Spatiotemporal ecological drivers of an aquatic plant community in a temporary tropical pool

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ABSTRACT

Ecological processes that extend over time and space organize plant communities, producing different spatiotemporal patterns of species aggregation (or non-aggregation). To investigate whether the spatiotemporal distribution patterns of the species are generated by interspecific competition and/or environmental filtering, we investigated the organization of an aquatic plant community in a temporary pool in the semiarid region of NE Brazil. For seven months (during the rainy season), we sampled aquatic plants along transects in the pool and measured limnological parameters. The spatial structure of the community changed significantly over time. The input and permanence of species in the community varied according to the stage of flooding of the pool. This leads to the expectation that the species would have overlapping niches, causing interspecific competition to increase and exclude less efficient competitors. Indeed, we found that the species coexisting in the pool were only slightly phylogenetically related, an evidence of interspecific competition. Therefore, in the temporary pool, the spatiotemporal organization of the aquatic plant community appears to be driven by simultaneous action of ecological abiotic and biotic processes that operate in an antagonistic fashion.

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1. Introduction

Biotic and/or abiotic ecological processes can act in the spatiotemporal organization of plant communities, shaping the community structure through different mechanisms that drive distinct patterns of spatiotemporal species aggregation or non-aggregation (Bullock et al., 2001; Hobbie et al., 2003; Legendre et al., 2010a). These spatiotemporal patterns are formed according to the species that are established in the community, which interact with one another and the environment, in events that are made possible when the habitat persists for a sufficient time for alternating populations to exist (Jocqué et al., 2007). Inter-specific relations that arise as species respond to environmental variations inherently depend on their evolutionary histories (Losos, 1996; Webb et al., 2002; Cavender-Bares et al., 2006; Kembel and Hubbell, 2006; Ives and Helmus, 2010). As phlyogenetically related species might have similar niches, they should not occur at the same time and space to avoid competition. However, phlyogenetically related species that exhibit similar ecophysiological requirements should coexist in the same space and time if they share the same limiting environmental factors (Webb et al., 2002).

To investigate the ecological processes underlying the spatiotemporal patterns of density and diversity in plant communities, it is essential to monitor trends in the variation of the abundance of individuals and species richness through the space and time. Concerning this proposal, temporary aquatic plant communities in seasonal pools represent, unlike perennials, a more feasible model for monitoring the entire process of community organization during a short favorable season. In general, temporary aquatic plant communities develop in locations where the environmental conditions can vary greatly over short periods. This requires that species are able to respond to environmental changes in a short time

and, consequently, results in rapid evolution of dynamic stages (Van der Valk, 1981; Gawne and Scholz, 2006). A good example of this dynamic are the aquatic plant communities that grow abundantly in temporary tropical pools during the short period when water is available (Casanova and Brock, 2000; Coops et al., 2003; Gawne and Scholz, 2006; Tabosa et al., 2012). Due to the seasonal climate, temporary tropical pools have an annual cycle of flood and drought, which causes extreme variations in the quantity and quality of water (Schefer and Jeppesen, 2007; Schefer and Van Ness, 2007).

In the temporary tropical pools, the initial flooding triggers species dynamics through germination from seed bank or resprouting from underground structures. Initially, density and diversity of the aquatic plants increase, but the always-changing water conditions lead to fast dynamics, which are maintained until the end of the desiccation period. Throughout the lasting of the temporary pool, the operation of environmental filters and/or competition alters the relationships of dominance among the species (Maltchick and Pedro, 2000). Towards the end of the rainy season, the water depth of the pool decreases, causing variation in important limnological parameters for aquatic plants, e.g., salinity and turbidity, which can render the aquatic environment less favorable for species development (Van der Valk, 1981; Gawne and Scholz, 2006; Schefer and Jeppensen, 2007; Schefer and van Ness, 2007). Furthermore, the competition strategies of aquatic plants are quite different from each other when they are under different environmental conditions (Gopal and Goel, 1993).

In this study, we followed the dynamic stages of an aquatic plant community in a temporary tropical pool in the semiarid region of Brazil to answer the following questions: (1) Do the species spatial distribution patterns significantly change along the duration of the temporary pool? (2) If so, what ecological processes, abiotic (environmental filtering) and/or biotic (competition), shape the community structure over time? Our hypothesis is that the spatiotemporal distribution of the aquatic plants in the pool is determined by the interaction of interspecific competition and environmental filters, since water varies over time in quantity and quality. We believe that during the desiccation of the pool the physicochemical changing of the aquatic environment could act as an agent of species selection, favoring different taxa in different dynamic stages. Besides, we also expect that interspecific competition, such as for water and space, becomes more intense over time, gradually limiting the co-existence of phylogenetically related species.

2. Material and methods

2.1. Study system

The study was conducted in a temporary pool ($4°11''13.04''$ S and $39°06''11.75''$ W), locally called Contendas pool, municipality of Caridade, state of Ceará, in the semiarid region of northeast Brazil, which is characterized by a strong seasonal climate. The regional climate is Koeppen's Bsh; semiarid, hot, with average temperature of the coldest month >18 °C and erratic rainfall that historically averages a total of 700 mm/year (Alvares et al., 2014). Due to high temperatures the entire year long, the evapotranspiration is generally twice or more the rainfall (Nimer, 1972). The pool has a rough area of 4.57 ha, and a perimeter about 923 m. The duration of the wet phase of the pool depends on the rainfall in each year, but historically it occurs from March to September (Fig. 1). The soil is predominantly stony and shallow (Litholic Neosol), and the maximum water depth in the center of the pool is 1 m at the peak of the wet phase. The life forms of the predominant species in the pool are therophytes and cryptophytes, which present themselves as plants rooted with floating leaves, emersed and, with a lower proportion, totally submerged (Tabosa et al., 2012). We sampled the pool over seven monthes, between March and September, since the beginning of the expansion until the complete contraction of the pool. During this period, we conducted thirteen surveys at fortnightly intervals. Fifteen parallel transects equally spaced at 15-m intervals were established from the margin to the center of the pool. Along each transect, we settled 20 equidistant sampling points at 10 m intervals. The aquatic plants were sampled using the point or needle method. At each sampling point, a needle (3 mm in diameter) was fixed with a bubble level to avoid tilt, and the plant species touched by the needle and the number of touches in each plant were recorded. We used the cover index (CI, Mantovani and Martins, 1990) to quantify the species abundance. The cover index of a species is the result of the sum of the absolute frequency (number of touches of the needle) and the absolute vigor (the ratio between the number of touches of the needle and the total number of sampling points).
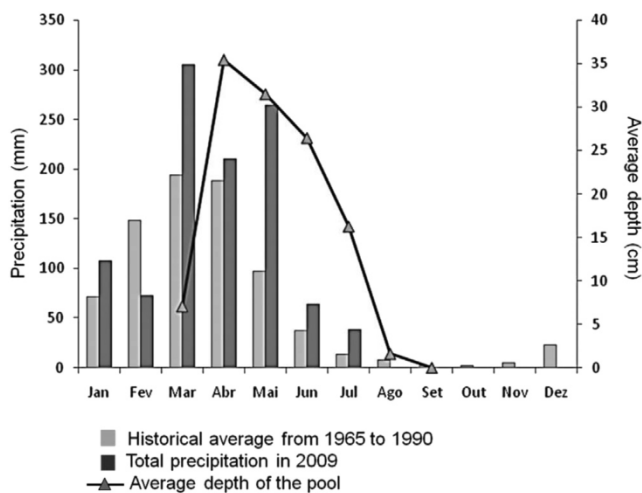
2.2. Description of the limnologic system

We described the aquatic environment through the limnological parameters alkalinity, conductivity, biochemical oxygen demand (BOD), total phosphorus, dissolved oxygen (DO), pH, nitrate, total nitrogen, and turbidity. We accepted that the rapid variation of these parameters over the desiccation of the pool could impose limits to the establishment and development of species (Kautsky, 1988). We collected water samples fortnightly at five different points of the pool, being two in the center and three in the edge of the pool. The samples were immediately transported to the laboratory in ice coolers. We measured pH with a Tecnal model Tec – 3mp potentiometer; turbidity with a Policontrol model AP 2000 turbidimeter; and conductivity with a Tecnopon model mCA 150p conductivimeter. These analyzes were performed as soon as the samples arrived in the laboratory. Nitrate concentrations were determined by the sodium salicylate method. We followed the protocol recommended by APHA (1998) to analyze the alkalinity, total phosphorus, DO and BOD, and by APHA (1989) to quantify the total nitrogen.

Fig. 1. Rainfall data of the region of the temporary pool *Contendas*, located in the semi-arid region of Brazil. Historical average precipitation from 1965 to 1990 (Varejão-Sila, 1990). Total precipitation in 2009 (FUNCEME, 2009).

Table 1
Cover index values of the plant species sampled along a temporary tropical pool's span in a semi-arid region in NE Brazil. Sampling trials were performed fortnightly.

Dynamic stage	Species	Sampling time[a]												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Early species	*Angelonia* sp.	1.67	*	*	*	*	*	*	*	*	*	*	*	*
	Croton sp.	1.67	*	*	*	*	*	*	*	*	*	*	*	*
	Digitaria ciliaris (Retz.) Koeler	1.33	*	*	*	*	*	*	*	*	*	*	*	*
	Echinochloa polystachya (Kunth) A. Hitch.	1.33	*	*	*	*	*	*	*	*	*	*	*	*
	Senna sp.	0.67	*	*	*	*	*	*	*	*	*	*	*	*
	Heliotropium elongatum (Lehm.) Willd.	*	2	2.67	*	*	*	*	*	*	*	*	*	*
	Callisia filiformis (Martens & Galeotti) D. R. Hunt.	*	0.67	0.67	*	*	*	*	*	*	*	*	*	*
	Panicum dichotomiflorum Michx.	*	0.67	0.67	*	*	*	*	*	*	*	*	*	*
	Sesbania sp.	1.33	*	0.67	*	1.33	0.67	*	*	*	*	*	*	*
Permanent species	*Echinochloa colona* (L.) Link.	25.3	11.3	7	4	0.67	1.33	1.33	1.33	*	*	*	*	*
	Discolobium hirtum Benth.	*	0.67	1.33	*	2.33	1.33	1.33	2.33	1	0.67	0.67	1.33	1.33
	Eleocharis mutata (L.) Roem. and Schult.	48	27	48.3	38	54	59	58	75	86.7	92	99	83	40.3
	Neptunia oleracea Lour.	6.33	7.66	12.7	8	4	3.67	1.67	2	3.33	4	3.33	2.33	5.67
	Borreria scabiosoides Cham. & Schltdl.	6.33	8.33	6	7.33	8.33	6.33	6	9.33	8.67	7.33	4.67	1	*
	Nymphaea lasiophylla Mart. & Zucc.	3.33	52	80	71	70.7	59.7	62.3	49.3	29.7	10.7	*	*	*
Sporadic species	*Chamaecrista* sp.	1.33	1.33	*	*	*	*	0.67	*	*	*	*	*	*
	Utricularia foliosa L.	1.33	*	0.67	*	3.33	0.67	*	1.33	*	*	0.67	*	*
	Thalia geniculata L.	5.66	*	*	0.67	*	*	1.33	0.67	0.67	0.67	1.33	2	*
	Senna obtusifolia (L.) H.S.Irwin and Barneby	2.33	*	*	*	*	*	0.67	*	0.67	*	*	*	*
	Aeschynomene filosa Mart. ex Benth.	*	*	1.33	0.67	*	*	*	5.67	3.33	8	3.67	2	*
	Eleocharis interstincta (Vahl) Roem. and Schult.	*	*	0.67	*	*	*	0.67	0.67	0.67	2	1.33	*	0.67
	Echinodorus subalatus (Mart.) Griseb.	*	*	0.67	*	*	*	0.67	*	*	*	0.67	*	*
Late species	*Eichhornia heterosperma* Alexander	*	*	*	*	*	0.67	*	*	*	*	*	*	*
	Bacopa aquatica Aubl.	*	*	*	*	*	1.33	2	4.67	8.33	2.67	*	*	*
	Scleria virgata (Nees) Steud	*	*	*	*	*	*	1.33	*	*	*	*	*	*
	Apalanthe granatensis (Humbl. and Bonpl.) Planch.	*	*	*	*	*	*	0.67	0.67	2	4.67	*	*	*
	Hydrocleys martii Seub.	*	*	*	*	*	*	1.33	*	*	0.67	0.67	*	*
	Eleocharis barrosii Svenson	*	*	*	*	*	*	1.33	5.67	4.67	4.67	3.33	*	*
	Paspalum orbiculatum Poir.	*	*	*	*	*	*	0.67	0.67	0.67	*	0.67	*	*
	Utricularia hydrocarpa Vahl	*	*	*	*	*	*	*	0.67	1.33	*	*	*	*

[a] The asterisk (*) indicates that the aquatic plant has not occurred at that time.

2.3. Identifying spatiotemporal patterns

To investigate whether species spatial distribution patterns significantly change along the temporary pool's span, we tested for the presence of spatiotemporal interaction of both the whole community and each species. In this task, we used the algorithm proposed by Legendre et al. (2010a), which performs an analysis of variance of ecological data obtained repeatedly but lacking replicate samples. To solve this problem, the algorithm creates artificial replicates by means of statistical strata taken from neighboring samples. Initially, we computed a matrix of species CI values with 3900 points (15 transects × 20 points × 13 sampling times) and ran the algorithm Model 5, with 999 permutations, implemented in the function STImodels (STI package; Legendre et al., 2010b) for R statistical language v2.15.3 (R Development Core Team, 2008). Interaction is statistically significant when $p < 0.05$.

2.4. Identifying ecological drivers

To assess which ecological processes (abiotic filtering or biotic competition) could more strongly shape the community structure over time, we performed two set of analysis. First, to investigate the role of abiotic filtering, we related the community descriptors to the variation of the limnological parameters. As community descriptors, we considered each species' cover index (CI) in each sampling time and the phylogenetic community dissimilarity (PCD) between consecutive sampling times. The phylogenetic community dissimilarity (Ives and Helmus, 2010) describes the differences between the samples by means of two components: one non-phylogenetic (PCDc) or floristic, which only considers the shared species among the samples; and another phylogenetic (PCDp), which takes into account the phylogenetic relationship among the species that are not shared among the samples. We calculate the PCD, PCD_C and PCD_P using the function *pcd*, available in package *picante* (Kembel et al., 2010) for R statistical language v2.15.3 (R Development Core Team, 2008).

Then, to assess the role of competition, we correlated the degree of co-occurrence of species to the phylogenetic distance among them (Cavender-Bares et al., 2006). If competition is an important ecological spatiotemporal process, then coexisting species should have little or no phylogenetic relationship among them, since, considering the phylogenetic conservatism, the weak kindred would avoid excessive overlapping niches (Webb et al., 2002). On the other hand, if the coexisting species have a closer phylogenetic relationship among themselves, then the assembly of the community could be assumed to have been driven by environmental filters, selecting species with similar physiological and ecological requirements (Webb et al., 2002). We quantified the degree of species co-occurrence by means of the checkerboard measure (Diamond, 1975), which computes pairs of species that do not coexist among different samples. Checkerboard values were correlated to the phylogenetic distances using the function *comm.phylo.cor*, also available in package *picante* (Kembel et al., 2010) for R language. By the one-tailed test, the observed correlation value was considered significant when it fell in the top 5% of the null distribution constructed under 999 randomizations.

2.5. Phylogenetic data

To analyze the community phylogenetic pattern, we constructed a phylogenetic tree for the 30 plant species using the Phylomatic module (Webb and Donoghue, 2005) in the program Phylocom (Webb et al., 2008). Phylogenetic distances (in millions of years) among the taxa were based on the estimated age of the clades as
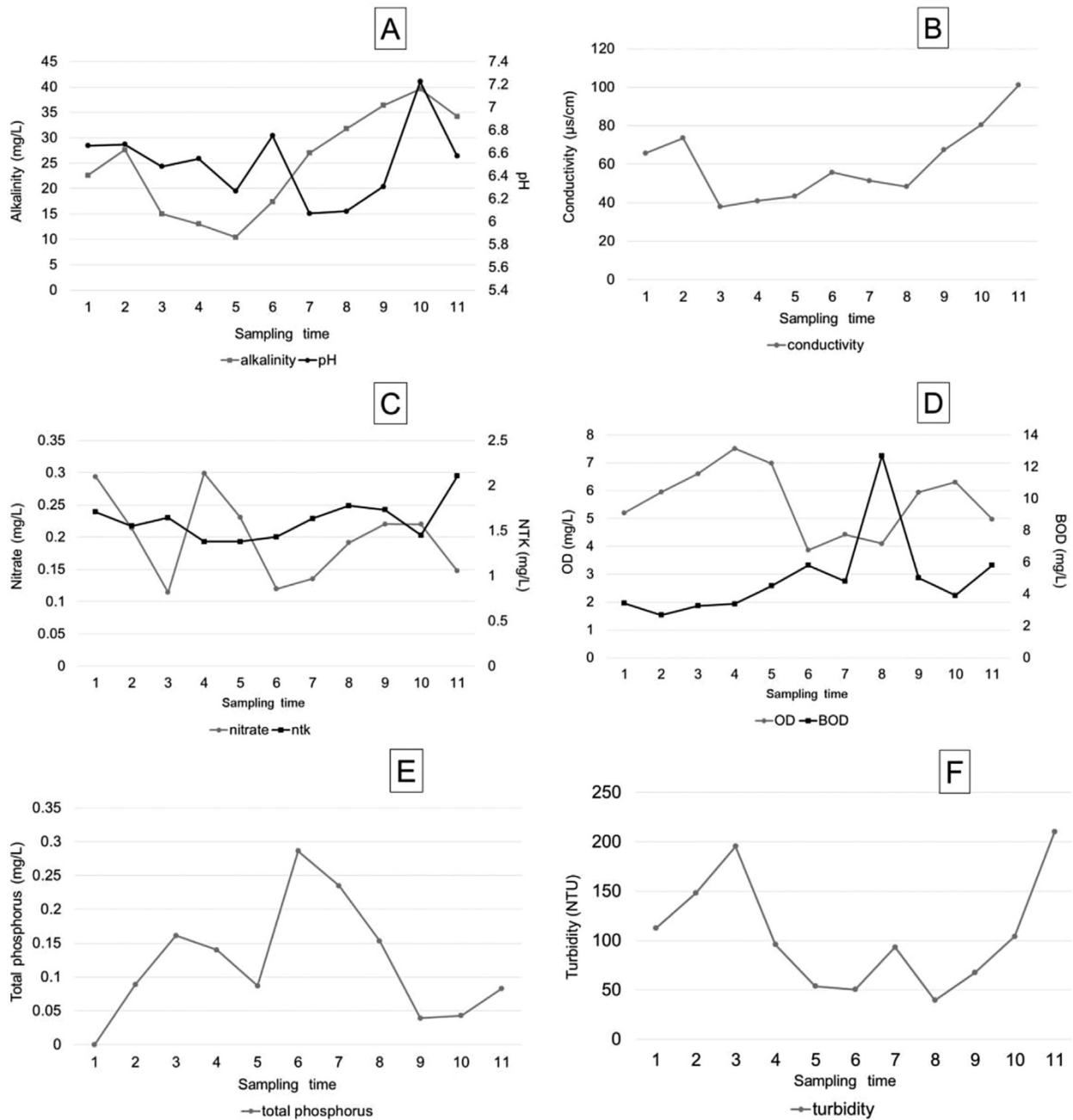
Fig. 2. Variation of limnological parameters in the *Contendas* temporary pool over the period of flood and drying. Alkalinity and pH (A), conductivity (B), nitrate and total nitrogenous-NTK (C), OD and BOD (D), total phosphorus (E), and conductivity (F). In sampling time, from one to six corresponds to the expansion of the pool, seven to 11 corresponds to the contraction of the pool. At 12 and 13 sampling time, there were not water in the pool.

calculated by Wikiström et al. (2001). Where there was no information for a clade, its age was estimated in order to minimize the variation between divisions (nodes) using the bladj algorithm in Phylocom. The Poaceae family showed polytomies that were resolved by distributing the genera into subfamilies according to Teerawatananon et al. (2009).

3. Results

In all 13 sampling trials, we recorded 30 species belonging to 14 families. We classified the species in four categories taking into account the dynamic stage in which they predominated. 1) Initial species were those that appeared at the beginning of the flood and

remained by the first half of the sampling trials. 2) Permanent species were those present during the entire pool's span. 3) Sporadic species appeared and disappeared without regularity at any of the dynamic stages. 4) Finally, late species were those recorded only in the second half of the sampling trials and remained in the community until the pool drying (Table 1).

During the flooding phase of the pool, we observed an increase in the availability of nutrients such as total phosphate, nitrate and total nitrogen (slight increase). During the start and the progress of the drying process of the pool, there was an increase in the concentration of nutrients (nitrogen and phosphate) as well as the conductivity and turbidity again (Fig. 2).

The spatial structure of the community changed significantly

Table 2

Spatiotemporal variation of aquatic plants species in a temporary tropical pool, located in a semi-arid region of Brazil. A significant correlation coefficient (r) indicates that the species has changed its position in the space of the community over time.

Species	r[a]
Aeschynomene filosa	0.23
Angelonia sp.	0.24
Apalanthe granatensis	0.26*
Bacopa aquatica	0.23
Borreria scabiosoides	0.24*
Callisia filiformis	0.26*
Chamaecrista sp.	0.24
Croton sp.	0.23
Digitaria ciliaris	0.41*
Discolobium hirtum	0.25*
Echinochloa colona	0.29*
Echinochloa polystachya	0.35*
Echinodorus subalatus	0.25
Eichhornia heterosperma	0.25
Eleocharis barrosii	0.22
Eleocharis interstincta	0.23
Eleocharis mutata	0.26*
Heliotropium elongatum	0.24
Hydrocleys martii	0.24
Neptunia oleracea	0.24
Nymphaea lasiophylla	0.34*
Panicum dichotomiflorum	0.21
Paspalum orbiculatum	0.23
Scleria virgata	0.25*
Senna obtusifolia	0.23
Senna sp.	0.20
Sesbania sp.	0.25*
Thalia geniculata	0.23
Utricularia foliosa	0.22
Utricularia hydrocarpa	0.24

[a] The asterisk (*) indicates significate values at $\alpha = 5\%$.

Table 3

Multiple correlation coefficients (r) and regression coefficients (b) from stepwise regression with forward selection between descriptors of tropical aquatic plant community and the following limnological variables: alkalinity (alk), conductivity (con), biochemical oxygen demand (BOD), total phosphorus (pho), dissolved oxygen (DO), pH, nitrate (nit), total nitrogen (ntk), and turbidity (tur). PCD = phylogenetic community dissimilarity measure between sampling times. PCDc = composicional component of PCD; PCDp = phylogenetic component. The environmental variable that has recently been added to the model is in bold.

Community descriptor	Limnological variable	r	b[a,b]
Cover index	**nit**	0.46	−0.06
	nit, **con**	0.64	23.32
	nit, con, **pH**	0.66	2.33
	nit, con, pH, **BOD**	0.69	−2.34
	nit, con, pH, BOD, **tur**	0.69	11.24
	nit, con, pH, BOD, tur, **pho**	0.88	15.44
	nit, con, pH, BOD, tur, pho, **alk**	0.98	30.08*
	nit, con, pH, BOD, tur, pho, alk, **OD**	0.99	−376.95*
	nit, con, pH, BOD, tur, pho, alk, OD, **ntk**	0.99	−193.27
PCD	**OD**	0.33	0.01*
	OD, **tur**	0.38	−0.03*
	OD, tur, **nit**	0.41	0.01*
	OD, tur, nit, **BOD**	0.41	−0.01
	OD, tur, nit, BOD, **alk**	0.45	−0.1*
	OD, tur, nit, BOD, alk, **ntk**	0.47	0.02
	OD, tur, nit, BOD, alk, ntk, **pH**	0.47	0.69
	OD, tur, nit, BOD, alk, ntk, pH, **con**	0.47	−0.14
	OD, tur, nit, BOD, alk, ntk, pH, con, **pho**	0.48	0.33
PCDc	**OD**	0.28	0.01*
	OD, **nit**	0.35	−0.08*
	OD, nit, **alk**	0.4	0.01*
	OD, nit, alk, **ntk**	0.4	−0.02
	OD, nit, alk, ntk, **BOD**	0.41	−0.09
	OD, nit, alk, ntk, BOD, **pH**	0.42	0.01
	OD, nit, alk, ntk, BOD, pH, **tur**	0.43	0.714
	OD, nit, alk, ntk, BOD, pH, tur, **con**	0.44	−0.09
	OD, nit, alk, ntk, BOD, pH, tur, con, **pho**	0.45	0.34
PCDp	**tur**	0.5	−0.01*
	tur, **com**	0.5	0.11*
	tur, con, **OD**	0.52	0.02
	tur, con, OD, **pH**	0.57	0.02*
	tur, con, OD, pH, **alk**	0.57	−0.01*
	tur, con, OD, pH, alk, **nit**	0.58	−0.05*
	tur, con, OD, pH, alk, nit, **ntk**	0.58	−0.02*
	tur, con, OD, pH, alk, nit, ntk, **pho**	0.58	−0.02*
	tur, con, OD, pH, alk, nit, ntk, pho, **BOD**	0.59	0.11*

[a] In multiple regression, the direction of the relationship between the dependent and independent variables is given by the regression coefficients (b), also named beta coefficients.

[b] The asterisk (*) indicates significate values when p < 0.05.

over time (r = 0.22; p = 0.001). Specifically, spatial structure of 11 species populations (36.6% of the total) changed significantly their spatial distribution along the desiccation of the pool, while 19 species (63.4% of the total) did not show any significant changes (Table 2).

Changes in community structure were related to the variations in the physicochemical properties of the water. The total CI varied randomly over time ($R^2 = 0.16$; p > 0.05) but was significantly positively related to the alkalinity and negatively to the DO (Table 3). PCD increased over time ($R^2 = 0.44$; p < 0.001) and was positively related to the DO and nitrate and negatively related to the alkalinity and turbidity. PCDc increased over time ($R^2 = 0.47$; p < 0.001) and was positively related to the alkalinity and DO but negatively to the nitrate. PCDp varied randomly over time ($R^2 = 0.01$; p > 0.05) and was positively related to the conductivity, DO, BOD and pH, and negatively to the alkalinity, phosphate, nitrate, total nitrogen, and turbidity (Table 3).

The checkerboard co-occurrence measure, which quantified the number of pairs of species that did not co-exist among sampling times, was negatively correlated to the phylogenetic distance (r = −0.10; p < 0.01). Therefore, the coexistence was greater among phylogenetically distant species.

4. Discussion

We found that in *Contendas* temporary pool, competition and environmental filters were the main ecological drivers that led the spatiotemporal distribution patterns of species in the aquatic plant community over time. Our results showed that, during desiccation of the *Contendas* temporary pool, the structure of the aquatic plant community varied in a non-random manner over time and space. The species composition and abundance of individuals varied over time such that the community was structured by initial, permanent, sporadic, and late species. Physicochemical variations of the aquatic environment over time influenced the abundance of the aquatic plants, and the floristic and phylogenetic composition. Interspecific competition was also a fundamental ecological driver in the assembling process of the community structure. Species that coexisted were phylogenetically less related to each other, so they probably had less niche overlap.

In *Contendas* temporary pool, the entry and persistence of species in the community were very heterogenous, having initial species such as *Callisia filiformis* (M. Martens & Galeotti) D.R. Hunt and *Echinochloa polystachya* (Kunth) Hitchc., which occurred only at the beginning of the increase in water depth. Other species were late, such as *Hydrocleys martii* Seub. and *Eleocharis barrosii* Svenson, and appeared during the desiccation period of the pool. Sporadic species were those infrequently recorded during sampling, such as *Echinodorus subalatus* (Mart.) Griseb. and *Scleria virgata* Steud., indicating the ephemerality of their populations. According to the

model proposed by Van der Valk (1981), species of temporary environments alternate from the beginning of the flooding period until desiccation of the pool is complete, due to abiotic changes that act as selective agents of the species according to the stage of succession. This temporary occupation of a habitat is widespread among aquatic plant species that grow in temporary tropical environments (Bove et al., 2003; França et al., 2003; Matias, 2007), emphasizing the role of abiotic processes in the organization of this type of community.

A change in the spatiotemporal structure of the community may have been a response of the species to the operation of ecological processes that could restrict their expectation of survival in the environment (Legendre et al., 2010b). In the *Contendas* temporary pool, the variation of limnological parameters partially explained the spatiotemporal change of the aquatic plants (36.6%). The alkalinity of the water, which was due to the presence of bicarbonates, had a positive effect on the total CI of the species. Aquatic plants, especially submerged ones, are able to increase their production rates by using bicarbonate as a source of inorganic carbon, compensating for the low availability of carbon dioxide (CO_2) in freshwater lakes (Maberly and Spence, 1983; Vestergaard and Sand-Jensen, 2000). Ever increasing levels of DO had a negative effect on total CI for each sampling week. Once the plants produce oxygen during photosynthesis, the negative effects on the CI would suggest that the competition would be acting on a growing population of submerged aquatic plants. Alternate explanation may be an effect of increased algal growth on the water surface, increasing DO and reducing the light penetration into the deeper layers of the pool where the submerged aquatic plants are.

During desiccation of the aquatic environment in seasonal wetlands, there is an increase in the concentrations of nutrients, salt, aquatic plants, and herbivores, making the environment less favorable for many species of aquatic plants. Consequently, they are eventually excluded from the community because of the inability to adapt to environmental conditions or by competition (Thormann et al., 1998; Wantzen et al., 2002; Gawne and Scholz, 2006). In the *Contendas* temporary pool, both the species composition and phylogenetic structure of the community were related to the variations in the water quality. Floristic dissimilarity increased when DO and alkalinity increased. As explained in the previous paragraph, competition among submerged plants could resulting in the exclusion of similar species, since they have similar ecophysiological requirements. In fact, the phylogenetic similarity of the species that were not shared (PCDp) between sampling times decreased as a function of increasing DO, suggesting that phylogenetically related taxa avoided the coexistence.

Besides light, the CO_2 availability in temporary pools can also be a limiting factor for the growth of aquatic plants, because its concentration in the water can be reduced by the slow diffusion in the environment, rapid absorption by aquatic plants and stored in the form of bicarbonates and/or carbonates (Maberly and Spence, 1983). Therefore under low concentrations of CO2, we expect an increase in the number of species that use bicarbonate as an alternative source of carbon. Maybe, the increased in the total CI as a function of increasing alkalinity could be evidence that the number of plants metabolizing bicarbonate as CO2 source may have increased in the community.

In seasonal wetlands, variations in the conditions of the aquatic environment can act as strong environmental filters of species (Van der Valk, 1981; Thormann et al., 1998; Gawne and Scholz, 2006), promoting aggregation of phylogenetically related species that are able to co-exist under the same environmental pressures. For example, PCDp decreased as the water became more alkaline, that is, phylogenetic similarity between sampling times increases in response to increased alkalinity. The number of species that were phylogenetically related and able to use bicarbonate as a carbon source could have increased when the water became more alkaline, pointing out the environmental filter action. The more categorical evidence that interspecific competition would act on the species succession was the non-random pattern of temporal coexistence exhibited by aquatic plants. The number of pairs of mutually exclusive species increased as the phylogenetic distance between species decreased, indicating that they coexisted for longer when the phylogenetic distance between them was small.

Our results showed that the species of aquatic plants changed their position in the space of *Contendas* pool over time, probably as a way to occupy portions of the spatiotemporal habitat where the competition and/or environmental conditions were less limiting. Yet, the input and permanence of species in the community was very heterogenous over time, suggesting that many of them depended on specific biotic and/or abiotic conditions exhibited by the distinct stages of succession. There is no doubt that the physicochemical variation of the pool water had a significative influence in the number of individuals of aquatic plants as well as in the floristic and phylogenetic composition. The physicochemical variation would have acted as a selecting factor of species with similar ecophysiological requirements, favoring different species in distinct periods of the pools desiccation. At the same time, the change in water quality and the reduction in their quantity over time could drive the ecological processes related to competition among aquatic plants, especially among those with close phylogenetic relationship. Therefore, we conclude that the assembly of the aquatic plants community in the *Contendas* temporary pool was structured over time and space by simultaneous action of environmental filters and interspecific competition what drove the guilds of aquatic plant species.

Acknowledgments

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