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Original Paper

Phylogenetic structure of aquatic plant assemblages in a climate sequence

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Abstract

Floristic studies of aquatic plants and flora associated with aquatic ecosystems carried out in the Neotropical region have demonstrated the predominance and co-occurrence of the same plant families under different climatic conditions. One way to interpret this co-occurrence of groups with non-random patterns in assemblages is to understand their phylogenetic structure. Herein, we present an investigation that studied the rule of phylogenetic assembly on plants associated with reservoirs in a tropical climosequence in Northeast Brazil. We studied eight areas during the dry and rainy periods and characterized their climatic, chemical, and trace elements, as well as richness, diversity, and phylogenetic structure of their assemblages. We found a predominance of the families Fabaceae, Poaceae and Cyperaceae, especially in border areas. Among the species surveyed, we highlight those with amphibian life-form, autochoric-type dispersion syndrome and the taxa with patterns of wide geographical distribution. We observed that the seasonal effect ruled patterns of phylogenetic structure with tendency for non-co-familiarity. Water quality and sediment were the abiotic factors most efficient as predictors of richness and variations in phylogenetic metrics. In this sense, the family co-occurrence identified in the assemblages was less deterministic than expected through non-randomness, because temporally, guilds were distinctly structured in function of seasonality.

Key words: environmental chemistry, heliophytes, hydrophytes, phylogeny.

Resumo

Estudos florísticos de plantas e floras associadas a ecossistemas aquáticos realizados na região Neotropical têm demonstrado a predominância e coocorrência das mesmas famílias de plantas em diferentes condições climáticas. Uma forma de interpretar essa coocorrência de grupos com padrões não aleatórios em assembléias é entender sua estrutura filogenética. Aqui, apresentamos uma investigação que estudou a regra de montagem filogenética em plantas associadas a reservatórios em uma climosseqüência tropical no nordeste do Brasil. Estudamos oito áreas durante os períodos seco e chuvoso e caracterizamos seus aspectos climáticos, fatores químicos e elementos-traços, bem como a riqueza, diversidade e estrutura filogenética de suas assembleias. Encontramos predominância das famílias Fabaceae, Poaceae e Cyperaceae, principalmente nas áreas de borda. Dentre as espécies levantadas, destacamos aquelas com forma de vida anfíbia, síndrome de dispersão do tipo autocórico e táxons com padrões de ampla distribuição geográfica. Observamos que o efeito sazonal governou padrões de estrutura filogenética com tendência à não co-familiaridade. A qualidade da água e o sedimento foram os fatores abióticos mais eficientes como preditores de riqueza e variações nas métricas filogenéticas. Nesse sentido, a coocorrência familiar identificada nas assembléias foi menos determinística do que a esperada pela não aleatoriedade, pois temporalmente as guildas se estruturaram distintamente em função da sazonalidade.

Palavras-chave: quimica ambiental, heliófitas, hidrófitas, filogenia.

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Introduction

Floras associated with aquatic environments present co-occurrence of the same taxonomic groups, since the structure of their assemblages tends to repeat similarly throughout time (Boschilia *et al.* 2008) and space (Padial *et al.* 2008; Machado-Filho *et al.* 2015). This disagrees with the claim that biodiversity is determined from ecologically equivalent groups, which vary in a seasonal-spatial continuum under the influence of environmental conditions (Whittaker *et al.* 2001; Willig *et al.* 2003).

Although environmental conditions directly influence the composition of aquatic taxa (Bornette & Puijalon 2011) and the edges of these ecosystems (Machado-Filho *et al.* 2015), phylogenetic methods have been used to understand unexpected patterns in these plant assemblages (Gotelli & McCabe 2002; Les *et al.* 2003; Ackerley 2009; Flynn *et al.* 2011; Genung *et al.* 2014). In this context, the evolutionary approach has been incorporated into the community approach, advancing knowledge about phylogenetic structure (Webb & Donoghue 2005; Webb *et al.* 2008; Gerhold *et al.* 2015). Studies on the phylogeny of communities can help to better understand spatial co-occurrence patterns (phylogenetic redundancy) and low temporal variability (phylogenetic maintenance) in assemblies, even for floras associated with aquatic environments.

In general, investigations that hitherto dealt with patterns of diversity and structure of assemblages of strictly aquatic and border region plants from springs, were based on floristic and phytosociological surveys of richness, diversity, and abundance related to environmental variables (Matias & Nunes 2001; França *et al.* 2003; Terneus 2007; Peralta-Peláez & Moreno-Casasola 2009; Moreno-Casasola *et al.* 2010; Durán-Suárez *et al.* 2011; Kilca *et al.* 2011; Pereira *et al.* 2012; Machado-Filho *et al.* 2015). In addition, when analyzing their floristic lists it is apparent that these results refer to the non-random taxonomy and co-occurrence of the same plant groups (Mouillot *et al.* 2005; Boschilia *et al.* 2008).

The present study aimed to understand how environmental variables (climatic-geographic, water quality, and sediment) act in explaining co-occurrence and phylogenetic aggregation/dispersion of assemblages of truly aquatic plants and from the border of water bodies in a climosequence (humid-semi-arid) during periods of drought and rain. We hypothesized that (i) seasonality does not influence phylogenetic relationships, and (ii) there is a phylogenetic adjustment between the taxa forming these assemblages, which contributes to phylogenetic conservation.

Materials and Methods

Study area

The study was carried out in areas containing eight artificial water bodies, used for multiple activities including public water supply, in the state of Paraíba, northeastern Brazil and are located as follow: Marés (07°06’55”S, 34°51’40°W), Araçagi (06°50’51”S, 35°22’55”W), São Salvador (07°05’39”S, 35°13’58”W), Epitácio Pessoa (07°28’49”S; 36°08’02”W), Estado (07°03’27”S, 36°21’47”W), Camalaú (07°53’10”S, 36°49’25”W), Capoeira (07°05’19”S, 37°27’23”W) and São Gonçalo (06°46’4”S, 38°12’36”W). The water bodies were categorized into regions (or sectors) according to their geographic location aiming at inferring a climosequence: Littoral (L), always humid climate under the influence of the Atlantic Ocean; Borborema (B), high altitude with dry climate in summer, and Sertão (S), continental with dry climate in summer (Fig. 1).

Environmental climate information (average air temperature, average precipitation, average insolation, average air humidity), reservoir volume and continentality (smallest distance from sea level to each reservoir) (Tab. S1 available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>) for 2014 and were based on websites of the Executive Agency for Water Management of the state of Paraíba - AESA (2015), Climate-Data.Org (2015) and Cidade-Brasil (2015).

Data collection and organization

We collected botanical material during the period of October 2013 and December 2014, collecting from both periods of drought and rain. In each area two collections data were carried out in the dry period and two in the rainy season. Samples were collected from the water bank margins from 2 meters in the direction of water and 1 meter in the direction of mainland, and all plants within the sample perimeter were collected, including herbaceous and arboreal individuals in juvenile stages. This sampling followed the standard floristic methods of collecting material only in the fertile stage (presence of flower/fruit). The collections were always carried out on the same banks, but along the entire water body. Collection and herborization procedures were based on Bridson & Forman (2004), during the collection, the habit and life-form of the specimens were recorded.

Species identification was mainly based on specialized literature, as well as through comparisons with samples available in herbariums (EAN) and consultation with IPA specialists (acronyms according to Thiers, continuously updated). Those collected were incorporated into the IPA collection and duplicates expressed in the herbarium of the Center for Rural Health and Technology (CSTR, not indexed) of the Federal University of Campina Grande. The vouchers used to verify the identification of the collected botanical material are available on the species project platform link (CRIA 2017), with registration numbers 89421-99446 (IPA).

The botanical families were systematized according to the Angiosperm Phylogeny Group - APG IV (2016) and species names and authors were consulted in The Plant List database (2015).

Life forms of the species were designated according to Scuthorpe (1967) and the dispersion syndromes *sensu* Van del Pijl (1982) were based on the morphological description of the respective diaspores from field observations, consultation with specialized literature, or from the information contained on exsiccate labels in the PEUFR, IPA and EAN herbarium collections. To determine the geographic distribution of the taxa, in addition to specialized literature, the following websites were consulted: Global Biodiversity Information Facility (2015), Global Invasive Species Data Base (2015), JSTOR (2015), and Plant Science, a database of tropical plants at the Missouri Botanical Garden (Tropicos 2013).

Concurrently with the collections of botanical material, we collected water and sediment samples one in the dry season and the other in the rainy season following the sampling methods described in APHA (2005). The water samples (1.5 L) were collected subsurface of the top layer of water and stored in a polypropylene bottle. Sediment samples from each body of water

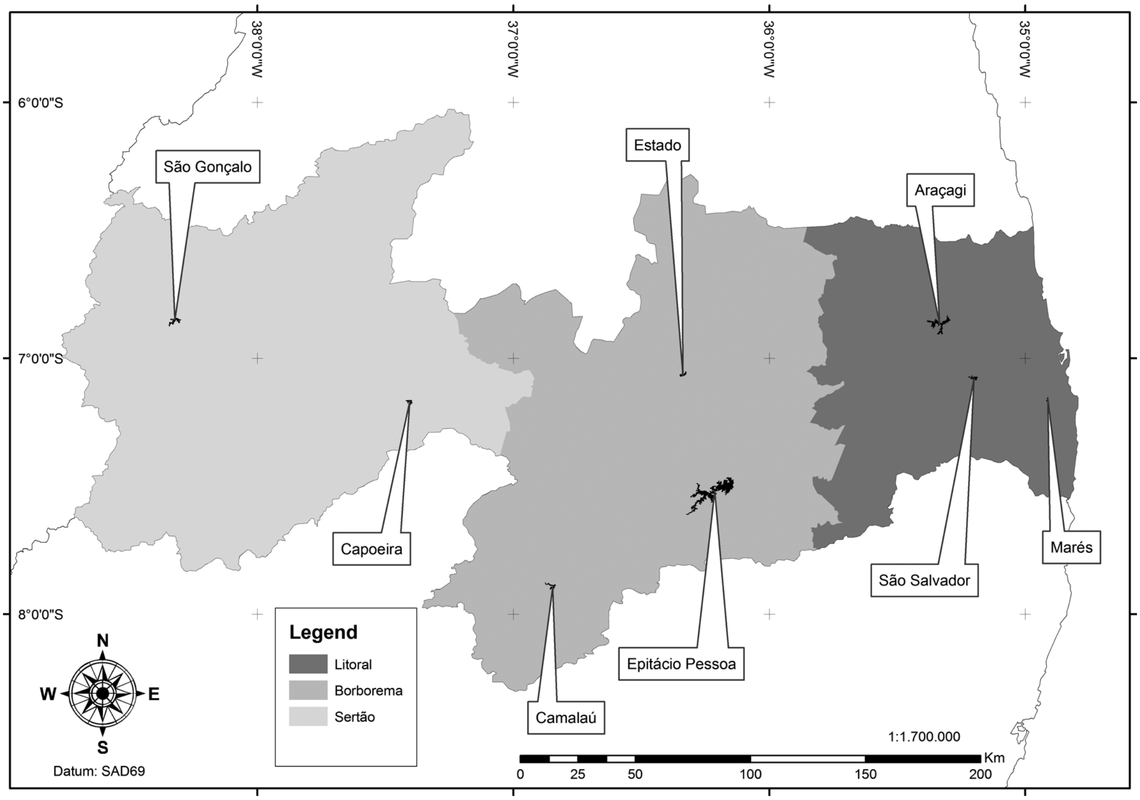

Figure 1 – Areas of study and climosequence analyzed in this study.

were compositely obtained, with three samples of 1 dm³ of sediment collected at random and at approximately equivalent distances, afterwards they were mixed into a single sample, which were stored in a dark plastic bag and transported to laboratory where they were refrigerated until processing.

Chemical and trace elements were measured in the water and sediment samples: pH (benchtop potentiometer - Analyzer), conductivity (benchtop conductivity meter -Analyzer), total nitrogen, total phosphorus, total organic carbon, calcium, magnesium (titulometry), all following the methods described in APHA (2005). The trace elements analyzed were: cadmium, copper, barium, manganese, lead, chromium, antimony, nickel and zinc - extracted by the 3051A method (USEPA 1998).

Calculation of phylogenetic metrics

We created a regional super-tree of kinship relationships of all the species identified in the eight reservoirs using the Phylomatic v.3 application (Webb & Donoghue 2005), from the most resolved phylogenetic tree of *Methaphyta* (R20120829), and formatted in newick. The internal nodes of the cladogram were calibrated through the Bladj algorithm in the Phylocom program (Webb *et al.* 2008), according to the age estimates considered by Bell *et al.* (2010). The cryptogamic taxa were excluded from these analyzes, since APG IV (2016) was used as an ancestral tree model. Afterwards, other trees were constructed corresponding to the plant assemblages in the dry/rainy periods, using the same procedures that constructed the regional super tree.

Phylogenetic diversity (DF) values were calculated using 999 permutations, which produced a theoretical null model through Phylocom (Webb *et al.* 2008). For the assemblages studied, we calculated the diversity metrics Mean Pairwise Distance - MPD - and Mean Nearest Taxon Distance - MNTD - and phylogenetic structure Net Relatedness Index - NRI - and Nearest Taxon Index - NTI (Webb *et al.* 2008), as well as the richness of the reservoirs. The MPD metric shows the average phylogenetic diversity, MNTD explains the species rate by genus, NRI indicates trends in aggregation (positive values) or dispersion (negative values) of the taxa in the assemblage, and NTI clarifies if the species tend to be more co-familiar (positive values) or not (negative values).

Statistical analysis

At first, the data were evaluated using the Shapiro-Wilk test. Then, we performed a factorial analysis (a + b) of variance (ANOVA) on the predictor variables and on the richness and phylogenetic metrics to test the seasonal (dry / rainy) and spatial (Coast / Borborema / Sertão) variation and then verified possible differences between spatial categories we used the Tukey test. In these steps we use the functions lm and aov in the R program. All climatic and physicochemical variables were tested for the dry and rainy seasons.

In order to select the predictor variables and their possible effects on the explanation of the phylogenetic richness and metrics, we utilized a Generalized Linear Model (GLM) test (McCullagh & Nelder 1989), which selected the most explanatory parsimonious models (AIC), as well as its explicability (R^2). For this test the Gaussian family was used for continuous data, such as MPD, MNTD, NRI and NTI, and the Poisson family for discrete data, such as richness. In the GLM analysis, the R package used was glm.

We used three separate GLM models (climatic-geographic, sediment, and water), since the number of cases ($n = 16$) was lower than the number of predictor variables tested (34), which made using a single model impossible.

Using the NRI and NTI phylogenetic structure metrics, we tested our hypotheses of this investigation, because as environmental selective pressures change the aggregation/phylogenetic dispersion and composition of coinciding families, it is inferred that the assemblages are conserved or change throughout time and space. With these analyzes we could verify if there was a significant difference between the assemblages temporally (rain and dry season), thus testing our first hypothesis, and spatially (different regions - Litoral, Borborema and Sertão), thus testing our second hypothesis. Both statistical procedures were performed for each context (special and temporal).

All statistical analyzes were performed in the program R (v.3.3.0).

Results

Abiotic variables

The water quality and sediment data did not show significant seasonal variations ($p > 0.05$). Only the climatic-geographical characteristics presented significant variation ($F = 35.47$, $R^2 = 0.71$, $p < 0.001$). The results of the ANOVA test

(Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>) confirmed that climatic and geographic parameters were significant for seasonal changes and spatial categories, with the exception of the volume of water bodies, which did not show significant spatio-temporality.

The average results of the chemical analysis for water and sediments in the reservoirs, in the dry and wet seasons, are presented in Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>.

Richness

The floristic survey resulted in the identification of 223 species (Tab. S3, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>), distributed in 152 genera, 50 families, and 23 orders. The families with the highest species richness were: Fabaceae (37 spp.), Poaceae (31 spp.), Cyperaceae (24 spp.), Asteraceae (15 spp.), Malvaceae (13 spp.), Amaranthaceae (11 spp.), Convolvulaceae (nine spp.), followed by Rubiaceae and Onagraceae (six species each), Commelinaceae (five spp.) and Polygonaceae (four spp.). All the other families (20% of the total) presented from one to three species each.

In relation to the regional pool of species, the richness sampled represents 57% of the species already cataloged for the state of Paraíba. In relation to the distribution of the richness in the different regions, 107 species were identified in the Litoral region (47 spp in Araçagi, 38 spp in São Salvador, and 22 spp in Marés), 123 species in the Borborema region (56 spp in Camalaú, 51 spp in Epitácio Pessoa, and 16 spp in Estado), and 96 species in the Sertão region (43 spp in São Gonçalo and 53 spp in Capoeira).

The most representative life-form was amphibian, presenting 180 species (91%), followed by aquatic life- forms *stricto sensu* immersed (3%), free floating (3%), fixed submerged (2%) and fixed floating (1%). The free submerged life form was not recorded. Regarding the dispersion syndromes, 55% autochoric species were observed, followed by 27% anemochoric, 11% zoochoric, and 7% hydrochoric.

We found the registered taxa were 24% cosmopolitan, followed by 21.5% pantropical, 17% neo-tropical, 9.4% endemic to the Caatinga/Cerrado region of Brazil, 8.5% had an uncertain distribution (species identified to genus or disjointed distribution), 8% occurred only in South America, 7.6% were disjoint with a Gondwanian distribution, and 3% occurred throughout the Americas.

The richness did not show significant variation for the climosequence or for the dry and rainy periods (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>). Compared to GLM models generated with richness and phylogenetic metrics, the richness equations had higher AICs, and were less parsimonious in climate-geographic and water models. The greatest explanations of richness were influenced by sediment attributes ($R^2 = 0.79$) and water quality variables ($R^2 = 0.86$) (Tab. S4, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>).

Phylogenetic metrics

The increase or decrease in the mean phylogenetic diversity (MPD), species rate by genus (NTMD), phylogenetic aggregation or dispersion (NRI) or co-familiarity (NTI), in terms of seasons, presented more randomized results than expected by chance (Tab. S5, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>). The ANOVA test (Tab. S5, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>) did not show any significant variation throughout time or space for any of the phylogenetic metrics evaluated.

The effect of seasonality seems to have caused a conspicuous decrease in phylogenetic diversity during the rainy season in the Littoral, whereas in other regions the seasonal effect did not cause a great variation in the MPD metric. The MNTD metric increased the distance between closely related species in the rainy season in the Littoral, decreased in the dry season of the Borborema, and remained stable in the Sertão region. No defined trends were observed for spatial or seasonal phylogenetic aggregation or dispersion, since the expected pattern for this metric was more random than desired. Finally, the NTI metric showed an association between the more subordinate taxa for the same families, which were more frequent in the dry period (Fig. 2).

The most parsimonious predictive models (lower AIC values) generated in GLM analysis indicated that water quality had greater explanatory power for MPD ($R^2 = 0.999$), MNTD ($R^2 = 0.894$) and NTI ($R^2 = 0.894$), followed by models of sediment and climatic-geographic characteristics (Tab. S4, available on supplementary material <https://doi.org/10.6084/m9.figshare.21357501.v1>). Only the NRI metric ($R^2 = 0.989$) was explained more parsimoniously by the sediment.

Discussion

In view of our two suggested hypotheses, we can verify that: first hypothesis was rejected, as seasonality influences the formation of different floristic guilds, that is, groups of species that are related more remotely than by chance; in relation to the second hypothesis, the phylogenetic maintenance of the groups in relation to the temporal factor was not observed, although spatially certain species co-occur, this low similarity does not interfere in the phylogenetic structure in assemblage.

Our results indicated that the Fabaceae, Poaceae, Cyperaceae and Asteracae families were the most diverse among the assemblages of plants, which corroborates with other surveys from the Neotropical region (Padial *et al.* 2008; Machado-Filho *et al.* 2014, 2015). Although anemochoric diaspores are the most expected, based on registered families (Van der Pijl 1982), this study observed that autochoric species predominated, that is, with less dispersal mobility, most species have a wide geographic distribution, and that they should probably establish mutualistic dispersal strategies with several animals (Bascompte & Jordano 2006).

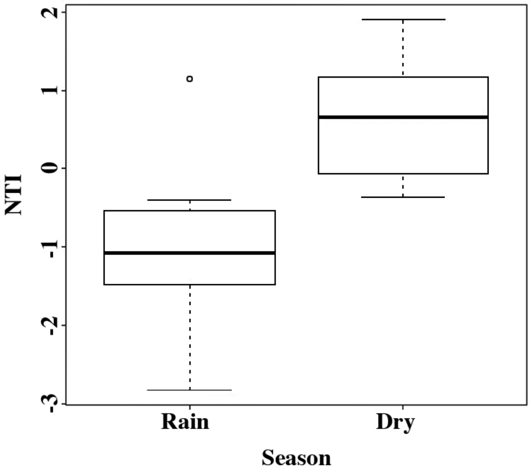

Figure 2 – Seasonality and Nearest Taxon Index (NTI) in the analyzed assemblages.

Agents of dispersion evolved along with the angiosperms about 180 million years ago, which resulted in different dispersion strategies (Vander Wall & Longland 2005). These strategies may, in some cases, involve two or more scatter periods. Due to this, the historical reconstruction of these events can be determined through several factors, such as time and anthropic interference (Robledo-Arnuncio *et al.* 2014).

Herein, the majority of species registered with amphibian life form are interesting when considering assembly rules, since the proportion of aquatic taxa *stricto sensu* is not very significant (9% in total). This fact leads us to believe that tropical aquatic ecosystems are composed of species that preferentially inhabit flooded or shallow regions at the border of water sources because they present specific homoplasias (Armstrong *et al.* 1994; Braendle & Crawford 1999), or are opportunists that easily obtain water and nutrients (Sabino *et al.* 2015) or, probably, because they encounter potential dispersors (Charalambidou *et al.* 2005; Correa *et al.* 2007). Furthermore, the amphibian habit also offers the advantage of greater mobility in the terrestrial landscapes, which causes a vicarious effect on the aquatic plants *stricto sensu*.

Our results also indicate that seasonality interferes with the phylogenetic structure of these assemblages, since different family guilds are formed by the seasonal changes of drought and rain, eliminating the idea of "taxonomic redundancy" for these groups of plants.

In spatial terms, "taxonomic redundancy", as seen in surveys of floristic listings for these types of assemblages analyzed, was observed through the MPD phylogenetic diversity metrics. Such redundancy could be related to the fact that a large number of the species have wide geographical distributions and, as these groups are well distributed, could have reflected in the results of close MPD. This data is very important, as it suggests that climatic gradients (that is, larger scale; atmospheric temperature and annual precipitation) select organisms that must present functional traits corresponding to environmental conditions, and then these assemblages are once again selected now by environmental characteristics (that is, smaller-scale substrate characteristics or water quality). This is what we saw when we analyzed the environmental and physicochemical and oligochemical parameters.

This characteristic of "taxonomic redundancy" was not observed throughout time, since our results indicated non-random orientations greater than expected by chance and in relation to the seasonality in the assembly rule of the assemblages analyzed. Contrary to our hypothesis, the NTI metrics showed formations of family guilds organizing themselves in distinct ways, specific to the dry season (generating greater co-familiarity) and rainy season (gathering other botanical groups). An example of this was the group of annual herbaceous plants surrounding the water bodies, which are often not present during the dry season, especially in the Sertão region.

The so-called "phylogenetic adjustment" (evoked as an amortization effect to conserve the structure of these types of plant assemblages, by replacing more evolutionarily related species with one another when their closest relative "disappears") was not perceived in the analysis since the seasonal disturbance caused substitution of taxa by phylogenetically distant taxa. Plants located in water-land transition regions behaved differently from that observed by Webb (2000), since the trend towards phylogenetic aggregation was more associated with the rainy season when the terrestrial region was flooded.

Regarding the effect of seasonality on plant assemblages, the majority of studies that address this theme are related to biomass parameters (Hrivnák *et al.* 2009; Kufner *et al.* 2011) or abundance of species (Guridi *et al.* 2004; Durán-Suárez *et al.* 2011), neglecting relative changes in the composition and structures of these assemblages. This is interesting because, among the most investigated strategies to detect patterns in biodiversity, there is the search for substitute groups which represent patterns of variation of species richness (Allen *et al.* 1999), and our results indicate that the effects of seasonal disturbance potentially govern distinct family groupings in the dry and rainy periods.

Herein, the most parsimonious explanatory models of the relationships between predictor variables, richness, and phylogenetic metrics showed that water quality parameters (nutrients and trace elements) and sedimentological parameters were the most important factors in explaining the assembly rules. In this sense, several investigations have attempted to explain the richness of aquatic plants, mainly through the relationship between the water quality of the environment (França *et al.* 2003; Terneus 2007; Peralta-Peláez & Moreno-Casasola 2009; Moreno-Casasola *et al.* 2010; Durán-Suárez *et al.* 2011; Pereira *et al.* 2012) and the sediment attributes (Clarke & Wharton 2001; Costa & Henry 2010; Kissoon *et al.* 2015).

The GLM estimation analysis strongly suggested that the oligochemical attributes of the sediment are more related to the phylogenetic assembly rules than to the water quality conditions. This needs to be explored in future studies. The results of this work can serve to establish a preliminary geochemical prognosis of some reservoirs in Paraíba, since we verified seasonal changes in the phylogenetic structure of the assemblages strongly associated with sediment attributes. As few studies have evaluated the environmental toxicity caused by the presence of trace elements in the environment directly influencing aquatic spermatophyte plants (Küpper *et al.* 2007; Vardanyan *et al.* 2008), there is a lack of establishing an environmental quality standard for tropical freshwater sediments, this ecotoxicological effect is not yet fully clarified.

Finally, the climatic-geographic model showed little explanation about phylogenetic variables. Several researchers have already discussed the importance of these variables on productivity (Mulholland *et al.* 1997; Santamaria & Van Vierssen 1997) and the trophic degree (Mckee *et al.* 2002) for these freshwater ecosystems. However, our results indicated that these climatic-geographic features did not explain the biological variables analyzed, since these taxa are widely distributed geographically and are already well adapted to several climatic ecotypes. The natural history of the ancestors of these taxa, which emerged and developed in arid and warm climates and were later modified by several climatic changes throughout the past 65 million years (Soltis & Soltis 2004), can explain this model in which climate/geography does not impose a barrier on the phylogenetic assembly rule in these assemblages of tropical plants.

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