

# Article

# Influence of *Eichhornia crassipes* (Mart) Solms on a Tropical Microcrustacean Community Based on Taxonomic and Functional Trait Diversity

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Abstract: Macrophytes are important structural attributes of freshwater ponds and wetlands, affecting zooplankton community composition. One of the best-known macrophytes in the world is Eichhornia crassipes, which, due to its high reproductive rate, can quickly occupy large areas of aquatic environments. However, there have been few assessments of the direct effect of this macrophyte, in the absence of predators, for tropical zooplankton communities. The aim of this study was to evaluate the influence of *E. crassipes* on microcrustacean community structure using species and functional diversity, the latter providing an important tool to evaluate the response to changes in resource availability along an environment gradient. We also evaluated which functional traits were favored when the structural niche offered by submerged parts of the macrophytes was present. We conducted a 30 day mesocosm experiment (117 m<sup>3</sup>) with and without the presence of floating macrophytes (Eichhornia crassipes) inserted along one edge of the mesocosms. Treatment effects on microcrustacean density and community structure using taxonomic and functional classification approaches were assessed. There was a positive association between macrophyte presence and microcrustacean diversity for both diversity types, showing that the presence of macrophytes enhanced the niche availability for the microcrustacean community, likely through changes to resource diversity through habitat structure provision. In the presence of macrophytes, the abundance of species with the following feeding traits increased: burrowing, benthic habitat preference, and herbivore-detritivore and omnivore-carnivore trophic groups. Results showed that the species capable of using the niche offered by submerged macrophyte structures had benthic traits, enabling their co-existence with species possessing primarily pelagic traits. Using a functional approach, our study demonstrated that Eichhornia crassipes can structure microcrustacean communities and promote diversity, likely via increased habitat diversity, which enables the co-existence of species possessing different adaptations to acquiring resources available in the environment.

**Keywords:** free-floating plants; habitat complexity; littoral zone; mesocosm; zooplankton; horizontal distribution



#### 1. Introduction

In aquatic ecosystems, the presence of macrophytes has important structuring consequences for microcrustacean communities because their physical characteristics alter habitat structure in ways that can influence resource availability and resource quality [1,2]. It has been reported that for cladocerans, the habitat architecture is an important factor influencing composition [3]. For example, macrophytes increase the availability of attachment surfaces for species that require a substrate for locomotion such as benthic cladocerans, or for species able to use submerged structures to settle and filter water from a stationary position. Macrophytes can increase resources for detritivores because their submerged structures accumulate sediments or detritus [3]. Moreover, macrophytes can also offer a novel prey source for omnivorous or carnivorous microcrustaceans because of increases in associated microorganisms [4]. Macrophytes are reported as essential for increases in diversity of fish fauna because of the greater supply of food resources, but also by offering refuge against predation from larger visual hunting fish [5]. Such changes that indirectly promote resource heterogeneity and higher resource availability may explain greater microcrustacean diversity in littoral zones of aquatic ecosystems, even in the absence of predators, especially where macrophytes are more abundant [6]. Some studies have demonstrated a role for macrophytes as mediators in the interaction between prey and aquatic predators [2–7], with zooplankton using plants as a refuge against predation by fish [8,9]. However, zooplankton may also avoid macrophyte areas when fish predation is intense in these areas [7].

One of the most notorious macrophytes in the world is *Eichhornia crassipes* (Mart) Solms, which, due to its high reproductive rate, can quickly occupy large areas of aquatic environments [10,11]. Because of this, these plants are considered to be pests capable of causing damage to fish production and water quality [11]. Knowing the influences of these plants on all components of aquatic communities is important in understanding how their extreme biomass affects the ecosystems that they invade and inhabit.

A major influence of macrophytes on zooplankton community structure is to promote an increase in microcrustacean taxonomic species richness. However, taxonomic richness may not be sufficient in capturing changes in niche dimensions related to resource availability that lead to compositional shifts, but perhaps not to richness shifts. Furthermore, taxonomic diversity does not consider mechanistically the ways in which species may be adapted to the novel niches offered by *Eichhornia* in particular, which is a free-floating plant. Functional trait diversity can thus be a more useful tool whereby species identities are replaced by trait combinations that reflect the various means of resource exploitation and, ultimately, the niche space occupied by species in the community [12–14]. Evaluating community compositional shifts (relative species abundances) with macrophytes, as well as the traits of the dominant species, allows us to identify the niches introduced by the submerged structures when *Eichhornia* colonizes.

A community with greater resource use trait diversity could allow more efficient resource exploitation by a community through complementarity [15,16], and could thus augment overall productivity, as has been shown in diatom communities [17]. To evaluate niche complementarity, functional diversity indices are useful tools by which greater values indicate the presence of taxa capable of exploring a greater variety of niche dimensions, indicating a reduction in competition for common resources [15].

In this study, we evaluated how the presence of the free-floating plant *Eichhornia crassipes* influences the functional structure of microcrustacean communities via changes in resource availability and habitat heterogeneity. We examined species traits related to the use of resource niches provided by macrophytes, and explored with the outcome for functional diversity. The aim of the study was to contribute to understanding the role of macrophytes *E. crassipes* in structuring microcrustacean communities, which ultimately influence ecosystem functioning through nutrient cycling in aquatic environments [17–19].

#### 2. Materials and Methods

#### 2.1. Experimental Design

We conducted an experiment using 12 earth pond mesocosms located in the Aquaculture Center, São Paulo State University (UNESP), Brazil (21°15′22′′ S, 48°18′48′′ W) in the autumn of 2011. Mesocosms were 1.50 m deep, 13 m long, and 6 m wide (totaling an area of 78 m<sup>2</sup> and a volume of 117 m<sup>3</sup>) and were thus long enough to allow for zone differentiation between littoral and pelagic areas with macrophyte manipulations. The mesocosms were filled with pond water and had established microcrustacean communities prior to macrophyte addition, with the most abundant taxa being *Bosmina longirostris* (O. F. Muller, 1785); *Diaphanosoma spinulosum* Herbst, 1967; *Argyrodiaptomus furcatus* (Sars, 1901); and *Thermocyclops decipiens* (Kiefer, 1929). The water was not replenished during the experiment. To observe the influence on microcrustacean community structure, replicated (six times) macrophyte treatments were established, either with or without the presence of *Eichhornia crassipes*. When present, macrophytes were inserted along one edge of the mesocosm, simulating a small lentic environment with a vegetated littoral zone. The experimental design with treatments and sampling sites in the littoral and pelagic zones are shown in Figure 1.





*Eichhornia crassipes* were obtained from cultivated macrophyte beds at Universidade Estadual Paulista (UNESP), Jaboticabal campus, where the experiment was performed. Before transplantation, macrophyte roots were washed with water to avoid contamination of mesocosms with organisms from the cultivation area. About 50 individuals of *E. crassipes* were inserted into each pond of the treatment with macrophytes. Because *E. crassipes* is a floating species, a 6 m bamboo stake was used to retain the macrophytes 2 m away from the mesocosm edges. Following the introduction of macrophytes on 1 April 2011, the mesocosm communities were left unperturbed for 30 days before microcrustacean samples were collected on 1 May 2011. After 1 month, the macrophytes multiplied and covered an area

of 12 m<sup>2</sup> in each the macrophyte treatment ponds; their roots grew to a depth of about 40 centimeters below the water surface. The experimental period corresponded to the first month of the dry season (April to September) in this tropical, hot, and rainy region, according to the Köppen–Geiger climate classification [20]. To isolate the effect of macrophytes on zooplankton community structure, predators such as fish were excluded and *Chaoborus* larvae were not observed.

#### 2.2. Sampling

Samples of water and zooplankton were collected from two locations in each mesocosm: from the pelagic zone in the center and in the littoral zone close to one of the mesocosm edges. In macrophyte-containing mesocosms, littoral samples were taken from the middle of the macrophyte stand. In the control treatment (no macrophytes), the zone close to the margin was sampled as the corresponding zone. In this way, it was possible to standardize the sample method and observe whether the effect on the zooplankton community resulted from the presence of macrophytes and not from the proximity to the pond margin. Samples were collected at noon and at midnight, resulting in four subsamples from each mesocosm—two spatial and two temporal points. This methodology ensured that communities were thoroughly sampled, taking into account potential vertical and horizontal diel migration of the microcrustaceans [21–23].

To sample microcrustaceans, 75 L from the water column was pumped from each location and time point using a bilge pump (Jabsco, model 34600-0000, ITT Jabsco, Costa Mesa, CA, USA). Water was filtered through a 45 µm mesh net, and organisms were anesthetized with carbonated water and fixed with 4% buffered formalin. In the laboratory, microcrustacean taxonomic identification was performed using light microscopy and taxonomic keys to identify species [24–26] on 2.5 mL subsamples. At least 60 individuals of the most abundant species were counted in each subsample, and the total number of subsamples counted was determined by satisfying the condition that the CV (coefficient of variation) of the densities was less than 0.2 [27]. When there was a low overall density of organisms, the entire sample was counted. Male and female copepods, nauplii, and copepodites were enumerated separately.

At the time of zooplankton sampling, limnological factors were also analyzed to determine whether there were any changes in the physical and chemical characteristics of the mesocosms because of macrophyte inclusion. Using a multiparameter probe (Horiba U-10—Horiba Ltd., Kyoto, Japan) in the littoral and pelagic zones, we measured temperature, dissolved oxygen, pH, and conductivity.

#### 2.3. Functional Traits

Feeding type, average body size, habitat preference, and trophic group are zooplankton traits that can be readily used for functional diversity analyses [28]. All traits were based on literature data.

#### 2.3.1. Feeding Type

This trait captures the manner by which species or groups obtain their food (Table 1). It is the most complex trait and we included some types in our classification. Cladoceran feeding types were classified as follows [29]: *Daphnia-type filtration*, when filtering occurs in a stationary position with the filtering apparatus on the third and fourth legs; *Sida-type*, which is similar to *Daphnia-type*, but the apparatus is located on the first five legs; and *Bosmina-type*, which is characterized by active horizontal swimming and a less developed filtering apparatus on the thoracic appendages. Copepods can be classified into two types: *raptorial* for animals that actively capture and kill prey, and *stationary suspension* for organisms that are more passive and swim less. We also included two other classifications: *burrowing type*, which digs into the substrate to feed on periphyton or detritus on mud, consisting of most chydorids [30–33], and *attached type*, species that attach to substrates such as macrophytes from which they filter water to feed [29].

Feeding Types	Abbreviations				
Daphnia filtration	d.filt				
<i>Sida</i> filtration	s.filt				
Bosmina filtration	b.filt				
Raptorial	raptorial				
Stationary suspension	stat.susp				
Burrowing	burrow				
Attached	attach				
Size	Class				
0.1 to 0.5 mm	class A				
0.6 to 1.0 mm	class B				
1.1 to 1.5 mm	class C				
1.6 to 2.0 mm	class D				
Habitat P	reference				
Benthic	benthic				
Open water	open.water				
Vegetation	vegetation				
Open water vegetation	open.water.vegetation				
Trophic	Group				
Herbivore	herb				
Herbivore-detritivore	herb.detr				
Omnivore	omnivore				
Omnivore-carnivore	omnivore.carnivore				

Table 1. Microcrustacean functional traits and their abbreviations.

#### 2.3.2. Body Size

Average body size is a continuous trait (Table 1). However, for the statistical comparison of densities between treatments, microcrustaceans were divided into four size classes: (A) 0.1 to 0.5 mm, (B) 0.6 to 1.0 mm, (C) 1.1 to 1.5 mm, and (D) 1.6 to 2.0 mm. The classes were determined on the basis of maximum sizes of microcrustacean species obtained from the literature.

#### 2.3.3. Habitat Preference

Habitat preference for microcrustaceans consisted of three general categories: *benthic, open water* (pelagic), and *vegetation*, for those associated with macrophytes (Table 1). Some species, such as *Moina minuta* Hansen, 1889, occupy both littoral and open water habitats, and were thus classified as *open water-vegetation*.

#### 2.3.4. Trophic Group

We applied main categories on the basis of primary prey sources: *herbivore, omnivore, carnivore,* and *detritivore* (Table 1). We considered omnivores to be organisms that feed on a variety of materials including plants, animals, algae, and fungi. For species with food preferences that span more than one prey type, combined groups were created: *omnivore–carnivore* and *herbivore–detritivore,* as recommended by Barnett et al. [28]. As no exclusively carnivorous species were found, we classified as *omnivorous–carnivorous* those that, although also feeding on algae, had a diet more similar to that of a predator. To classify an organism as *herbivore–detritivore* or *carnivore–omnivore* we used the criteria established by Barnett et al. [28] to differentiate species that were more carnivorous than others.

#### 2.4. Diversity Indices

Diversity indices for the microcrustacean taxonomic data included species richness (S), Shannon–Wiener diversity (H'), and community evenness (J'). These indices were calculated on

abundance (#/L) data from the microscope counts. All the taxonomic diversity indices were calculated using the *Vegan* package in R [33,34] (R Foundation for Statistical Computing, Vienna, Austria).

We used analogous functional diversity indices—functional richness (*FRic*), functional evenness (*Eve*), and functional dispersion (*FDis*). All traits (Table 1) were used to create the species × trait matrix. *FRic* represents the volume of the functional space occupied by the community and *FEve* is the regularity of abundance in this volume [12]. *FDis* represents the mean distance in multidimensional trait space of individual species to the centroid of all species; it can account for relative species abundances by shifting the position of the centroid to that of the more abundant species and then weighting distances of individual species by their relative abundance [6]. All the functional indices were calculated using the *FD* package in R [34,35], applying distance matrices based on Gower's index.

Individuals with the same trait were pooled and densities among groups were compared to detect whether the macrophytes influenced the abundance of individuals possessing some specific trait.

#### 2.5. Statistical Analyses

#### 2.5.1. Niche Complementarity

SES (standardized effect size) for functional richness was calculated because it excludes the effect of species richness from the analyses, besides being a good test to detect increases in niche complementarity along an ecological gradient [15]. The species density matrix used in this null model analysis consisted of the mean of species densities across the four samples taken from each mesocosm (littoral, pelagic, day, and night) resulting in a matrix with the densities of populations from six mesocosms with macrophytes and six mesocosms without macrophytes. The SES ranking was calculated for each mesocosm following the methodology proposed by Gotelli and Entsminger [36], where the observed values of functional richness was compared with those expected from matrix swap null models, calculated with the independent swap algorithm described in Gotelli and Entsminger [36]. This statistical procedure generated a ranking number whereby the functional richness in each mesocosm was compared with means of random values created for all community combinations.

The SES ranking that resulted for each mesocosm was compared using an independent *t*-test to assess whether mesocosms with macrophytes had greater functional diversity than that expected by chance (n = 6, degrees of freedom = 5), thereby indicating the presence of functional complementarity. The SES ranking was calculated using the 'ses.mpd' and 'ses.mntd' functions from the *picante* package [34] in R statistical software [33].

#### 2.5.2. Potential Drivers of Functional and Species Diversity

Species richness (*S*), Shannon–Wiener diversity (*H'*), Simpson's dominance (D), functional richness (*FRic*), functional uniformity (*FEve*), and functional dispersion (*FDis*) were calculated for each subsample (littoral, pelagic on day and night period). The influence of macrophytes and environmental variables on functional and species diversity was evaluated using generalized additive models (GAM) with integrated smoothness estimation, where all the functional and the species diversity parameters (dependent variables) were modelled with the temperature, concentrations of dissolved oxygen, water conductivity, and pH (independent variables). There were no statistical differences between parameters from both treatments. All models identified the mesocosm (tank) and the littoral and pelagic zones (habitat) with the day (time) included as a random effect. Model selection was using the AIC (Akaike information criterion), adjusted  $R^2$ , and the significant estimates of the independent variables. All statistical analyses were performed with the package *mgcv* in R statistical software [33–38].

#### 2.5.3. Density Comparison for Species and Functional Groups

To evaluate the responses of individual species or functional groups to macrophytes, subsample densities were pooled according to the statistical analysis performed. Trait densities were log-transformed prior to analyses to reduce heteroscedasticity. For the comparison of species and

functional groups densities between treatments, the four subsampled densities from each mesocosm were pooled, resulting in six replicates for each treatment (with and without macrophytes). Comparisons were performed using a two-way ANOVA with treatment and zones as factors. There were no statistical differences between zooplankton densities from day and night samples and thus we pooled the day and night subsamples. It was expected that in the presence of macrophytes, the distribution of species and functional groups would be different between littoral and pelagic zones, whereas these zones would be more similar in mesocosms without macrophytes. The results enabled the identification of macrophyte effects on specific traits. All the statistical analyses were performed using R statistical software [34].

### 3. Results

Across all samples, a total of two calanoid copepod, two cyclopoid copepod, and eight cladoceran species (from the Sididae, Bosminidae, Moinidae, Daphiniidae, Ilyocryptidae, and Macrothricidae families) were identified (Table 2).

Cladocerans	Abbreviation
Diaphanosoma spinulosum Herbst, 1967	disp
Pseudosida bidentata Herrick, 1884	psbi
Bosmina longirostris (O. F. Muller, 1785)	bolo
Moina minuta Hansen, 1889	momi
Ceriodaphnia cornuta Sars, 1886	сесо
Simocephalus serrulatus (Koch, 1841)	sise
Ilyocryptus spinifer Herrick, 1882	ilsp
Macrothrix paulensis (Sars, 1901)	mapa
Copepods	Abbreviation
Thermocyclops decipiens female (Kiefer, 1929)	thdef
Thermocyclops decipiens male	thdem
Mesocyclops meridianus female (Kiefer, 1926)	mesmef
Mesocyclops meridianus male	mesmem
Argyrodiaptomus furcatus female (Sars, 1901)	arfuf
Argyrodiaptomus furcatus male	arfum
Notodiaptomus iheringi female (Wrigth, 1935)	noihf
Notodiaptomus iheringi male	noihm
Calanoid copepodid	coca
Cyclopoid copepodid	cocy
Copepod nauplii	naup

Table 2. List of microcrustacean species found in the experimental mesocosms and their abbreviations.

## 3.1. Community Structure and Environment Variables

There were no significant treatment differences in the mean levels of any environment variables (p > 0.05; Figure S1). Species richness (S) (Figure 2a) and diversity (H') (Figure 2c) decreased linearly with pH, but were higher in the presence of macrophytes than in the control (Figure 2b,d). Functional richness (*FRic*) decreased linearly with water conductivity (Figure 2e), whereas functional dispersion (*FDis*) decreased linearly with water temperature (Figure 2g). Both *FRic* and *FDis* were higher in the presence of macrophytes than in the control (*Feve*) nor taxonomic indicators (J) of evenness were associated with macrophytes, nor with limnological variables.





**Figure 2.** Relationships between: (**a**) species richness (*S*) and pH, adjusted  $R^2 = 0.42$ ;  $F_{3,22} = 214.59$ ; (**b**) species richness (*S*) by treatment ( $S = 5.0131 + s(1.4836, Macro) + s(1.0, pH) + a_i$ ;  $a_i N(0, 1.372)$ ); (**c**) Shannon species diversity (*H'*) and pH, adjusted  $R^2 = 0.3$ ;  $F_{3,22} = 106.07$ ; (**d**) Shannon species diversity (*H'*) by treatment ( $H = 0.852 + s(0.308, Macro) + s(1.0, pH) + a_i$ ;  $a_i N(0, 0.357)$ ); (**e**) functional richness (*FRic*) and conductivity, adjusted  $R^2 = 0.29$ ;  $F_{3,22} = 47.1$ ; (**f**) functional richness (*FRic*) by treatment (*FRic* = 0.097 +  $s(0.0508, Macro) + s(1.0, Conduct.) + a_i$ ;  $a_i N(0, 0.0403)$ ); (**g**) functional dispersion (*FDis*) and temperature, adjusted  $R^2 = 0.26$ ;  $F_{3,22} = 90.81$ ; (**h**) functional dispersion (*FDis*) by treatment (*FDis* = 0.122 +  $s(0.0519, Macro) + s(1.0, Temp.) + a_i$ ;  $a_i N(0, 0.0572)$ ). Obs.: only statistically significant results are shown; other variables presented in the Supplementary Materials (Tables S1–S5).

#### 3.2. Density of Species and Functional Groups

In the presence of macrophytes, significantly greater abundances of species were observed, including those able to attach and burrow to feed, those with benthic habitat preference, and those belonging to herbivore–detritivore, and omnivore–carnivore trophic groups (Figure 3 and Table 3). Reduced densities of species preferring the open water habitat, from the omnivore trophic group and from the largest, class D body size (1.6 to 2.0 mm) were observed in the mesocosms with macrophytes (Table 3).



**Figure 3.** Mean logarithmic densities (± Standard Error (SE)) of functional traits in the littoral and pelagic habitats by macrophyte treatment.

**Table 3.** Two-way ANOVA results comparing log density of each functional group by treatment (with macrophytes and control), by zones (littoral and pelagic), and for the interaction of treatment and zone. Trait abbreviations as in Table 1.

Functional Trait	Treatment				Zone		<b>Treatment</b> × <b>Zone</b>					
	F	р	df	F	р	df	F	р	df			
			Feeding	Types								
attached	5.923	0.019	1	7.570	0.009	1	10.710	0.002	1			
b.filtr	12.526	0.001	1	-	-	1	-	-	1			
burrow	12.972	0.001	1	4.111	0.049	1	-	-	1			
d.filtr	-	-	1	-	-	1	-	-	1			
raptorial	-	-	1	-	-	1	-	-	1			
s.filtr	-	-	1	-	-	1	-	-	1			
stat.susp	4.545	0.039	1	-	-	1	-	-	1			
	Habitat Preference											
benthic	12.972	0.001	1	4.111	0.049	1	-	-	1			
open.water	5.378	0.025	1	-	-	1	-	-	1			
open.water.vegetation	-	-	1	-	-	1	-	-	1			
vegetation	4.305	0.04	1	-	-	1	-	-	1			
			Trophic	Group								
herb	-	-	1	-	-	1	-	-	1			
herb.detr	12.972	0.001	1	4.111	0.049	1	-	-	1			
omnivore	7.196	0.010	1	-	-	1	-	-	1			
omnivore.carnivore	14.243	< 0.001	1	-	-	1	-	-	1			
Size Class												
class.A	-	-	1	-	-	1	-	-	1			
class.B	-	-	1	-	-	1	-	-	1			
class.C	-	-	1	-	-	1	-	-	1			
class.D	118.521	< 0.001	1	-	-	1	-	-	1			

The distribution of some functional groups between the littoral and pelagic zones of the mesocosms was significantly affected by the presence of macrophytes (Figure 3 and Table 3). The omnivore–carnivore trophic group presented equal abundances in the littoral and pelagic zones with macrophytes (none of this group were present in the control). Class D (1.6 to 2.0 mm) microcrustaceans were more abundant in the pelagic zones of mesocosms without macrophytes. All other groups varied significantly by zone only when macrophytes were present; the omnivore trophic group and open water habitat traits were more abundant in the ponds without macrophytes, whereas the attached, the herbivore-detritivore trophic group, benthic habitat preference, and burrowing feeding were more abundant in littoral zones with macrophytes over the pelagic zones (Figure 3).

The cladocerans *Pseudosida bidentata* Herrick, 1884; *Ilyocryptus spinifer* Herrick, 1882; *Bosmina longirostris*; and *Macrothrix paulensis* (Sars, 1901), and the copepod *Mesocyclops meridianus* (Kiefer, 1926) occurred at greater densities in mesocosms with macrophytes (Figure 4 and Table 4). Species with reduced densities in the presence of macrophytes were the cladoceran *Ceriodaphnia cornuta* Sars, 1886; copepod nauplii; and the copepod *Argyrodiaptomus furcatus*. With respect to zone differentiation, the cladoceran *Ilyocryptus spinifer* was more abundant in littoral zones, irrespective of treatment, and *Pseudosida bidentata* was more abundant in littoral zones of mesocosms with macrophytes (Figure 4 and Table 4).



**Figure 4.** Mean logarithmic densities ( $\pm$  SE) by species in the littoral and pelagic habitats by macrophyte treatment.

The SES rankings showed a positive value in the macrophyte treatment (Figure 5), with a significant result (p < 0.05) for the *t*-test, comparing the macrophyte treatments. A significantly more positive value in the SES ranking indicated a higher functional diversity than expected by chance, implying a higher niche complementarity in mesocosms with macrophytes.

Smaailaa	Treatment				Zone			Treatment $\times$ Zone		
Species	F	р	df	F	р	df	F	p	df	
Disp	-	-	1	-	-	1	-	-	1	
Bolo	12.526	< 0.001	1	-	-	1	-	-	1	
Mapa	20.444	< 0.001	1	-	-	1	4.033	0.050	1	
Ilsp	8.256	0.006	1	7.345	0.009	1	-	-	1	
Psbi	11.139	0.001	1	4.187	0.046	1	4.187	0.046	1	
Momi	-	-	1	-	-	1	-	-	1	
Sise	5.923	0.019	1	7.57	0.008	1	10.71	0.002	1	
Ceco	9.124	0.004	1	-	-	1	-	-	1	
Noihm	-	-	1	-	-	1	-	-	1	
Noihf	-	-	1	-	-	1	-	-	1	
Arfuf	118.521	< 0.001	1	-	-	1	-	-	1	
Arfum	56.446	< 0.001	1	-	-	1	-	-	1	
Thdef	-	-	1	-	-	1	-	-	1	
Naup	7.515	0.008	1	-	-	1	-	-	1	
Cocy	1.223	0.008	1	-	-	1	-	-	1	
Coca	-	-	1	-	-	1	-	-	1	

**Table 4.** Two-way ANOVA results comparing log species density by treatment (with macrophytes and control), by zone (littoral and pelagic), and for the interaction of treatment and zone. Trait abbreviations as in Table 2.



**Figure 5.** Box plots showing the means and standard errors of rankings of standardized effect sizes (SES) for functional diversity comparing the two treatments (p-value < 0.001).

#### 4. Discussion

The density of individuals with certain functional traits varied between experimental treatments, enabling us to identify which microcrustacean niche dimensions were affected by *Eichhornia crassipes* macrophytes. This was possible because the traits reflect how niche space is used by species in the community [12]. Thus, increases in density of individuals with the attached feeding type and benthic traits, as we observed for the benthic habitat and herbivore detritivore food preference traits, indicated that macrophytes such as *E. crassipes* increased resource opportunities for benthic species unable to efficiently exploit pelagic zones. Thus, although their presence may restrict the local niche of pelagic species, *E. crassipes* are capable of enhancing the niche for other species of microcrustaceans, enabling a greater functional diversity across ponds with both types of zones.

Benthic cladocerans, such as Chydoridae, Macrothricidae, and Ilyocryptidae, are composed of species that have morphological specializations, allowing them to explore the niche offered by submerged structures of macrophytes. Antennae are usually used as an oar to move along a substrate or mud, and the carapaces have morphological adaptations on the ventral margin to permit crawling on surfaces [30]. Most benthic species are able to swim only short distances [30], and the submerged branches and roots of macrophytes as *E. crassipes* can be used as a substrate for attachment. These submerged structures form a tangled complex of branches of different sizes, shapes, and thicknesses

that provide increased availability of microhabitats and niches. For submerged aquatic vegetation (SAV), the increase in zooplankton biomass and functional diversity was also related to the increased availability of habitats and ecological niches provided by submerged macrophyte structures [39]. Increased abundance of organisms in the macrophyte mesocosms with the attached feeding type, benthic habitat preference, as well as the herbivore–detritivore trophic grouping together reflects their feeding strategy consisting of scraping the surfaces of submerged branches of macrophytes for periphyton or accumulated detritus on macrophyte roots [3].

In addition to increasing the foraging area for benthic species, macrophyte-associated microorganisms can also represent novel food resources for predacious microcrustaceans [5], potentially explaining a higher density of omnivore–carnivore trophic group found in the macrophyte treatment. In our study, copepods classified as omnivore–carnivore were represented by the cyclopoid *Mesocyclops*, a benthic genus, adapted to living among macrophytes, and with a high plasticity for prey preference [40,41]. Even a small increase in food quality via novel micro-organism introductions with macrophyte addition could have enabled the density increase in this trophic group.

Unlike benthic species, filter feeders could not exploit the novel niches offered by macrophytes in littoral zones. Species with the vegetation trait (e.g., of the genera: *Simocephalus* and *Diaphanosoma*) possess a feeding apparatus similar to pelagic species, allowing capture of suspended solids in the water column, but with the additional ability to attach to the submerged structures of macrophytes and filter feed from a stationary position [31,32,42]. Such species are often found in the middle of macrophyte stands [28]. In our study, all species categorized as preferring vegetation habitat—*Pseudosida bidentate*, *Simocephalus serrulatus* (Koch, 1841), and *Macrothrix paulensis*—increased in density in *E. crassipes* stands, indicating the role of these plants in increasing the habitat availability.

Macrophyte forms (floating vs. submerged) may influence resources available for microcrustaceans because the physical assistance offered by each depends on the shape and structure that remains submerged [5], potentially differentially influencing microcrustacean functional groups [39]. The floating form as *E. crassipes* has submerged roots and stolons, which retain a large amount of detritus that is highly suitable for benthic species use [3], but not for pelagic filter feeders. For pelagic species, submerged macrophytes may offer a better overall habitat, as their growth form allows for some light penetration and phytoplankton growth, also offering greater interstitial space for filtration [7,43] (although this depends on the biomass density of the macrophytes). Thus, the floating macrophytes used in our experiment likely did not adequately increase the foraging area available for microcrustaceans possessing the vegetation habitat trait (primarily filter feeders), explaining the lack of treatment effect.

For the truly pelagic filter feeders with habitat preference for open areas, we detected an avoidance of macrophyte zones, with lower densities of these species and traits in the macrophyte treatment and in their littoral zones. For truly pelagic species, macrophytes may be preferred over open water areas, primarily as a refuge against visual predation from fish in pelagic zones [7], predators that were absent in our study. For pelagic species, the avoidance of macrophyte stands is related to a decrease in phytoplankton production due to light limitation [9,44], thereby diminishing resources for filter feeders such as *Ceriodaphnia* and calanoid copepods. In addition, the presence of macroinvertebrate predators [45,46] and small fish [47] in macrophyte stands may also cause pelagic species to avoid these sites.

The abundances of the copepod *A. furcatus* were reduced from positive to almost zero densities with the addition of macrophytes. These taxonomic shifts are associated with the feeding habit of Diaptomidae, a group with a feeding preference for larger phytoplankton and even small planktonic invertebrates, such as rotifers [48]. Macrophytes generally reduce phytoplankton production [38] and change their composition [49], and thus food quality and quantity may have been reduced for such diaptomids, negatively affecting their abundance.

Species and functional diversity indices responded positively to macrophyte presence, although some environmental variables also showed influences. However, irrespective of any environmental effects associated with macrophyte addition, the presence of the macrophyte itself showed a significant beneficial effect on microcrustacean diversity. These findings indicate that resources related to food and habitat structure promoted by macrophytes played an important role in the changes observed in the zooplankton community structure.

With an analysis of community structure, it was possible to evaluate increases in diversity in the macrophyte treatment, as well as to infer that a greater niche space was occupied by the community on the basis of the traits that were most responsive, reflecting an increase in resource and physical heterogeneity offered by macrophyte structures. This conclusion is based on the fact that the responsive traits of microcrustaceans were those related to feeding and specifically to the morphology of appendices used to filter suspended solids, scrape solid surfaces, or actively prey on other organisms [22,29,31,42], as well as functional traits that reflect resource requirements for each species [28].

Species using alternate resource types can be favored by macrophyte presence, as we observed for benthic species, which are normally otherwise unable to inhabit the water column. Thus, an increase in niche complementarity, as observed through augmented functional trait diversity, enabled a more complete resource exploitation by the community. Greater niche complementarity between species and macrophytes was also evidenced by a greater variation in functional group densities between littoral and pelagic zones, observable only in the macrophyte treatment. Furthermore, some functional groups were present in macrophyte-covered littoral zones, indicating a likely increase in resource niche dimensionality and a greater species complementarity.

Functional traits and niche complementarity are significant factors influencing community assembly, and the influence of macrophytes on these will in turn have implications for ecosystem functioning. For plankton communities, functional diversity has been associated with an increase in productivity [17]. The shifts in our microcrustacean communities should have consequences for pond ecosystem functioning because of the important role that these organisms play in linking trophic levels and in recycling nutrients [19,50,51].

The main goal of this study was to verify whether *E. crassipes* increased the diversity of predator-free microcrustacean communities through increases in habitat heterogeneity and functional complementarity of species. Through the null model comparison, it was possible to confirm that zooplankton functional diversity increased in the presence of the floating macrophyte *E. crassipes*, promoting changes in the zooplankton community structure. Our observations further indicated a greater niche complementarity in mesocosms with *Eichhornia crassipes*. This plant is considered to be a pest of aquatic ecosystems in many parts of the world [11] and its increase in abundance can result in a profound change in biodiversity of the aquatic ecosystem. The zooplankton community is considered as a link between producers and consumers in aquatic food chains. Changes in its structure can have a cascading effect throughout the aquatic biota. In addition to the direct effect of macrophytes on zooplankton, demonstrated in this study, several other studies have demonstrated the indirect effects of macrophytes on the interaction between zooplankton and its predators, generating many questions that will certainly be addressed in future studies.

#### 5. Conclusions

Shallow ecosystems in the tropics are abundant and usually contain extended littoral zones with a high diversity of microcrustaceans. Our study demonstrated that the effect of *Eichhornia crassipes* on extending the resource base alone was sufficient in altering taxonomic and functional diversity and composition, independent of any supplementary effects that macrophytes may have on predation rates, which could further enhance such shifts. It also contributes to future studies about the trophic interactions mediated by macrophytes, which are still little known in the tropics.

**Supplementary Materials:** The following are available online at http://www.mdpi.com/2073-4441/11/11/2423/s1: Figure S1: Average of limnological variables in mesocosms with and without macrophytes. Table S1: Statistical results of modeling analysis for *S* (species richness) and the independent variables. Table S2: Statistical results of modeling analysis for *FRic* (functional richness) and the independent variables. Table S3: Statistical results of modeling analysis for *FRic* (functional richness) and the independent variables. Table S4: Statistical results of modeling analysis for *FEve* (functional evenness) and the independent variables. Table S5: Statistical results of modeling analysis for *FEve* (functional dispersion) and the independent variables.

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