






## Environmental heterogeneity in wetlands increases alpha and beta diversity of cladocerans (Crustacea, Branchiopoda) at local and regional scale

A heterogeneidade ambiental em áreas úmidas aumenta a diversidade alfa e beta de cladóceros (Crustacea, Branchiopoda) em escala local e regional

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**Abstract: Aim:** The goal of this study was to investigate the effect of habitat heterogeneity on diversity on a local and regional scale. We tested two hypotheses: (i) the habitat diversity, given by quantity of microhabitat by macrophytes richness, increases the alpha diversity of organisms that live in those environments; (ii) the habitat heterogeneity, given by compositional difference of microhabitat, increases the beta diversity of organisms that live in those environments. **Methods:** Samples contained cladocerans and macrophytes were collected in six wetlands from the Brazil Central during dry and rainy seasons, in Brazilian National Park (BNP) and Formosa Instruction Field (FIF). **Results:** In local scale (wetlands) the number of macrophyte morphospecies shows the positive effect on alpha diversity of cladoceran; the compositional difference of the microhabitat positively affected the beta diversity in three wetlands studied. In regional scale, the number of macrophyte morphospecies showed the positive effect on alpha diversity; the beta diversity was higher in the BNP than in the FIF. **Conclusions:** Our findings suggest that the species richness and dissimilarity of aquatic macrophytes increased to alpha and beta diversity of cladocerans on the local and regional scales. Thus, cladocerans richness was correlated with the number of microhabitats and the variability between microhabitats in wetlands.

**Keywords:** Chydoridae, microcrustaceans, microhabitats, wetlands.

**Resumo: Objetivo:** O objetivo deste estudo foi investigar o efeito da heterogeneidade do habitat na diversidade de cladóceros em escala local e regional. Nós testamos duas hipóteses: (i) a diversidade de habitat, dada pela quantidade de microhabitat, aumenta a diversidade alfa de organismos que vivem nesses ambientes; (ii) a heterogeneidade de microhabitat, dada pela diferença de composição do microhabitat, aumenta a diversidade beta dos organismos que vivem nesses ambientes. **Métodos:** Amostras de cladóceros e de macrófitas foram coletadas em seis áreas úmidas do Brasil Central, durante as estações seca e chuvosa, no Parque Nacional de Brasília (BNP) e no Campos de Instrução



de Formosa (FIF). **Resultados:** Em escala local (áreas úmidas), o número de morfoespécies de macrófitas mostrou um efeito positivo na diversidade alfa de cladóceros; a diferença de composição do microhabitat afetou positivamente a diversidade beta em três áreas úmidas estudadas. Em escala regional, o número de morfoespécies de macrófitas mostrou efeito positivo na diversidade alfa; a diversidade beta foi maior em BNP do que em FIF. **Conclusões:** Nossos resultados indicam que a riqueza e dissimilaridade de espécies de macrófitas aquáticas aumentaram a diversidade alfa e beta de cladóceros em escala local e regional. Assim, a riqueza de cladóceros foi correlacionada ao número e a variabilidade de microhabitats em áreas úmidas.

**Palavras-chave:** Chydoridae, microcrustáceos, microhabitats, áreas úmidas.

## 1. Introduction

The role of macrophytes in structuring aquatic communities is an increasingly relevant question when concerning the factors that govern diversity in freshwater aquatic ecosystems. The aquatic macrophytes play an important role to invertebrates because provide complex interaction among abiotic and biotic which support the biodiversity, such as: structural complexity and heterogeneity of microhabitats (Pelicice et al., 2008; Thomaz et al., 2008); permanent habitat for some species (littoral species) while foraging area to others (planktonic species).

At the same time, macrophytes support the food to invertebrates because is the habitat of periphyton algae, support predatory interactions (Burks et al., 2002). In fact, the presence of macrophytes is related to patterns of distribution, foraging, ecomorphology and diversity of both vertebrates and invertebrates (Rennie & Jackson, 2005; Hornung & Foote, 2006; Agostinho et al., 2007; Hansen et al., 2011; Deosti et al., 2021; Espinosa-Rodríguez et al., 2021; Quirino et al., 2021).

Macrophytes are remarkably diverse, with many species exhibiting a variety of lifestyles and morphologies (Vieira et al., 2007; Padial et al., 2009; Hinojosa-Garro et al., 2010; Thomaz & Cunha, 2010; Lucena-Moya & Duggan, 2011). These characteristics also favor the formation of different microhabitats, which in turn lead to an increased spatial heterogeneity and a potential association with an increased diversity of aquatic invertebrates (Nogueira et al., 2003; Braghin et al., 2016).

Among such invertebrates, the microcrustaceans of the Superorder Cladocera stand out for the high number of species that associate with macrophytes, especially when compared to pelagic zone (Castilho-Noll et al., 2010; Forró et al., 2008; Gebrehiwot et al., 2017; Smirnov, 1992, 1996). Many studies evaluated the structure and aspects of cladoceran assemblages in macrophyte-dominated environments (*e.g.*, Whiteside & Harmsworth, 1967; Hann & Turner, 2000; Elmoor-Loureiro,

2007; Sousa et al., 2009). However, most of these studies did not evaluate any possible correlations between the number of macrophyte species and the diversity of these microcrustaceans.

The number of macrophyte species in multispecific bank might be more important than structural complexity of a monospecific bank compound by one macrophyte species, considered highly complex, for instance. This can occur because the biological diversity of macrophytes in multispecific banks, resulting mainly from competition and abiotic interactions, also supports many ecological interactions in those communities that use the macrophytes as microhabitats to realize at the least one step of their life cycle. The mechanism raised here suggests that heterogeneity given by multispecific banks goes beyond the structural complexity because increase the biological complexity, *i.e.* increase the chances for more ecological interactions to happen, resulting in higher biodiversity.

This highlights the gaps in the knowledge regarding cladoceran diversity and its association with the aquatic vegetation, even though these two components of the aquatic biota represent good models to test ecological hypotheses, including those related to the environmental heterogeneity theory. The wetlands of the Cerrado in central Brazil are excellent environments to evaluate the spatial heterogeneity provided by the aquatic vegetation and its effects on cladoceran diversity, because they are densely colonized by macrophytes and harbor diverse microcrustacean communities (Reid, 1984, 1987, 1993; Sousa & Elmoor-Loureiro, 2008).

We aimed to investigate the effect of habitat heterogeneity on diversity on a local and regional scale. The following hypotheses were evaluated: (i) the habitat diversity, given by quantity of microhabitat by richness of macrophytes, increases the alpha diversity of organisms that live in those environments; (ii) the habitat heterogeneity, given by compositional difference of microhabitat, increases the beta diversity of organisms that live in those environments.

## 2. Material and Methods

### 2.1. Study Area, sampling and identification of *Cladocera*

The study was performed in central Brazil, in two areas harboring unaltered Cerrado fragments. The Brasília National Park (BNP) and the Formosa Instruction Field (FIF). The BNP is located in the Federal District and is its largest Integral Protection Conservation Unit with 42,389 hectares. On this study, three wetland areas were sampled inside the BNP: Henrique pond (HE - 15°41'18"S 47°56'10"W), Exército pond (EX - 15°44'44,3"S 47°58'49,1"W) and Peito de Moça pond (PM - 15°45'05,8"S 48°01'33,2"W).

The FIF is an area administered by the Brazilian Army, located in the state of Goiás, border the Federal District to the east and the state of Minas Gerais to the South. The FIF comprises a large and well-preserved Cerrado fragment, and harbors many aquatic ecosystems such as lotic systems, lagoons and wetlands. In this study, we sampled the following natural wetlands inside the FIF: Cabocla I pond (CBI - 15°48'16,6"S 47°14'58,8"W), Cabocla II pond (CBII - 15°48'22,6"S 47°14'10,6"W) and Grande pond (GR - 15°49'37,3"S 47°13'50,8"W). All the sampled wetlands are densely covered with macrophytes. Cladocerans were collected through a gradient of depth and using a plankton net dragged among aquatic vegetation; the experimental design and protocols for cladoceran sampling and identification follow Sousa et al. (2014).

### 2.2. Physical and chemical variables

We measured 11 physicochemical water parameters: temperature, pH, electrical conductivity, dissolved oxygen, turbidity, dissolved solids, suspended solids, total nitrogen, dissolved inorganic nitrogen, reactive soluble phosphorus, and total phosphorus. Measurements of temperature, pH, electrical conductivity and dissolved oxygen were taken in the field using specific probes. For all other variables, we collected 5L of water using a manual suction pump. The methods used for the remaining variables followed the *Standard methods for examination of water and wastewater* (APHA, 2005). Dissolved inorganic nitrogen corresponded to the sum of the amounts of nitrate (N-NO<sub>3</sub><sup>-</sup>), nitrite (N-NO<sub>2</sub><sup>-</sup>) and ammonium (N-NH<sub>4</sub><sup>+</sup>).

### 2.3. Macrophyte sampling and identification

We collected macrophytes following the experimental design described in Sousa et al. (2014, p. 145):

[...] a transect was installed from the lowest depth of water table toward the center of the water body and sample points were chose based in changes in the depth or in macrophyte assemblage; in each sampling point, a perpendicular line up to 24 m was established for data collection.

Thus, were collected least two specimens of each macrophyte morphospecies observed within perpendicular line. All vegetal material collected was herborized following the usual procedure for terrestrial plants, except for submerged macrophytes, which were stored in 90% ethanol. We identified the plant material to the lowest possible taxonomic level, using specialized literature (Pott & Pott, 2000; Munhoz et al., 2011). Afterwards, we deposited them in the herbarium of the Universidade de Brasília. A list of the macrophytes encountered is found in Sousa (2012).

### 2.4. Statistical analyses

Species richness for both cladocerans and macrophytes for each wetland were compared using a sample-based rarefaction analysis. Our experimental design was realized in two scales: in the local scale the grain was in each wetland (HE, EX, PM, CBI, CBII, and GR) whereas in the regional scale the grain was in each area (BNP and FIF).

The effect of habitat heterogeneity on cladoceran alpha diversity was tested using a General Linear Model, where: cladoceran species richness was dependent variable; macrophyte species richness was independent variable; and, each scale was the variable conditioned. The homoscedasticity was assessed by visual inspection of residuals. Normality was tested with a shapiro-test of the residuals model and the linearity using the significance of linear coefficient. For this analysis, all data were log x+1 transformed and evaluated with a regression analysis.

The effect of the habitat heterogeneity on cladoceran beta diversity was tested using a Mantel Test with 999 randomizations. We estimated the habitat heterogeneity among sites computing the Jaccard dissimilarity matrix of the macrophyte composition. The cladoceran beta diversity was computed using the Jaccard dissimilarity matrix.

Moreover, on a regional scale, we also measured the variability of species composition of cladocerans for the wetlands in the BIP and FIF. To do so, the *betadisper* function of the Vegan package was used to check the observed dispersion homogeneity related to species composition. Following that, we performed a permutation test (999 randomizations) to evaluate if there are significant differences among

the areas concerning dissimilarity (Anderson et al., 2006). All analysis was performed in the R environment using the vegan package.

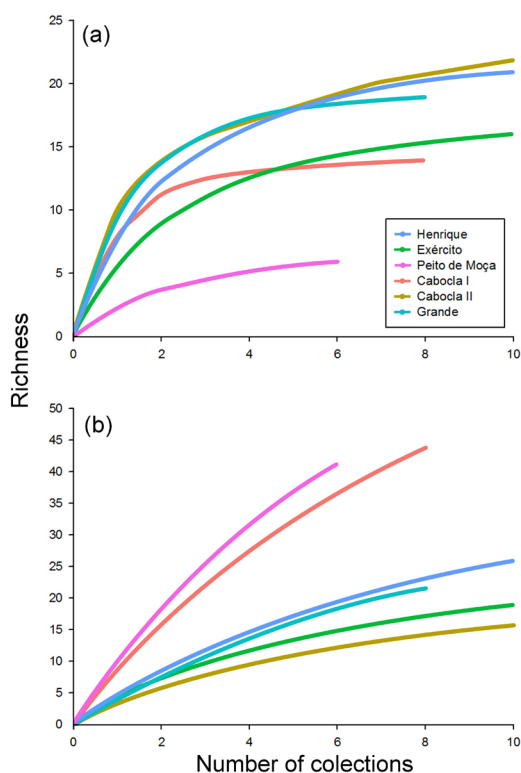
### 3. Results

#### 3.1. Physicochemical parameters

The Table 1 shows the results regarding the physicochemical water parameters. The sampled wetlands exhibit, on average, low levels of electrical conductivity and dissolved oxygen. The pH values found indicate slightly acidic waters, with values always below six. Regarding the nutrients, the studied areas exhibit low levels of nitrogen and phosphorus, on average.

#### 3.2. Local effect of the diversity of habitat on taxonomic diversity of Cladocera

The rarefaction analysis showed the highest cladoceran richness in CBII, followed by HE, GR, EX, CBI, and PM (Figure 1a) wetlands. The number of macrophytes varied between wetlands: the minimum was 14 morphospecies in CBII and the maximum 43 species (Figure 1b). Regardless of the wetland, the number of macrophyte shows the positive effect on alpha diversity (ANCOVA; coefficient = 0.816; p-value < 0.001;  $R_{Adj}^2 = 0.76$ )



**Figure 1.** (a) Sample-based rarefaction analysis to cladoceran for the wetlands studied. (b) Sample-based rarefaction analysis to macrophytes for the wetlands studied.

**Table 1.** Mean, standard deviation and variation coefficient for the physicochemical water parameters in wetlands of the Brasília National Park and Formosa Instruction Field.

	Wetland					
	HE	EX	PM	CBI	CBII	GR
	(N=10)	(N=10)	(N=6)	(N=8)	(N=10)	(N=8)
Water temperature (°C)	25.50±3.09 12.11%	24.34±1.78 7.30%	24.22±2.95 12.17%	24.81±1.06 4.28%	22.33±3.72 16.68%	27.11±4.42 16.30%
Electrical conductivity (µS cm <sup>-1</sup> )	4.93±2.05 41.60%	4.78±1.24 25.86%	7.75±2.87 36.89%	5.74±1.58 27.51%	5.07±0.95 18.78%	4.88±2.36 48.48%
Dissolved oxygen (mg L <sup>-1</sup> )	4.88±0.75 15.45%	5.51±0.99 17.89%	4.97±0.55 11.13%	4.73±0.82 17.25%	3.73±0.74 19.83%	4.79±0.90 18.73%
pH	5.11±0.21 4.08%	5.50±0.44 7.97%	5.57±0.41 7.52%	5.02±0.11 10.84%	5.39±0.27 5.07%	5.72±0.49 8.58%
Inorganic nitrogen (µg L <sup>-1</sup> )	96.27±48.74 50.63%	91.91±43.94 47.81%	87.15±25.39 29.13%	127.68±47.49 37.20%	174.88±87.18 49.85%	110.71±29.30 26.43%
Total nitrogen (µg L <sup>-1</sup> )	178.88±106.72 59.60%	197.40±108.57 54.85%	164.47±119.58 72.66%	123.88±56.73 45.80%	173.35±86.94 50.15%	117.35±32.72 27.88%
Soluble reactive phosphorus (µg L <sup>-1</sup> )	1.58±0.95 60.18%	5.53±10.13 183.5%	1.07±0.12 11.35%	4.03±2.58 64.04%	2.96±1.67 56.42%	2.99±1.94 65.06%

HE = Henrique Pond; EX = Exército Pond; PM = Peito de Moça Pond; CBI = Cabocla I Pond; CBII = Cabocla II Pond; GR = Grande Pond.

(Figure 2). The compositional difference of the microhabitat positively affected the beta diversity of CBI, LE, and LH, while that negatively affected the beta diversity in PM (Table 2).

3.3. Regional effect of the habitat diversity on species richness

Regardless of the protected areas, the number of macrophyte shows the positive effect on alpha diversity (ANCOVA; coefficient = 0.463; p-value < 0.001;  $R^2_{Adj} = 0.36$ ) (Figure 3). The compositional difference of the microhabitat in regional scale positively affected the beta diversity (Table 3). Beta diversity was higher in the BNP than in the FIF ( $F = 10.384$ ;  $p = 0.002$ ) (Figure 4).

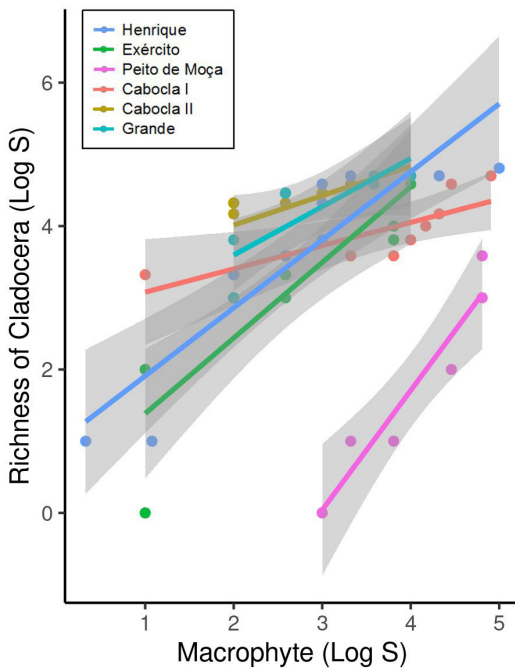


Figure 2. Cladoceran species richness in relation to macrophyte species richness in local scale.

Table 2. Mantel test between distance compositional matrix of macrophytes and distance compositional matrix of Cladocera. Both matrices were computed based on Jaccard dissimilarity.

	R-Mantel	p-value
CBI	0.39	<b>0.024</b>
CBII	0.08	0.321
EX	0.35	<b>0.031</b>
GR	0.05	0.372
HE	0.35	<b>0.05</b>
PM	-0.57	<b>0.03</b>

HE = Henrique Pond; EX = Exército Pond; PM = Peito de Moça Pond; CBI = Cabocla I Pond; CBII = Cabocla II Pond; GR = Grande Pond.

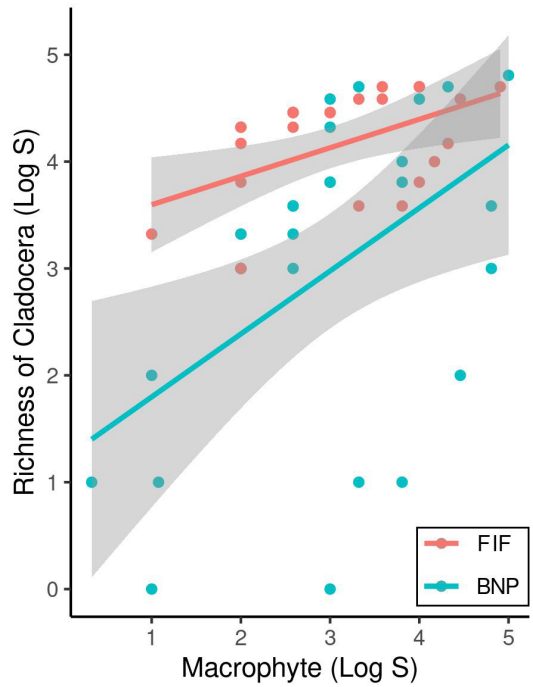


Figure 3. Cladoceran species richness in relation to macrophyte species richness in regional scale. BNP = Brasília National Park; FIF = Formosa Instruction Field.

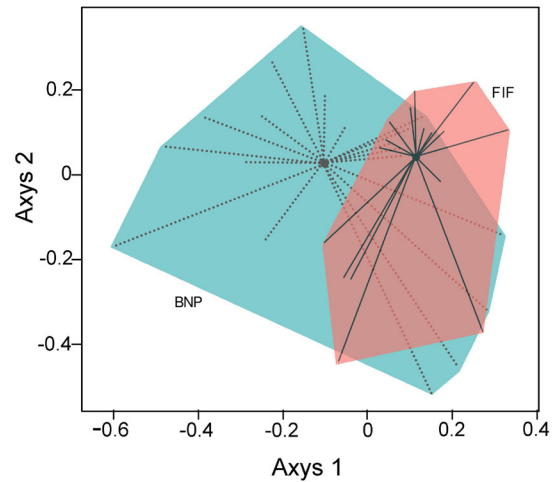


Figure 4. Principal coordinate analysis of the centroid distance resulting from the *betadisper* function. BNP = Brasília National Park; FIF = Formosa Instruction Field.

Table 3. Mantel test between distance compositional matrix of macrophytes and distance compositional matrix of Cladocera. Both matrices were computed based on Jaccard dissimilarity.

	R-Mantel	p-value
BNP	0.20	<b>0.007</b>
FIF	0.16	<b>0.019</b>

BNP = Brasília National Park; FIF = Formosa Instruction Field.

#### 4. Discussion

According to Fonseca et al. (2018), the wetlands studied should be considered poor in nutrients, thus, might be classified as oligotrophic environments. Such result is a pattern related to pristine water bodies in Brazilian Cerrado (Reid, 1984; Fonseca & Mendonça-Galvão, 2014). At the same time, the reduced concentration of nutrients in the studied wetlands seem to have not a negative effect on the diversity due high observed richness of algae, cyanobacteria, testate amoebae, macrophytes and microcrustaceans (Fonseca et al., 2018).

We recorded that the species richness and dissimilarity of aquatic macrophytes increased to alpha and beta diversity of cladocerans on the local and regional scales. We argue that the availability of microhabitats (macrophyte species richness) supports more ecological niches and, therefore, it favors more and different species. Moreover, the heterogeneity of microhabitats (higher macrophyte beta diversity) increased the cladoceran turnover, because the higher microhabitats variation also allows a higher number of different cladoceran species to share the same site. The habitat mosaic provided by aquatic macrophytes affects the species composition and distribution of aquatic invertebrate assemblages (Sakuma & Hanazato, 2002; Geraldts & Boavida, 2004; Walseng et al., 2006; Castilho-Noll et al., 2010; Braghin et al., 2016; Kuczyńska-Kippen & Joniak, 2016). The macrophytes are a strong indicative of spatial heterogeneity and complexity because different species of macrophytes can be spatially arranged in a particular manner in each water body according to factors such as depth levels and the life-history aspects of the species considered (Gledhill et al., 2008; Kuczynska-Kippen, 2009).

Another attribute related to species as functional units is that not all individuals belonging to them exhibit the exact same morphological features, are in the same developmental stage or display the same health conditions, which grants these individuals different conditions and provides habitats with different resources (Cronk & Fennessy, 2001; Trochine et al., 2009). This can lead to a type of ecological relationship as those reported in the wetlands of our study, especially because cladocerans tend to be a dominant fauna in environments with presence of macrophytes (Braghin et al., 2016; Gebrehiwot et al., 2017).

Macrophytes increases ecological complexity through higher resource availability because it provides a range of surfaces for colonization by numerous organisms, including periphytic algae

and closely related organisms, bacteria, ciliates, flagellates (Schwarzbold, 1990; Meerhoff et al., 2007; Buosi et al., 2011), which works as food resource to cladocerans. Macrophytes also are recognized to be the home of more dense and diverse zooplankton communities (Gebrehiwot et al., 2017) because they reduce the foraging activity of planktivorous fish (Thomaz et al., 2008) and serve as a refuge for zooplankton against predation (Burks et al., 2002). Altogether, such ecological features might be related to the high diversity of organisms found inhabiting macrophytes.

In the regional scale, we found positive association between cladoceran beta diversity and macrophyte dissimilarity suggesting that cladoceran beta diversity in the studied wetlands are the result of habitat differentiation provided by the aquatic vegetation. According to Shmida & Wilson (1985), one of the main determinants of species composition variability is habitat diversity. Our results support this statement, considering that aquatic macrophytes displayed a high relative importance for the dissimilarity of cladoceran species: the increase in the vegetation dissimilarity implies in an increase in habitat diversity and in the distribution of different ecological niches, generating a similar response for the phytophile fauna. In other words, the variability in cladoceran species composition followed the habitat structure modifications generated by the aquatic vegetation (Choi et al., 2014).

More recently, investigations have highlighted the importance of shallow wetlands (Scheffer et al., 2006; Gledhill et al., 2008), such as those from our study. Some studies indicate that these wetlands support a considerable portion of the aquatic biodiversity in the landscape scale (e.g., Boix et al., 2008; Céréghino et al., 2008; Gebrehiwot et al., 2017), harboring a high level of species endemism and an elevated number of rare species when compared to other aquatic environments (Fonseca et al., 2018), such as large lakes. In this sense, the results brought here show an elevated diversity of cladoceran species sustained mainly by different environmental settings and corroborate with the necessity to conserve aquatic vegetation of littoral water bodies and wetlands.

In conclusion, we found that the number of macrophytes and compositional difference of the microhabitat positively affected the alpha and beta diversity of Cladocera in local and regional scales. The beta diversity was higher in the Brazilian National Park than in the Formosa Instruction Field. Thus, our findings suggest that aquatic

macrophytes displayed a high relative importance for cladoceran species in the wetland studied due to an increase in habitat diversity.

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## Data availability

The data that support the findings of this study might be found in Sousa (2012) and Sousa et al. (2014).

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