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Breaking the misconception of a dry and lifeless semiarid region: the diversity and distribution of aquatic flora in wetlands of the Brazilian Northeast

Lígia Queiroz Matias[1*], Felipe Martins Guedes[2], Hugo Pereira do Nascimento[1] and Júlia Caram Sfair[1]

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ABSTRACT

The semiarid region of northeastern Brazil possesses a set of wetlands characterized by hydrographic basins with deficient drainage networks, a few large and permanent lotic systems and several permanent and temporary lagoons. Aquatic plants are widely distributed in these wetlands and the present study aims to determine if those of Ceará state have similar species compositions and differences in species richness. We hypothesized that lentic ecosystems would have more species and different growth forms of aquatic angiosperms than lotic ecosystems. A total of 1619 records of aquatic angiosperms in 43 wetland areas were analysed. The most representative families were Cyperaceae, Poaceae, Fabaceae, Alismataceae, Malvaceae, Nymphaeaceae and Pontederiaceae. Most of the species are helophytes and bottom-rooted emergent hydrophytes. Permanent lentic ecosystems had the highest number of exclusive species (27.85 %), followed by temporary lentic ecosystems (20.54 %). Contrary to our hypothesis, the different aquatic ecosystems were found to possess distinct species compositions and different proportions of growth forms, and all wetland types contributed to the macrophyte richness of the study area, although they differ in species richness. Therefore, conservation plans for the native aquatic macrophyte biota should include all wetland ecosystems in the semiarid state of Ceará.

Keywords: biodiversity, floristic richness, hydrophytes, macrophytes, seasonal aquatic ecosystems

Introduction

Arid regions are traditionally perceived as relatively simple ecosystems, with low species diversity (McNeely 2003). However, the conclusions about the patterns of diversity in these regions can differ widely depending on the taxon analysed and the peculiarities of the geographical areas (MacKay 1991). If we consider that in temporary pools, the spatial structure of the aquatic plant community changes significantly during the rainy season according to the stage of flooding (Ferreira *et al.* 2015), would the diversity of aquatic plants in the semiarid region be differentiated between the lentic and lotic systems?

Wetlands in semiarid zones of northeastern Brazil are influenced by climatic seasonality and unpredictable flood pulses, which present multiannual frequency and low amplitude (Junk *et al.* 2014). A biogeographic delineation approach of South American freshwater ecosystems considered the extreme Northeast of Brazil as the "Ecoregion

1 Centro de Ciências, Departamento de Biologia, Universidade Federal do Ceará, 60440-900, Fortaleza, CE, Brazil
2 Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, 50670-901, Recife, PE, Brazil

* Corresponding autor: lqmatias@ufc.br

Northeastern Caatinga and Coastal drainages" (Abell *et al.* 2008), with a predominance of aquatic systems albeit of low water volume, but functional in terms of regulation of the regional hydrological regime and maintenance of biodiversity (Junk *et al.* 2014). Particularly in this ecoregion, Ceará state presents the largest flood area (24,339.65 ha) and the largest number of temporary lagoons (2,930) (Maltchick *et al.* 1999). Therefore, these temporary lagoons, together with the hydrographic basins with a deficient drainage network and the permanent lentic systems of coastal formations (Claudino-Sales & Peulvast 2002), characterize the set of wetlands in the state.

Temporary lagoons have a cyclical nature, involving alternating rainy and dry seasons, which favours the succession of different species in processes of flooding and drought (Tabosa *et al.* 2012). In contrast, the permanent lagoons, given the stability of the water column, have plant communities associated with the depth of the euphotic zone, as this is a determining factor for the extension of the habitats of macrophytes (Wetzel 2001). Furthermore, in artificial ecosystems like weirs, aquatic plant assemblages are more associated with nutrient concentrations than with water depth (Paiva *et al.* 2014).

On the other hand, lotic systems in the Brazilian semiarid region are characterized by flash floods during the rainy season that can vary according to rainfall, *i.e.*, the water can flow for weeks in small streams or months in larger rivers during the 'wet phase' (Maltchick & Medeiros 2006). During the dry season or "drying phase", water flow ceases, leading to the formation of strings of disconnected temporary pools along the riverbed where the aquatic biota survives (Medeiros & Maltchick 1999). In addition, due to the absence of the river-floodplain system, only the main river channel keeps the temporary pools in the dry season, resulting in less habitat availability for aquatic organisms (Maltchick & Medeiros 2006).

Along the coast of Ceará, permanent and temporary aquatic systems originate in interdune and deflated dune areas, as a result of flooding during the rainfall period or the rise of the water column in less permeable soils, and are located mainly between old Quaternary dunes and Tertiary Formations (also known as "Formação Barreiras" [Claudino-Sales & Peuvast 2002]). In addition to these, permanent lentic ecosystems originate from the barrage of rivers in the vicinity of their mouths due to the accumulation of sand carried by the wind (forming the "lagamares"), or by abandoned meanders and marginal lagoons located along corridors of the main rivers that reach the coast (Silva *et al.* 2007).

Aquatic plants occur both in coastal environments (Matias *et al.* 2003; Moro *et al.* 2014) and in temporary and permanent aquatic systems, natural or artificial, located in the semiarid region (Paiva *et al.* 2014; Albuquerque *et al.* 2020). In shallow lagoons, plant communities occupy the entire water column, forming strata of submerged hydrophytes, overlaid by bottom-rooted emergents with floating leaves and/or stems, and by bottom-rooted emergents above the water surface (Tabosa *et al.* 2012). In deep permanent reservoirs and lagoons, the communities occur at shallower depths and periodically flooded banks (Matias *et al.* 2003; Paiva *et al.* 2014). In lotic ecosystems, species richness is lower in systems with deficient drainage, and communities are influenced by the flood intensity (Pedro *et al.* 2006).

Growth forms vary according to the stability of the water column, with the presence of submerged forms in permanent lentic systems being more common (Matias *et al.* 2003; Moro *et al.* 2014; Paiva *et al.* 2014) while the bottom-rooted emergents and bottom-rooted emergents with floating leaves and/or stems share the water surface in temporary lentic systems (Tabosa *et al.* 2012).

On the other hand, the dynamics of the water column in permanent lotic systems constitute a strong environmental filter to colonization by aquatic plants, which depend on marginal areas, such as an underwater banks or places with water between the spit and the shore, which are protected from strong turbulence (Sculthorpe 1967). The bottom-rooted emergent and bottom-rooted submerged forms occur in these marginal habitats (Koehler & Bove 2004), whilst haptophytes are restricted to habitats with accentuated unevenness (Silva *et al.* 2015). And, in temporary lotic systems, the occurrence of two phases of hydrological disturbance (flooding and drought) exert a strong influence so that angiosperms with bottom-rooted submerged or free-floating forms are observed in the areas of river resurgences or permanent river puddles (Maltchick & Medeiros 2006; Maltchick & Bianchini 2006).

Considering that aquatic plants are widely distributed in wetlands, the present study analyses if aquatic systems of Ceará state tend to show similarity in species composition and differences in species richness and growth forms. We hypothesize I) that lentic ecosystems, natural or artificial, will exceed lotic ecosystems in the number of species (richness). However, as rivers present drainage deficiency and discontinuity (having stability of the water column for only a few months), we expect that II) lentic and lotic ecosystems present similarity in species composition and differences in the proportions of growth forms.

Materials and methods

Data source

All records of angiosperms (number of species in each area) from wetlands of Ceará state were obtained through systematic inventories carried out in the state, collections were performed during the wet seasons from 2000 to 2020 and are published elsewhere and we also included data (number of species) from Iguatu wetlands from unpublished studies (Tab. 1). In the case of these unpublished studies, all species were sampled in Iguatu wetlands along the shoreline

of the lagoons using three transects 50 m apart, from the margin to the furthermost area of the macrophyte stand, close to the limnetic zone. Plants were sampled in a belt transect ca. 1 m wide using traditional plant sampling tools (scissors, shovels and hoes), given that the depth of the water column (less than 1 m) did not require any other apparatus.

Nomenclatural data were updated based on IPNI (http://www.ipni.org/), Flora do Brasil 2020 (http://reflora.jbrj.gov.br), Tropicos (http://tropicos.org) and The Plant List (http://theplantlist.org). Identifications made by specialists were considered and others had their identifications updated based on the specific literature for each family. The new records and origin status (native or exotic) were based on Flora do Brasil 2020 (2020), in order to highlight the main invasive species, we annotated this information after each scientific name in the species list (Moro *et al.* 2012). Growth forms were classified following Cook (1990) as the following: (1) Hydrophytes: bottom-rooted submerged (RS), bottom-rooted emergent (RE), bottom-rooted emergent with floating leaves and/or stems (RLF), free-swimming submerged (FS), free-floating emergent (FE), and (2) Helophytes (Hel).

For the similarity analysis, the following 43 wetland habitats were selected: 9 Permanent Lentic (PLE), 11 Temporary Lentic (TLE), 8 Permanent Lotic (PLO), 7 Temporary Lotic (TLO) and 8 Artificial Lentic (ALE) ecosystems (Fig. 1, Tab. S1 in supplementary material).

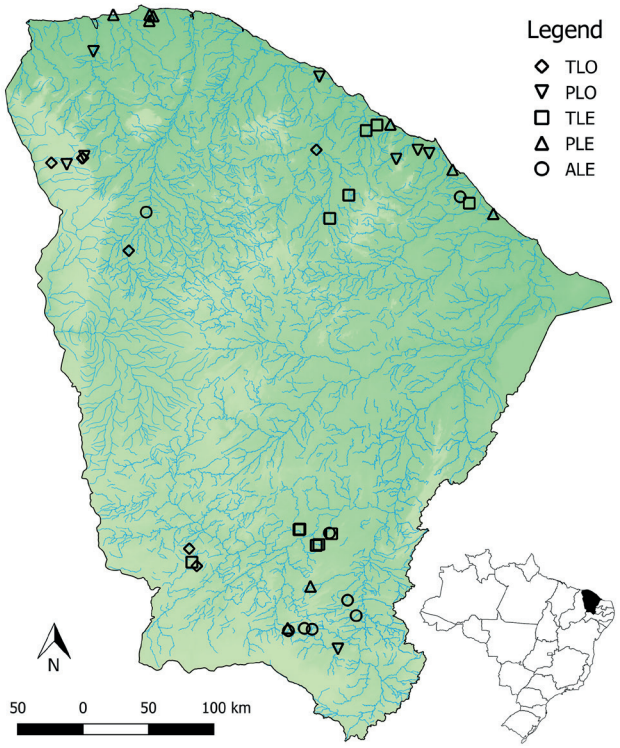

Figure 1. Map of the localization of the 43 selected wetland areas. ALE = Artificial Lentic ecosystem; PLE = Permanent Lentic ecosystem; PLO = Permanent Lotic ecosystem; TLE = Temporary Lentic ecosystem; TLO = Temporary Lotic ecosystem.

Statistical analyses

To compare the richness among the five different ecosystems (PLE, TLE, PLO, TLO and ALE) we used the extrapolation approach based on the Hill number with q = 0 (Chao *et al.* 2014), using the iNEXT package (Hsieh *et al.* 2013) in R software (R Development Core Team 2020). We performed 1000 randomizations and calculated the confidence interval at 95 %.

We calculated the distance of species composition among the 43 ponds and rivers with the Jaccard dissimilarity index. The distance matrix was related to their features (lentic or lotic and permanent, temporary or artificial) with a PERMANOVA approach, which is a multivariate analysis of variance for dissimilarity data with permutations (Anderson 2001; McArdle & Anderson 2001). PERMANOVA does not have the assumption of normal distribution, being characterized as a non-parametric analysis more powerful than the analysis of similarity (ANOSIM) and the Mantel test in detecting differences in real communities (Anderson & Walsh 2013). PERMANOVA also assumes independent observations, it can use categorical or continuous independent variables, and it uses a permutation test (Anderson 2001). We used the "adonis" function with 10,000 replications, followed by the "betadisper" function in the "vegan" package (Oksanen *et al.* 2019) in R software (R Development Core Team 2020).

To understand the proportion of growth forms, considering the interaction of lotic/lentic and temporary/artificial/permanent ecosystems, we calculated the Scheirer-Ray-Hare test, which is a non-parametric test analogous to the two-way ANOVA when their assumptions are not met (Sokal & Rohlf 1995). We used the proportion of growth forms because the number of sampled units of Permanent Lentic (9), Temporary Lentic (11), Permanent Lotic (8), Temporary Lotic (7) and Artificial Lentic (8) were different and, thus, not comparable concerning the absolute number of species in each growth form.

Additionally, we performed the *post-hoc* pairwise Dunn test (Sokal & Rohlf 1995). The Scheirer-Ray-Hare test was calculated with the "rcompanion" package (Mangiafico 2019) and the Dunn test with the "FSA" package (Ogle *et al.* 2020), both in R software (R Development Core Team 2020).

Results

Our sampling of aquatic angiosperms is represented by 44 families, 108 genera and 219 species (Tab. 1). The most representative families were Cyperaceae (23 %), Fabaceae (10 %), Poaceae (9 %), Alismataceae (5 %), followed by Araceae, Nymphaeaceae and Pontederiaceae (4 % each) (Fig. 2A). Most of the species are helophytes (58 %) and bottom-rooted emergent hydrophytes (22 %) (Fig. 2B). Of the species in this study, 21 are new records for Ceará state (Flora do Brasil 2020 2020), most representatives of Poaceae (7 spp.).

The greatest values for species richness were found in permanent (162 spp.) and temporary lentic (107 spp.) ecosystems, followed by artificial lentic ecosystems (86 spp.). Temporary (32 spp.) and permanent lotic (51 spp.) ecosystems presented the lowest richness (Fig. 3). Six species occurred in all five ecosystems: *Echinodorus subalatus*, *Pistia stratiotes*, *Neptunia plena*, *Nymphaea amazonum*, *Ludwigia helminthorrhiza* and *Ludwigia leptocarpa*. Permanent lentic ecosystems showed the largest number of exclusive species (61 or 27.85 %), followed by temporary lentic (45 or 20.54 %), artificial lentic (14 or 6.39 %), permanent lotic (12 or 5.47 %) and temporary lotic (8 or 3.65 %). Most of the species (123 or 56.16 %) occurred exclusively in non-artificial lentic ecosystems.

The five ecosystems have different species compositions ($F = 1.25$; $R^2 = 0.03$; $P = 0.03$), but no significant dispersion ($F_{4.38} = 0.87$; $P = 0.48$), indicating that the difference among the five ecosystems is greater than the difference within the ecosystems (Fig. 4; Tab. 2). Temporary aquatic systems tend to have higher proportions of free-swimming submerged and bottom-rooted emergents with floating leaves and/or stems (Fig. 5A and B, Tab. S2 in supplementary material), whereas lentic ecosystems tend to have higher proportions of bottom-rooted submerged forms than lotic ecosystems (Fig 5C, Tab. S2 in supplementary material). On the other hand, helophytes tend to show different proportions among the different ecosystems (Fig. 5D, Tab. S2 in supplementary material).

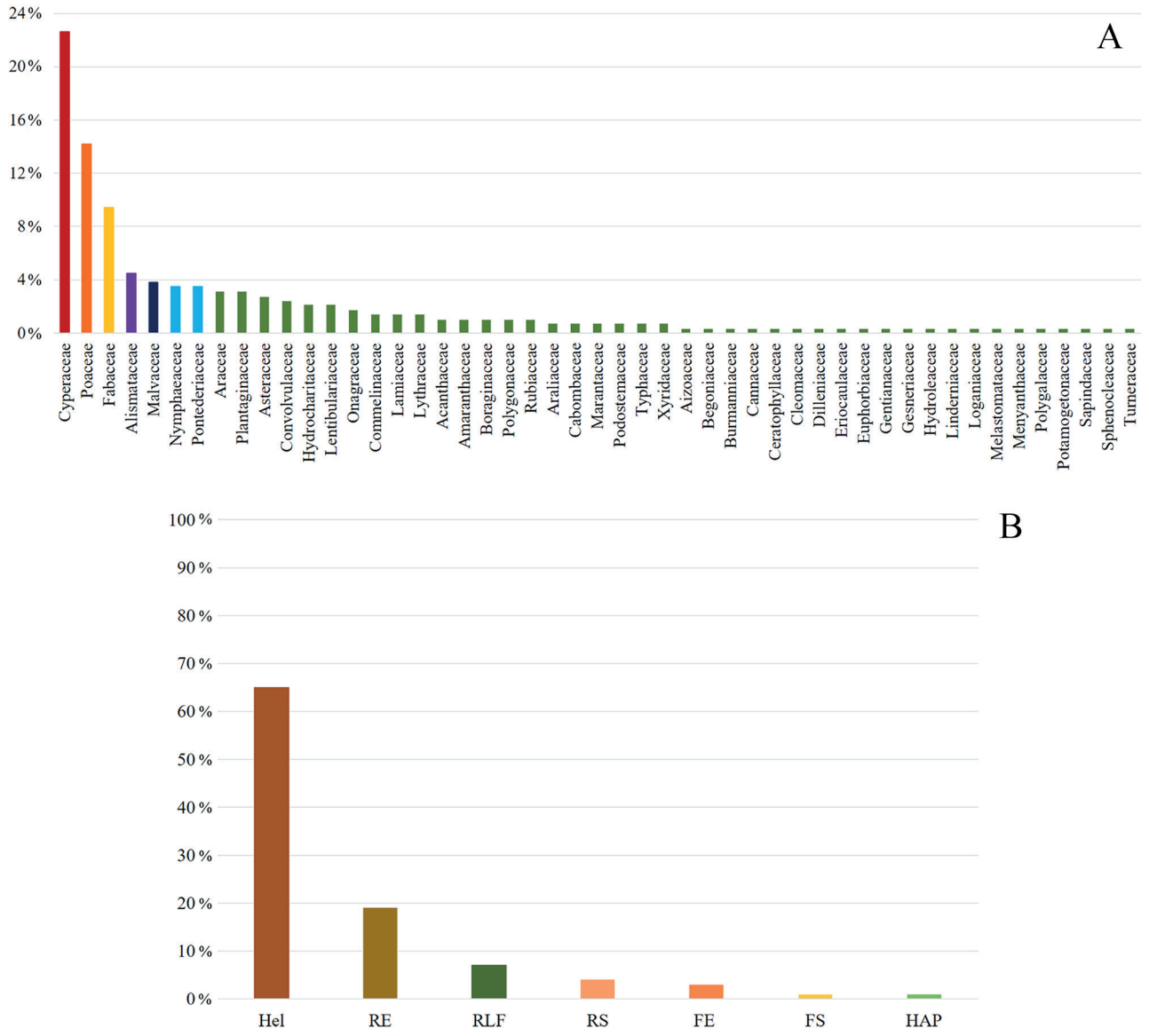

Figure 2. A. Percentage of species richness per family in the study areas. **B**. Percentage of growth forms (Cook 1990) of aquatic angiosperms in the study areas. (Hel) Helophytes; (RE) Bottom-rooted emergent; (RLF) Bottom-rooted emergent with floating leaves and/or stems; (RS) Bottom-rooted submerged; (FE) Free-floating emergent; (FS) Free-swimming submerged; (HAP) Haptophytes.

Table 1. Floristic list of species collected in aquatic ecosystems in Ceará state, northeastern Brazil. The growth forms (GF) were classified following Cook (1990): (1) Hydrophytes: bottom-rooted submerged (RS), bottom-rooted emergent (RE), bottom-rooted emergent with floating leaves and/or stems (RLF), free-swimming submerged (FS), free-floating emergent (FE), haptophytes (HAP), and (2) Helophytes (Hel). PLE – Permanent Lentic ecosystem; TLE – Temporary Lentic ecosystem; PLO – Permanent Lotic ecosystem; TLO – Temporary Lotic ecosystem; ALE – Artificial Lentic ecosystem. (*) New record for Ceará state.

Family	Species	Occurence indication	GF	PLE	TLE	PLO	TLO	ALE
Acanthaceae	*Hygrophila guianensis* Nees ex Benth. (*)	Guedes & Nascimento 2016	Hel	0	0	1	0	0
	Justicia laevilinguis (Nees) Lindau	Normando 2011	Hel	0	1	0	0	0
Aizoaceae	*Sesuvium portulacastrum* (L.) L.	Matias & Nunes 2001	Hel	1	1	0	0	0
Alismataceae	*Echinodorus glandulosus* Rataj	Matias & Sousa 2011	RE	0	1	1	1	0
	Echinodorus lanceolatus Rataj	Ibiapina-Santos 2016	RE	0	1	0	0	0
	Echinodorus palaefolius (Nees & Mart.) J.F. Macbr.	Matias & Sousa 2011	RE	0	1	0	0	0
	Echinodorus pubescens (Mart.) Seub. Ex Warm.	Ibiapina-Santos 2016	RE	0	1	0	0	0
	Echinodorus subalatus (Mart.) Griseb.	Tabosa *et al.* 2012; Moro *et al.* 2014; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RE	1	1	1	1	1
	Helanthium tenellum (Mart.) Britton	Matias *et al.* 2003	RE	1	0	0	0	1
	Hydrocleys martii Seub.	Tabosa *et al.* 2012; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RLF	1	1	0	0	0
	Hydrocleys nymphoides (Willd.) Buchenau	Ibiapina-Santos 2016	RLF	1	1	1	0	0
	Limnocharis flava (L.) Buchenau	Ibiapina-Santos 2016	RE	1	1	0	0	0
	Limnocharis laforesti Duchass. ex Griseb.	Ibiapina-Santos 2016	RE	0	1	0	0	1
	Sagittaria guayanensis Kunth.	Matias & Sousa 2011	RLF	1	1	0	0	0
	Sagittaria planitiana G. Agostini	Matias & Sousa 2011	RE	1	1	1	0	0
Amaranthaceae	*Alternanthera brasiliana* (L.) Kuntze	Matias & Nunes 2001	Hel	0	0	1	0	0
	Alternanthera tenella Colla	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Amaranthus spinosus L. (*)	Ibiapina-Santos 2016	Hel	0	1	0	0	0
Araceae	*Landoltia punctata* (G. Mey.) Les & D.J. Crawford	Andrade *et al.* 2013	FE	1	0	0	0	0
	Lemna aequinoctialis Welw.	Ibiapina-Santos 2016	FE	1	1	0	0	1
	Lemna minuta Kunth.	Ibiapina-Santos 2016	FE	0	1	0	0	0
	Montrichardia arborescens (L.) Schott (*)	Andrade *et al.* 2013	RE	1	0	0	0	0
	Montrichardia linifera (Arruda) Schott	Moro *et al.* 2014	RE	1	0	1	0	0
	Pistia stratiotes L.	Paiva *et al.* 2014; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	FE	1	1	1	0	1
	Spirodela intermedia W. Koch	Andrade *et al.* 2013	FE	1	0	0	0	1
	Wolffia columbiana Karsten	Ibiapina-Santos 2016	FE	1	1	0	0	0
	Wolffiella welwitschii (Hegelm) Monod	Ibiapina-Santos 2016	FE	1	1	0	0	1
Araliaceae	*Hydrocotyle bonariensis* Lam. (*)	Moro *et al.* 2014	Hel	1	0	0	0	0
	Hydrocotyle verticillata Thunb. (*)	Guedes & Nascimento 2016	Hel	1	0	0	0	0
Asteraceae	*Eclipta prostrata* (L.) L.	Ibiapina-Santos 2016	Hel	1	1	1	0	1
	Erechtites hieracifolius (L.) Raf. ex DC.	Guedes & Nascimento 2016	Hel	1	0	0	0	1
	Mikania micrantha Kunth	Guedes & Nascimento 2016	Hel	1	0	0	0	0
	Spilanthes acmella (L.) L. (*)	Guedes & Nascimento 2016	Hel	0	1	0	0	0
Boraginaceae	*Euploca polyphylla* (Lehm.) J.I.M. Melo & Semir	Guedes & Nascimento 2016	Hel	1	1	0	0	0
Burmaniaceae	*Burmannia capitata* (Walter ex J.F. Gmel.) Mart.	Matias *et al.* 2003	Hel	0	1	0	0	0

Table 1. Cont.

Family	Species	Occurence indication	GF	PLE	TLE	PLO	TLO	ALE
Cabombaceae	*Cabomba aquatica* Aubl.	Ibiapina-Santos 2016	RS	1	1	1	0	0
	Cabomba haynesii Wiersema	Ibiapina-Santos 2016	RS	0	1	0	0	1
Cannaceae	*Canna glauca* L.	Ibiapina-Santos 2016	RE	1	1	0	0	0
Ceratophyllaceae	*Ceratophyllum demersum* L.	Moro *et al.* 2014; Paiva *et al.* 2014; Ibiapina-Santos 2016	FS	1	1	1	0	1
Cleomaceae	*Tarenaya spinosa* (Jacq.) Raf.	Paiva *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	1	1	1
Commelinaceae	*Callisia filiformis* (M. Martens & Galeotti) D.R. Hunt	Tabosa *et al.* 2012	Hel	0	1	0	0	0
	Commelina difusa Burm.f.	Matias & Nunes 2001	Hel	0	1	1	0	0
	Dichorisandra perforans C.B. Clarke	Guedes & Nascimento 2016	Hel	0	0	1	0	0
	Tripogandra glandulosa (Seub.) Rohweder(*)	Guedes & Nascimento 2016	Hel	0	0	1	0	0
Convolvulaceae	*Aniseia martinicensis* var. *ambigua* Hallier f.	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Camonea umbellata (L.) A.R. Simões & Staples	Normando 2011	Hel	0	0	1	0	0
	Ipomoea asarifolia (Desr.) Roem. & Schult.	Matias *et al.* 2003; Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	1
	Ipomoea carnea subsp. *Fistulosa* (Mart. Ex Choisy) D. F. Austin	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Ipomoea nil (L.) Roth	Ibiapina-Santos 2016	Hel	0	1	0	0	0
Cyperaceae	*Bulbostylis capillaris* (L.) C.B. Clarke	Matias & Nunes 2001	Hel	1	1	0	0	0
	Cyperus aggregatus (Willd.) Endl.	Matias *et al.* 2003; Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	1
	Cyperus amabilis Vahl	Matias *et al.* 2003	Hel	1	0	0	0	0
	Cyperus articulatus L.	Moro *et al.* 2014	Hel	1	1	0	0	0
	Cyperus blepharoleptos Steud.	Paiva *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	1
	Cyperus brevifolius (Rottb.) Endl. ex Hassk.	Moro *et al.* 2014	Hel	1	0	0	0	0
	Cyperus compressus L.	Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	0
	Cyperus digitatus Roxb.	Ibiapina-Santos 2016	Hel	1	1	0	0	1
	Cyperus esculentus L.	Ibiapina-Santos 2016	Hel	1	1	1	0	1
	Cyperus fugax Liebm.	Guedes & Nascimento 2016	Hel	1	0	0	0	0
	Cyperus iria L.	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Cyperus ligularis L.	Matias *et al.* 2003; Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	1
	Cyperus luzulae (L.) Retz.	Guedes & Nascimento 2016	Hel	0	1	1	0	0
	Cyperus macrostachyos Lam.	Ibiapina-Santos 2016	Hel	1	1	1	0	1
	Cyperus metzii (Hochst. ex Steud.) Mattf. & Kük.	Moro *et al.* 2014	Hel	1	1	0	0	0
	Cyperus obtusatus (J. Presl & C. Presl) Mattf. & Kük.	Matias *et al.* 2003; Moro *et al.* 2014	Hel	1	1	0	0	0
	Cyperus odoratus L.	Moro *et al.* 2014	Hel	0	1	1	0	0
	Cyperus polystachyos Rottb.	Matias *et al.* 2003; Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	1
	Cyperus rotundus L.	Moro *et al.* 2014	Hel	1	0	0	0	0
	Cyperus sphacelatus Rottb.	Normando 2011	Hel	1	1	0	0	0
	Cyperus surinamensis Rottb.	Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	0
	Cyperus uncinulatus Schrad. ex Nees	Moro *et al.* 2014	Hel	1	1	0	0	0
	Eleocharis acutangula (Roxb.) Schult.	Albuquerque *et al.* 2020	RE	1	0	0	0	0
	Eleocharis atropurpurea (Retz.) J.Presl & C. Presl	Matias *et al.* 2003	RE	1	1	0	0	0

Table 1. Cont.

Family	Species	Occurence indication	GF	PLE	TLE	PLO	TLO	ALE
Cyperaceae	*Eleocharis elegans* (Kunth) Roem. & Schult.	Normando 2011	RE	0	1	0	0	0
	Eleocharis equisetoides (Elliott) Torr.	Moro *et al.* 2014	RE	1	0	0	0	0
	Eleocharis flavescens (Poir.) Urban	Ibiapina-Santos 2016	RE	0	1	0	0	0
	Eleocharis geniculata (L.) Roem. & Schult.	Matias *et al.* 2003; Moro *et al.* 2014; Ibiapina-Santos 2016	RE	1	1	0	1	0
	Eleocharis interstincta (Vahl) Roem. & Schult.	Tabosa *et al.* 2012; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RE	1	1	0	0	1
	Eleocharis maculosa (Vahl) Roem. & Schult.	Normando 2011	RE	1	1	0	0	0
	Eleocharis mutata (L.) Roem. & Schult.	Matias *et al.* 2003; Tabosa *et al.* 2012; Albuquerque *et al.* 2020	RE	1	1	0	0	0
	Eleocharis nana Kunth	Normando 2011	RE	1	0	0	0	0
	Eleocharis plicarhachis (Griseb.) Svenson	Matias *et al.* 2003	RE	1	1	0	0	0
	Eleocharis retroflexa (Poir.) Urban	Normando 2011	RE	0	1	0	0	0
	Eleocharis sellowiana Kunth	Matias *et al.* 2003	RE	1	0	0	0	0
	Eleocharis subfoliata C.B.Clarke	Normando 2011	RE	1	0	0	0	0
	Fimbristylis littoralis Gaudich.	Normando 2011	Hel	1	0	1	0	0
	Fimbrystilis cymosa R. Br.	Matias *et al.* 2003; Moro *et al.* 2014	Hel	1	1	0	0	0
	Fimbrystilis dichotoma (L.) Vahl	Normando 2011	Hel	1	0	0	0	0
	Fimbristylis littoralis Gaudich.	Normando 2011	Hel	1	0	1	0	0
	Fimbrystilis vahlii (Lam.) Link	Normando 2011	Hel	1	0	0	0	0
	Fuirena robusta Kunth (*)	Moro *et al.* 2014	Hel	1	0	0	0	0
	Fuirena umbellata Rottb.	Matias *et al.* 2003	Hel	1	0	1	1	0
	Rhynchospora caracasana (Kunth) Boeckeler	Moro *et al.* 2014	Hel	1	0	0	0	0
	Rhynchospora contracta (Nees) J. Raynal	Normando 2011	Hel	1	0	0	0	0
	Rhynchospora exaltata Kunth	Moro *et al.* 2014	Hel	1	0	0	0	0
	Rhynchospora holoschoenoides (Rich.) Herter	Matias *et al.* 2003; Moro *et al.* 2014	Hel	1	1	0	0	0
	Rhynchospora riparia (Nees) Boeckeler	Matias *et al.* 2003	Hel	1	1	0	0	0
	Scleria bracteata Cav.	Normando 2011	Hel	0	0	1	0	0
	Scleria gaertneri Raddi	Guedes & Nascimento 2016	Hel	0	0	1	0	0
	Scleria hirtella Sw.	Guedes & Nascimento 2016	Hel	1	0	0	0	0
	Scleria macrophylla J. Presl & C. Presl(*)	Normando 2011	Hel	0	0	1	0	0
Dilleniaceae	*Tetracera wildenowiana* Steud. (*)	Guedes & Nascimento 2016	Hel	1	0	0	0	0
Euphorbiaceae	*Caperonia palustris* (L.) A. St.-Hil. (*)	Ibiapina-Santos 2016	Hel	1	1	0	0	1
Fabaceae	*Aeschynomene evenia* C. Wright & Sauvalle	Moro *et al.* 2014; Ibiapina-Santos 2016	RE	1	1	0	0	0
	Aeschynomene filosa Mart.	Tabosa *et al.* 2012; Ibiapina-Santos 2016	RE	0	1	0	0	0
	Aeschynomene rudis Benth.	Normando 2011	RE/Hel	0	1	0	0	0
	Centrosema brasilianum (L.) Benth	Ibiapina-Santos 2016	Hel	0	1	0	0	1
	Centrosema plumieri (Tupin. ex Pers.) Benth	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Chamaecrista diphylla (L.) Greene	Guedes & Nascimento 2016	Hel	1	1	0	0	0
	Chamaecrista ramosa var. *ramosa* (Vogel) H.S.Irwin & Barneby	Guedes & Nascimento 2016	Hel	1	1	0	0	0
	Desmodium triflorum (L.) DC.	Moro *et al.* 2014	Hel	1	0	0	0	0

Table 1. Cont.

Family	Species	Occurence indication	GF	PLE	TLE	PLO	TLO	ALE
Fabaceae	*Discolobium hirtum* Benth.	Tabosa *et al.* 2012	Hel	1	1	0	0	0
	Indigofera hirsuta L.	Matias *et al.* 2003	Hel	1	1	0	0	0
	Indigofera microcarpa Desv.	Moro *et al.* 2014	Hel	1	0	0	0	0
	Macroptilium lathyroides (L.) Urban	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Mimosa camporum Benth.	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Mimosa candollei R. Grether	Ibiapina-Santos 2016	Hel	0	1	1	0	0
	Mimosa misera Benth.	Normando 2011	Hel	1	0	0	0	0
	Neptunia oleracea Lour.	Tabosa *et al.* 2012; Moro *et al.* 2014; Paiva *et al.* 2014; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RLF	1	1	0	0	1
	Neptunia plena (L.) Benth.	Matias *et al.* 2003; Ibiapina-Santos 2016	RLF	1	1	1	0	1
	Parkinsonia aculeata L.	Normando 2011	Hel	1	1	0	0	0
	Senna alata (L.) Roxb.	Normando 2011	Hel	0	1	0	0	0
	Senna obtusifolia (L.) H.S. Irwin & Barneby	Tabosa *et al.* 2012	Hel	0	1	0	0	0
	Sesbania exasperata Kunth	Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Stylosanthes angustifolia Vogel	Matias *et al.* 2003; Moro *et al.* 2014	Hel	1	0	0	0	0
	Zornia latifolia Sm.	Matias *et al.* 2003	Hel	1	0	0	0	0
Gentianaceae	*Schultesia guianensis* (Aubl.) Malme	Matias *et al.* 2003	Hel	1	0	0	0	0
Heliotropiaceae	*Heliotropium elongatum* (Lehm.) I.M. Johnst.	Tabosa *et al.* 2012; Ibiapina-Santos 2016	Hel	0	1	0	0	0
Hydrocharitaceae	*Apalanthe granatensis* (Bonpl.) Planch.	Tabosa *et al.* 2012; Ibiapina-Santos 2016	RS	1	1	0	0	1
	Egeria densa Planch.	Moro *et al.* 2014	RS	1	1	0	0	1
	Egeria najas Planch.	Matias *et al.* 2017	RS	1	1	0	0	1
	Najas arguta Kunth	Matias *et al.* 2017	RS	0	1	0	0	1
	Najas conferta (A.Braun) A.Braun	Tabosa *et al.* 2012; Ibiapina-Santos 2016	RS	1	1	0	0	1
	Najas marina L.	Matias *et al.* 2017	RS	1	0	0	0	0
Hydroleaceae	*Hydrolea spinosa* L.	Moro *et al.* 2014; Ibiapina-Santos 2016	RE	1	1	1	1	1
Lentibulariaceae	*Utricularia cornuta* Michx.	Guedes & Matias 2020	Hel	1	0	0	0	0
	Utricularia erectiflora St.-Hil. & Girard.	Guedes & Matias 2020	Hel	1	1	0	0	0
	Utricularia foliosa L.	Tabosa *et al.* 2012; Ibiapina-Santos 2016; Guedes & Matias 2020	FS	1	1	0	0	1
	Utricularia gibba L.	Moro *et al.* 2014; Ibiapina-Santos 2016; Guedes & Matias 2020	FS	1	1	0	0	0
	Utricularia hydrocarpa Vahl.	Tabosa *et al.* 2012; Guedes & Matias 2020	FS	0	1	0	0	0
	Utricularia trichophylla Spruce ex. Oliv.	Guedes & Matias 2020	Hel	1	0	1	0	0
Loganiaceae	*Spigelia anthelmia* L.	Matias *et al.* 2003	RE	1	0	0	0	0
Lythraceae	*Ammannia latifolia* L.	Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	1	0	0
	Cuphea campestres Mart. ex Koehne	Tabosa *et al.* 2012	Hel	0	1	0	0	0
Malvaceae	*Malachra radiata* (L.) L.	Ibiapina-Santos 2016	Hel	1	1	0	0	0
	Melochia pyramidata L.	Ibiapina-Santos 2016	Hel	0	1	0	0	1
	Melochia tomentosa L.	Ibiapina-Santos 2016	Hel	1	1	1	0	1
	Waltheria indica L.	Ibiapina-Santos 2016	Hel	0	1	0	0	0

Table 1. Cont.

Family	Species	Occurence indication	GF	PLE	TLE	PLO	TLO	ALE
Marantaceae	*Thalia densibracteata* Petersen	Ibiapina-Santos 2016	RE	0	1	0	0	0
	Thalia geniculata L.	Tabosa *et al.* 2012; Ibiapina-Santos 2016	RE	1	1	0	0	0
Melastomataceae	*Pterolepis glomerata* (Rottb.) Miq.	Moro *et al.* 2014	RE	1	0	0	0	0
Menyanthaceae	*Nymphoides humboldtiana* (Kunth) Kuntze	Matias *et al.* 2003; Moro *et al.* 2014; Paiva *et al.* 2014; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RLF	1	1	0	0	1
Nymphaeaceae	*Nymphaea amazonum* Mart. & Zucc.	Moro *et al.* 2014; Albuquerque *et al.* 2020	RLF	1	1	1	0	1
	Nymphaea ampla (Salisb.) DC.	Sousa & Matias 2013	RLF	0	1	0	0	0
	Nymphaea jamesoniana Planch.	Ibiapina-Santos 2016	RLF	0	1	0	0	0
	Nymphaea lasiophylla Mart. & Zucc.	Matias *et al.* 2003; Tabosa *et al.* 2012; Moro *et al.* 2014; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RLF	1	1	1	0	1
	Nymphaea lingulata Wiersema	Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RLF	1	1	0	0	1
	Nymphaea prolifera Wiersema	Sousa & Matias 2013	RLF	1	0	0	0	0
	Nymphaea pulchella DC.	Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RLF	1	1	1	0	0
	Nymphaea rudgeana G. Mey.	Matias *et al.* 2003; Moro *et al.* 2014	RLF	1	0	0	0	0
	Nymphaea tenerinervia Casp.	Moro *et al.* 2014	RLF	1	1	0	0	0
Onagraceae	*Ludwigia erecta* (L.) H. Hara	Nascimento & Matias (2021)	Hel	1	1	0	0	0
	Ludwigia helminthorrhiza (Mart.) H. Hara	Moro *et al.* 2014; Paiva *et al.* 2014; Ibiapina-Santos 2016; Albuquerque *et al.* 2020; Nascimento & Matias (2021)	RLF	1	1	0	0	1
	Ludwigia hyssopifolia (G. Don) Exell	Moro *et al.* 2014; Ibiapina-Santos 2016; Nascimento & Matias (2021)	RE	1	1	1	1	1
	Ludwigia leptocarpa (Nutt.) H.Hara	Moro *et al.* 2014; Ibiapina-Santos 2016; Nascimento & Matias (2021)	Hel	1	1	1	0	1
	Ludwigia octovalvis (Jacq.) P.H.Raven	Matias *et al.* 2003; Nascimento & Matias (2021)	Hel	1	1	1	0	1
Plantaginaceae	*Angelonia biflora* Benth.	Paiva *et al.* 2014	Hel	0	0	1	0	0
	Bacopa angulata (Benth.) Loefgr. & Edwall	Moro *et al.* 2014	RE	1	0	0	0	0
	Bacopa aquatica Aubl.	Tabosa *et al.* 2012; Moro *et al.* 2014	RE	1	1	0	0	1
	Bacopa cochlearia (Huber) L.B.Sm.	Moro *et al.* 2014	RE	1	1	1	0	0
	Bacopa monnieri (L.) Wettst.	Moro *et al.* 2014	RE	1	0	1	0	0
	Scoparia dulcis L.	Paiva *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	1	0
	Stemodia foliosa Benth.	Guedes & Nascimento 2016	Hel	1	0	0	0	1
	Stemodia maritima L.	Paiva *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	1	0	1
Poaceae	*Aristida adscensionis* L.	Guedes & Nascimento 2016	Hel	0	1	0	0	0
	Aristida amazonensis Longhi-Wagner (*)	Guedes & Nascimento 2016	Hel	1	0	0	0	0
	Cyphonanthus discrepans (Döll) Zuloaga & Morrone(*)	Normando 2011	Hel	1	0	0	0	0
	Digitaria ciliaris (Retz.) Koeler	Tabosa *et al.* 2012	Hel	0	1	0	0	0
	Digitaria horizontalis Willd.	Normando 2011	Hel	1	0	0	0	0
	Echinochloa colona (L.) Link	Tabosa *et al.* 2012; Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Echinochloa polystachya (Kunth) Hitchc.	Tabosa *et al.* 2012; Paiva *et al.* 2014	Hel	1	1	0	0	1
	Eragrostis ciliaris (L.) R.Br.	Matias & Nunes 2001	Hel	1	0	0	0	0
	Hymenachne amplexicaulis (Rudge) Nees	Ibiapina-Santos 2016	RE	1	1	0	0	1
	Panicum dichotomiflorum Michx.	Tabosa *et al.* 2012	Hel	0	1	0	0	0

Table 1. Cont.

Family	Species	Occurence indication	GF	PLE	TLE	PLO	TLO	ALE
Poaceae	*Paspalidium geminatum* (Forssk.) Stapf	Matias *et al.* 2003; Moro *et al.* 2014	Hel	1	1	0	0	0
	Paspalum densum Poir.	Normando 2011	Hel	1	0	0	0	1
	Paspalum distichum L. (*)	Moro *et al.* 2014	Hel	1	0	0	0	0
	Paspalum orbiculatum Poir. (*)	Tabosa *et al.* 2012	Hel	0	1	0	0	0
	Paspalum repens P.J.Bergius	Moro *et al.* 2014; Ibiapina-Santos 2016	Hel	1	1	0	0	0
	Paspalum vaginatum Sw.	Matias *et al.* 2003; Moro *et al.* 2014	Hel	1	0	0	0	0
	Reimarochloa brasiliensis (Spreng.) Hitch(*)	Ibiapina-Santos 2016	Hel	1	1	0	0	0
	Rugoloa polygonata (Schrad.) Zuloaga	Normando 2011	Hel	1	0	0	0	1
	Sacciolepis myuros (Lam.) Chase (*)	Normando 2011	Hel	1	0	0	0	1
	Sporobolus virginicus (L.) Kunth(*)	Matias & Nunes 2001	Hel	1	0	0	0	0
	Urochloa arrecta (Hack. ex T.Durand & Schinz) Morrone & Zuloaga	Ibiapina-Santos 2016	Hel	1	1	0	0	1
Podostemaceae	*Apinagia gardneriana* Tul.	Guedes & Nascimento 2016	HAP	0	0	1	0	0
	Mourera aspera (Bong.) Tul. (*)	Guedes & Nascimento 2016	HAP	0	0	1	0	0
Polygalaceae	*Polygala appendiculata* Vell.	Moro *et al.* 2014	Hel	1	0	0	0	0
Polygonaceae	*Polygonum ferrugineum* Wedd.	Moro *et al.* 2014; Paiva *et al.* 2014; Ibiapina-Santos 2016	RE	1	1	1	0	1
	Polygonum hispidum Kunth	Ibiapina-Santos 2016	RE	1	1	0	0	1
Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	Paiva *et al.* 2014; Ibiapina-Santos 2016	FE	1	1	1	0	1
	Eichhornia diversifolia (Vahl) Urb.	Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RLF	0	1	0	1	0
	Eichhornia heterosperma Alexander	Tabosa *et al.* 2012; Ibiapina-Santos 2016; Albuquerque *et al.* 2020	RE	0	1	0	0	0
	Eichhornia paniculata (Spreng.) Solms	Albuquerque *et al.* 2020	RE	0	1	0	0	1
	Eichhornia paradoxa (Mart. ex Schult. & Schult.f.) Solms(*)	Sousa *et. al* 2018	RE	0	1	0	0	0
	Heteranthera oblongifolia Mart. Ex Schult. & Schult.f.	Tabosa *et al.* 2012; Ibiapina-Santos 2016	RE	1	1	0	0	0
	Heteranthera rotundifolia (Kunth) Griseb.	Sousa *et al.* 2018	RLF	0	1	0	0	0
	Heteranthera seubertiana Solms	Sousa *et al.* 2018	RE	0	1	0	0	0
	Hydrothrix gardneri Hook.f.	Tabosa *et al.* 2012	RS	1	0	0	0	1
	Pontederia parviflora Alexander	Ibiapina-Santos 2016	RE	1	1	0	0	0
Potamogetonaceae	*Potamogeton pusillus* L.	Ibiapina-Santos 2016	RS	1	0	0	0	1
Rubiaceae	*Richardia grandiflora* (Cham. & Schlecht.) Steud.	Matias & Nunes 2001	Hel	1	0	0	0	1
	Borreria scabiosoides Cham & Schltdl.	Tabosa *et al.* 2012; Ibiapina-Santos 2016	Hel	0	1	0	0	0
	Borreria verticillata (L.) G.Mey.	Matias *et al.* 2003	Hel	1	0	0	0	0
Sphenocleaceae	*Sphenoclea zeylanica* Gaertn.	Ibiapina-Santos 2016	Hel	0	1	0	0	0
Turneraceae	*Turnera weddelliana* Urb. & Rolfe (*)	Moro *et al.* 2014	Hel	1	0	0	0	0
Typhaceae	*Typha angustifolia* L.	Guedes & Nascimento 2016	RE	1	0	0	0	0
	Typha domingensis Pers.	Ibiapina-Santos 2016	RE	1	1	0	0	0
Xyridaceae	*Xyris jupicai* Rich.	Moro *et al.* 2014	Hel	1	0	0	0	0
	Xyris macrocephala Vahl	Matias *et al.* 2003; Moro *et al.* 2014	Hel	1	0	0	0	0

Discussion

Our hypothesis that lentic ecosystems present more species of aquatic angiosperms was confirmed. However, our results show that the different aquatic ecosystems present distinct species composition and different proportions of sets of growth forms (bottom-rooted submerged, bottom-rooted emergent, bottom-rooted emergent with floating leaves and/or stems, free-swimming submerged, free-floating emergent, haptophytes and helophytes) according to the ecosystem. This result does not corroborate the hypothesis that in permanent lentic ecosystems there would be a greater diversity of growth forms compared to the others.

Cyperaceae and Poaceae were the most representative families in the wetlands of Ceará state. These plant families also constitute the greatest richness of monocotyledons in the world (Bouchenak-Khelladi *et al.* 2014) and exhibit strong dominance in several wetlands worldwide (Sieben 2010; Rodríguez-Arias & Benavides 2016; Oliveira *et al.* 2019). Furthermore, the initial diversification of these plant groups occurred in the Paleogene (Bremer 2002), a period of intense rainfall and open landscapes (Cerling *et al.* 1998), probably in wetlands (Givnish *et al.* 2010). In addition, some Poales are restricted to aquatic ecosystems, such as Typhaceae, Xyridaceae and some genera of Eriocaulaceae (Bouchenak-Khelladi *et al.* 2014), which are also found in Ceará state.

Species of Cyperaceae, Poaceae, Fabaceae, Alismataceae and Malvaceae predominate in the wetland flora of Ceará and are mostly helophytes and bottom-rooted emergent hydrophytes. These growth forms stand out in lotic systems and the margins of lentic systems, habitats usually associated with primary succession. Notably, Cyperaceae and Poaceae species present efficient long-distance dispersal mechanisms and underground systems that allow for effective vegetative propagation (Goetghebeur 1998). Both families usually have the largest number of representatives in aquatic environments (Matias *et al.* 2003; Tabosa *et al.* 2012; Oliveira *et al.* 2019).

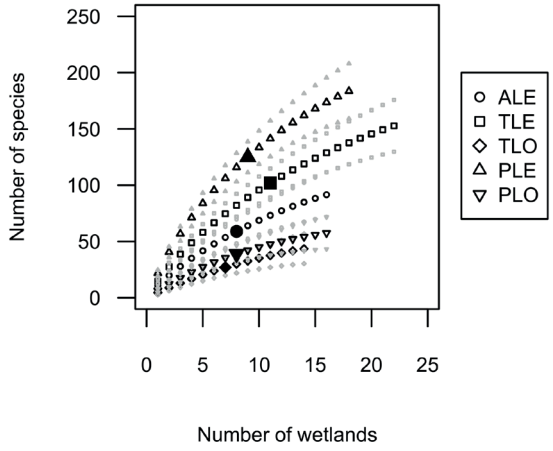

Figure 3. Rarefied and extrapolated (black symbols) number of species in the five ecosystems analysed. Confidence interval at 95% after 1000 randomizations (grey symbols, with the same shape of the correspondent rarefied and extrapolated number of species). The filled symbols are the observed number of species and have the same shape as the rarified and extrapolated number of species. The left side of the observed richness is the rarified and the right side is the extrapolated number of species. ALE = Artificial Lentic ecosystem; PLE = Permanent Lentic ecosystem; PLO = Permanent Lotic ecosystem; TLE = Temporary Lentic ecosystem; TLO = Temporary Lotic ecosystem.

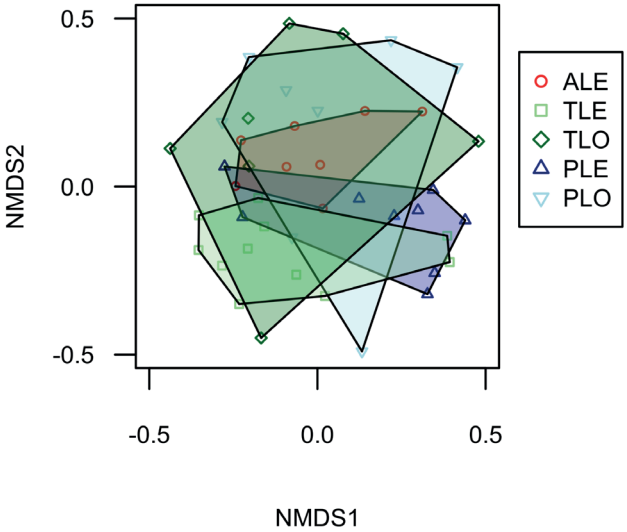

Figure 4. Nonmetric Multidimensional Scaling (NMDS) representing the grouping of the wetlands and their corresponding ecosystems. The PERMANOVA indicated the difference among the five ecosystems ($F = 1.25$; $R^2 = 0.03$; $P = 0.03$; Table 1). ALE = Artificial Lentic ecosystem; PLE = Permanent Lentic ecosystem; PLO = Permanent Lotic ecosystem; TLE = Temporary Lentic ecosystem; TLO = Temporary Lotic ecosystem. The stress of the NMDS is 0.29.

Table 2. Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA) results considering the five different habitats. The interaction is related the two factors: temporary/permanent/artifical and lotic/lentic. ALE = artificial lentic; PLE = permanent lentic; PLO = permanent lotic; TLE = temporary lentic; TLO = temporary lotic wetland.

	DF	Sum of the squares	Mean of the squares	F	R^2	P
Temporary (TLE, TLO)/ Permanent(PLE, PLO)/ Artificial (ALE)	2	1.22	0.61	1.36	0.06	0.001
Lentic (ALE, PLE, TLE)/ Lotic (PLO, TLO)	1	0.77	0.77	1.72	0.04	0.0002
Interaction	1	0.56	0.56	1.26	0.03	0.039
Residuals	38	16.99	0.44		0.86	
Total	42	19.54			1	

The greatest species richness was found in permanent and temporary lentic ecosystems with the largest number of exclusive species (56.16 %). The stability of the water column contributed to species with different growth forms being able to colonize these ecosystems, resulting in local dominance of one or a few species and evident zonation patterns along environmental gradients from shoreline to limnetic zone border as a function of the variation in water depth (Spence 1982; McCreary 1991).

In the shallow coastal zone, the co-occurrence of helophytes and bottom-rooted hydrophytes constitute a stratified vegetation (Den Hartog & Segal 1964), related to the typically strong competition among aquatic plant species (Gopal & Goel 1993). And, as a greater number of species tend to co-occur at shallower depths in lentic systems of Ceará (Matias *et al.* 2003), helophytes and bottom-rooted emergent hydrophytes, represented by the Cyperaceae, Poaceae, Fabaceae, Alismataceae and Malvaceae families, predominate along the banks of the aquatic ecosystems of the state. In the limnetic region, assemblages tend to constitute strata of free-swimming submerged forms according to a gradient of light intensity as a function of

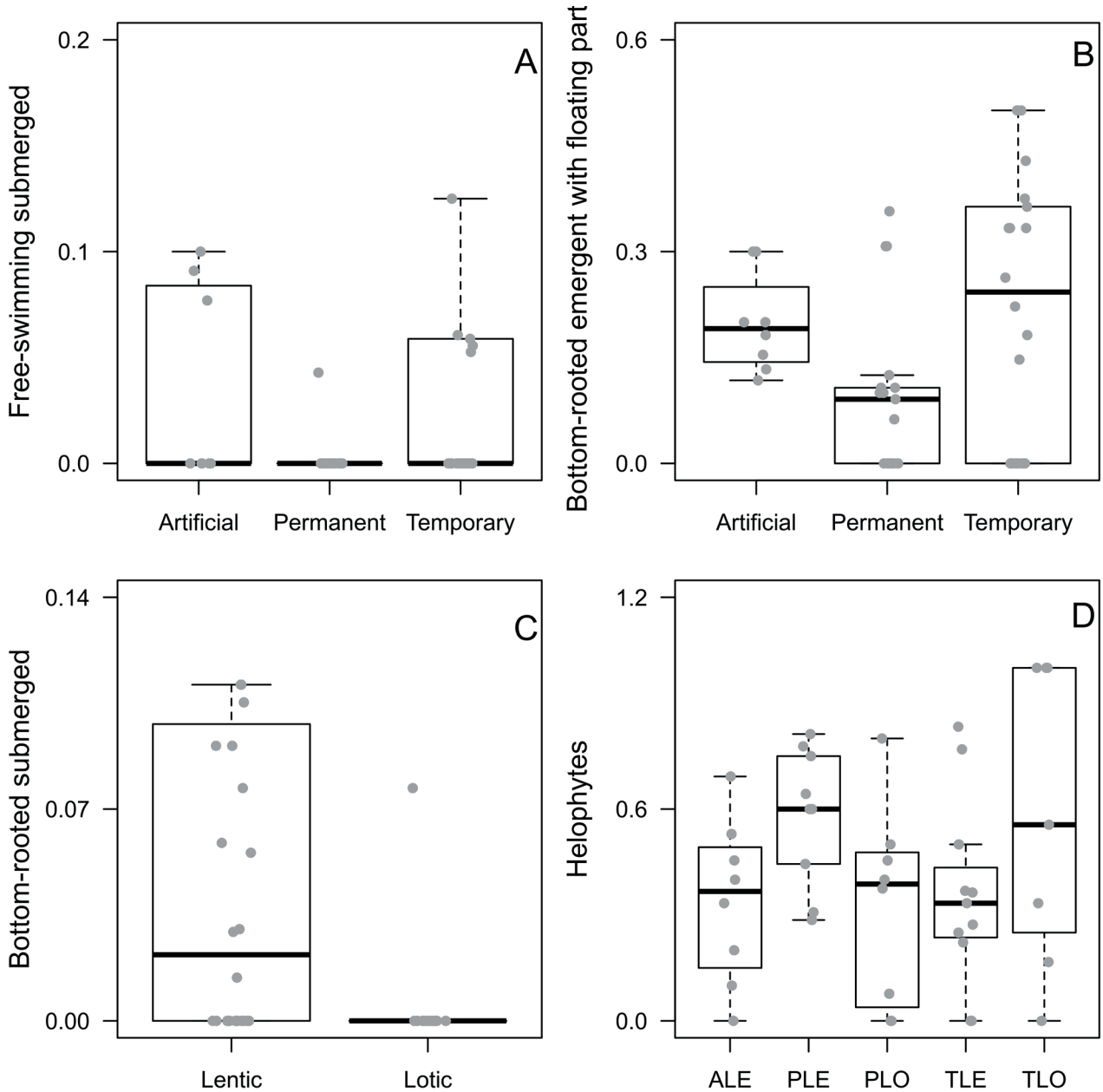

Figure 5. Boxplots showing the distribution of the proportion of growth forms among the aquatic ecosystems. **A-B.** Artificial, permanent, temporary; **C.** lentic and lotic; **D.** different combinations of both. We show only the significant results in Table S2 in supplementary material. ALE = Artificial Lentic ecosystem; PLE = Permanent Lentic ecosystem; PLO = Permanent Lotic ecosystem; TLE = Temporary Lentic ecosystem; TLO = Temporary Lotic ecosystem. Grey points: the proportions of the life-form in the aquatic ecosystems.

water depth (Rørslett & Agami 1987) and occasionally, free-floating and bottom-rooted submerged forms in the extremes of the water column (Spence 1982).

The free-floating species showed no significant difference in the proportion of records among the aquatic ecosystems, but the proportion of free-swimming submerged and bottom-rooted emergents with floating leaves and/or stems was different between the artificial and natural lentic systems, and between natural lentic and lotic ones. Submerged plants interact intrinsically with the functioning of aquatic ecosystems, mobilizing nutrients and providing habitats for smaller dominant omnivore-planktivores (Meerhoff *et al.* 2003). Bottom-rooted emergents with floating leaves and/or stems can occupy the entire water column, especially in shallow lakes, resulting in the vanishing of submerged plants by accumulation of organic matter in the sediment and eutrophication of the environment due to the high production of floating leaf blades (Klok & Velde 2017). Thus, these species assemblages affect, among other factors, the trophic levels of lentic ecosystems (Barko *et al.* 1986), resulting in a wide variation of growth forms.

The assemblages that compose the artificial aquatic systems include *Utricularia foliosa* and *Ceratophyllum demersum*, both free-swimming species. The shift in water flow allows submerged plants to form extensive vegetation banks that influence the dynamics of nutrients between water and sediment (Barbosa *et al.* 2020), constituting a common aspect in reservoirs of the Brazilian semiarid region. Other plants like *Ludwigia helminthorrhiza*, *Neptunia oleracea*, *N. plena*, *Nymphaea amazonum*, *N. lasiophylla*, *N. lingulata* and *Nymphoides humboldtiana* compose the assemblages of these systems as bottom-rooted emergents with floating leaves and/or stems. These species share a fast rate of vegetative reproduction, either by rhizomes or by stolons, so that in formations mixed with submerged macrophytes they present a pattern of relationship alternating between negative and positive interactions (Lycarião & Dantas 2017). Additionally, they are generalists, except for *N. ligulata* (Sousa & Matias 2013), and are found in most Brazilian regions (Flora do Brasil 2020 2020). Furthermore, there are fewer species in artificial systems than in natural lentic systems in Ceará state (14 or 6.39 % are common species).

On the other hand, the proportion of bottom-rooted submerged forms was different between the lentic and lotic systems, with records of the following species limited to lentic ecosystems: *Eriocaulon setaceum*, *Cabomba haynesii*, *Hydrothrix gardneri*, *Potamogeton pusillus* and all Hydrocharitaceae species, with restricted occurrence of *Najas marina* in permanent lentic ecosystems. Species with this growth form were not recorded in lotic systems, probably due to their vulnerability to complete their life cycle due to abiotic factors such as water currents (Power *et al.* 2016).

Aquatic plant richness is related to other environmental factors in lentic systems (Alahuhta *et al.* 2014; Ferreira *et al.* 2015), which makes it difficult to generalize about the diversity of these ecosystems (Bubíková & Hrivnák 2018). However, it is possible to observe that there is a set of exclusive species that are evolutionarily associated with these ecosystems. In this study, representatives of Nymphaeales (Cabombaceae, Nymphaeaceae), Monocotyledons (Alismataceae, Araceae, Hydrocharitaceae, Marantaceae, Potamogetonaceae, Pontederiaceae, Thyphaceae) and a few Eudicotyledons (Lentibulariaceae, Menyanthaceae, Hydroleaceae) have records limited to lentic ecosystems. Some of these families (Alismataceae, Araceae, Hydrocharitaceae, Lentibulariaceae, Pontederiaceae) have species with progressive adaptation to the aquatic environment, an evolutionary trend in monocots that is associated with vegetative differentiation more than in any other angiosperm group (Kremer & Andel 1995).

In temporary lentic ecosystems, different growth forms colonize the entire water column in a space-time dynamic, *i.e.*, these ecosystems have high species turnover (Tabosa *et al.* 2012). Thus, the species have not only overlapping niches, but are also phylogenetically related species and tend to compete among themselves (Ferreira *et al.* 2015). In these environments, few families did not have records, either because they are not associated with habitat specificity or because the populations are restricted to permanent lentic ecosystems (Araliaceae, Burmanniaceae, Linderniaceae, Potamogetonaceae, Xyridaceae), reflected by a considerable number of exclusive species (45 or 20.54 % are exclusive to temporary lentic ecosystems). This shows that natural temporary lentic ecosystems contribute to the maintenance of aquatic plant richness in Ceará state, being recognized that natural ponds contributed most to regional biodiversity, supporting significantly many more species, more unique species and more rare species than other waterbody types (Williams *et al.* 2003).

The hydrophytes that have records restricted to these ecosystems were *Eichhornia heterosperma*, *Eichhornia paradoxa*, *Heteranthera rotundifolia*, *Heteranthera seubertiana*, *Lemna minuta*, *Utricularia hydrocarpa*, and the species endemic to northeastern Brazil, *Echinodorus palaefolius* and *Echinodorus pubescens*.

In contrast, the movement of the water column in lotic ecosystems is considered a significant driver of macrophytes diversity (Lacoul & Freedman 2006; Bornette & Puijalon 2011) because water speed selects species with morphological adaptations like streamlined shapes, strap-like leaves or flat shoots (Chambers *et al.* 1991).Other adaptations include those that allow plants to attach firmly to the rocky substrate in rapid streams and waterfalls by specialized structures, such as disk-like holdfasts (haptera) found in Podostemaceae (Rutishauser *et al.* 2005), so that only *Apinagia gardneriana* and *Mourera aspera* have records limited to these ecosystems (Bubíková & Hrivnák 2018). In the present study, lotic ecosystems showed low values of richness and a low number of exclusive species (12 or 5.47 %).

The rivers of the semiarid region present wide variation in the water column due to rainfall irregularity, selecting species with high resistance and resilience in response to hydric disturbances (Maltchick & Pedro 2001). This may influence the low number of exclusive species, which tend to present mechanisms for survival in temporary environments based on ruderal strategies, due to the desiccation of the habitat and the consequent loss of biomass during the dry season (Albuquerque *et al.* 2020).

In temporary lotic systems, floods and droughts cause disturbances with different intensity, frequency and duration, determining the occurrence of aquatic communities. Therefore, species richness was lower in the puddles of the rivers and streams subject to flood events when compared to ponds (Pedro *et al.* 2006). This dynamic can explain the low richness found in the temporary rivers of Ceará, with the lowest number of exclusive species (8 or 3.65 %).

Artificial lentic ecosystems showed species richness (86 spp.) close to the richness of lotic systems (83 spp.), and lower than natural lentic systems (359 spp.). Considering only the hydrophytes, the species that occupy these systems tend to be generalists (*Echinodorus subalatus*, *Nymphaea amazonum, Neptunia plena, Ludwigia helminthorrhiza* and *L. leptocarpa*) or species with predominant occurrence in natural lentic ecosystems with free-floating growth form (*Lemna aequinoctialis*, *Pistia stratiotes*, *Spirodela intermedia*, *Wolffiella welwitschii*), free-swimming submerged (*Utricularia foliosa*), bottom-rooted submerged (*Cabomba haynesii*, *Apalanthe granatensis*, *Egeria densa*, *E. najas*, *Najas arguta*, *N. conferta*, *Potamogeton pusillus*) and bottom-rooted emergent forms (*Echinodorus subalatus*, *Helanthium tenellum*, *Bacopa aquática*, *Stemodia foliosa*, *S. marítima*, *Polygonum ferrugineum* and *P. hispidum*). These artificial systems exhibit irregular water level fluctuations related to the modifications of the reservoirs by human activity, being considered a special type of lentic environment (Hutchinson 1957), so that only a few species with free-floating forms have records from these environments in Ceará state: *Eichhornia crassipes*, *Lemna aequinoctialis* and *Spirodela intermedia*. The free-floating macrophytes tend to be limited by stream speed, being common in slow-flowing streams (Grinberga 2011), or when intercepted, tend to predominate in reservoirs (Paiva *et al.* 2014) mainly during the dry season (Lycarião & Dantas 2017).

Among the species that occur in all five ecosystems, *P. stratiotes* has a pantropical distribution, while *E. subalatus*, *N. amazonum, N. plena, L. helminthorrhiza* and *L. leptocarpa* are of wide distribution in Brazil (Flora do Brasil 2020 2020) and in the American continent (Tropicos® 2020). Some aquatic plants with wide distribution tend to present high levels of polymorphism and phenotypic plasticity related to environmental variables, allowing them to occur over a wide range of conditions (Lacoul & Freedman 2006). Wide morphological variability in populations occurring in Ceará has been described for *E. subalatus* (Matias 2007), *N. amazonum* (Sousa & Matias 2013) and *P. stratiotes* (Andrade *et al.* 2013), which explains how these species tend to occupy different aquatic environments.

Helophytes predominated in the aquatic systems of Ceará state, accounting for 65 % of the species. Vegetative reproduction is a predominant trait in this group, which may assure population maintenance at the ecological time scale (Li 2014). These species colonize the margins of aquatic systems forming assemblages that are affected by the dynamic of the substrate and the water (Deil *et al.* 2011). In addition to cryptophytic species, annual species occupy the margins of these systems, declining when the margins are little impacted by abiotic factors (*e.g.* waves) or when nutrients in substrate favour an increase in biomass and establishment of perennial rhizomatous helophytes (Hernández & Rangel 2009).

An unusual finding in this study was that only the proportions of helophytic species differed in relation to the five types of aquatic systems. Among all the factors, the interactions between terrestrial and aquatic environments can explain the distribution and abundance of aquatic plants in many interaction scenarios (Lacoul & Freedman 2006). Moreover, the organization of plant assemblages, regardless of the aquatic system type, may be influenced by biotic unpredictability, given that in arid regions ecological variability in life cycles is influenced by highly variable and unpredictable flow regimes and the impacts of land use and water resources (Choy *et al.* 2002).

The results showed that all waterbody types contributed to the macrophytes richness in the state, although lentic ecosystems have the highest richness values and exclusive species. So that the preservation of this flora must be considered not only for a specific type of aquatic ecosystem but for all possible types of freshwater habitats in Ceará state.

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