)	0.78 \pm 0.32	0.26 \pm 0.6	ns
pH	7.42 \pm 0.29	7.53 \pm 0.53	ns
Temperature ($^{\circ}C$)	28.35 \pm 2.25	28.17 \pm 2.35	ns
Secchi (m)	0.55 \pm 0.05	0.72 \pm 0.09	ns
Conductivity ($\mu S.cm^{-1}$)	286 \pm 28.08	310.25 \pm 43.43**	5.73
Turbidity (NTU)	73.22 \pm 23.49	43.5 \pm 23.78**	8.64
Total phosphorous ($mg.L^{-1}$)	2.31 \pm 0.27	1.5 \pm 0.17*	2.44
Orthophosphate ($mg.L^{-1}$)	2.14 \pm 0.04	1.11 \pm 0.08*	2.24

3.2. Evaluation of the Ecological Question

Stepwise regression analysis identified the limnological variables of TP and PO_4 to comprise the set of predictor variables (QM error = 0.70; $R^2 = 68.81$) for the variation of species richness in CR. However, the analyses of partial correlation indicated that the WLR in CR did not interfere with the correlation of richness with the limnological variables selected by stepwise regression (Table 3).

Table 3. Results (p) of the partial correlation between the limnological variables preliminarily indicated by the stepwise regression as predictors of richness or scores of NMDS. Legends: (SP) correlation excluding the covariable depth; (CP) correlation including the covariable depth.

Variables	Richness		Composition	
	SP	CP	SP	CP
Conductivity	-	-	0.028	0.080
Orthophosphate	0.026	0.332	0.017	0.200
Total phosphorous	0.041	0.205	0.028	0.044
Turbidity	-	-	0.001	0.059

The stepwise regression indicated the set of limnological variables COND, TUR, TP and PO_4 as explicative of the variation of the scores of axis 1 of the NMDS (QM error = 0.79; $R^2 = 72.45$). However, the partial correlation indicated that the WLR in CR did not exert influence in the correlation of these scores with the limnological variables selected by the stepwise regression (Table 3).

The cover of *P. geminatum*, *Salvinia auriculata* and *E. crassipes* exhibited a decline in the post-WLR period, while *L. helminthoriza* and *Polygonum ferrugineum* experienced an increase in cover (Table 1).

4. Discussion

Our results of species richness and composition confirmed our proposed hypothesis. The disturbance caused by WLR in tropical ecosystems modifies the species richness and composition of the aquatic vegetation [7, 12, 33]. According to the cited authors, the post-WLR modification of the aquatic vegetation is related, mainly, to changes in limnological variables. Regarding variation in the abiotic characteristics of the water in the post-WLR period in CR, we would expect that increased richness and change in floristic composition would be directly related to limnological variables. Indeed, the results of the stepwise regression showed that certain limnological variables, if correlated with richness and/or with the scores of the NMDS, could influence species richness and composition.

However, the results of the analyses of partial correlation revealed that the correlation between the limnological variables and the response variables (richness or scores of NMDS) were not altered by the WLR in the reservoir. Therefore, the limnological variables indicated by stepwise regression cannot be considered direct predictors of increase in species richness and changes to floristic composition due to WLR.

This inference allows us to establish an important assumption for future studies of environmental explicative predictors of biological processes of aquatic macrophytes: the functional relationship needs to be removed from the statistical relationship between limnological variables and the response variable. Under certain situations, the correlation between limnological variables and the response variable (pattern or biological process in question) is only statistical, and thus not related to the ecological question of the study. The need to understand the statistical and functional relationship between environmental variables and response

variables, aiming to the choice of environmental predictors has already been reported by [34] for tree species.

Due to the inexistence of a direct relationship between limnological variables and variation of ecological attributes (richness and floristic composition) post-WLR of CR, we considered that changes in the processes of interespecific interaction (especially competition) have influenced the variation in these ecological attributes. It is known that changes in the limnological characteristics caused by WLR favor whatever species are best adjusted to the new environmental condition [2, 33]. These changes alter the processes of interespecific interaction that, on the other hand, act in structuring the aquatic vegetation [13, 14]. In this context, the relationship of the limnological characteristics with the change in structure of the post-WLR aquatic macrophyte community becomes indirect, and the processes of interespecific interaction become the preponderant factors.

The results of cover of the species confirm the aforementioned inferences. The post-WLR reduction of cover of the weeds *E. crassipes*, *P. geminatum* and *S. auriculata* in CR indicates their disadvantage in physical competition and/or in utilization of resources. The new records of *E. densa*, *L. leptocarpa* and *L. helminthorriza* linked to increase in the cover of *C. odoratus* and *O. cubense* in the post-WLR period indicate their better adjustment to the new limnological conditions in CR.

The rapid filling and the historically unprecedented outflow of CR have lead us to assume that this event can be considered an intermediate disturbance and, therefore, the biological processes of the aquatic macrophytes could be explained by the intermediate disturbance hypothesis (IDH) [35]. According to this theory, after an intermediate event of alteration of the normality of the environmental conditions, the processes of interespecific interaction are modified, allowing the replacement or coexistence of species. Thereby, new species can colonize these environments, maximizing the richness in the ecosystem. Some researchers associate the IDH not just with a simple understanding of coexistence between species, but to a set of phenomena arising from various mechanisms of coexistence [36]. Anyway, the results of plant cover corroborate the IDH in CR and enhance the inference that interespecific interaction can restructure the aquatic macrophyte community in environments under WLR.

The limited variation in species richness and composition among the four sampling expeditions in the post-WLR period in CR suggests that this type of event could definitively restructure the aquatic vegetation. We believe that this restructuring is derived from increased potential niches and greater complexity of interespecific relationships [10, 12-15].

5. Conclusions

In synthesis, the results of our study suggest that limnological changes derived from WLR indirectly influence the structuring of aquatic macrophyte communities. Our results suggest that the limnological changes in CR interfere in the processes of interspecific competition and,

consecutively, lead to an increase in species richness and a change in species composition. In the case of rapid WLRs (e.g., what occurred in CR), the ecological processes of the aquatic macrophyte communities can be explained by the IDH, and they can definitively restructure the aquatic vegetation.

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