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Richness of Arbuscular Mycorrhizal Fungi in a Brazilian Tropical Shallow Lake: Assessing an Unexpected Assembly in the Aquatic-Terrestrial Gradient

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Abstract: Aquatic ecosystems are historically overlooked regarding the occurrence of Arbuscular Mycorrhizal Fungi (AMF). Tropical lakes in the southern hemisphere are generally impacted by human actions, such as those in Brazil, although they still preserve a great diversity of macrophyte species that can support AMF communities. Thus, the study aimed to test (i) whether AMF community structure (composition, richness, diversity, dominance, and evenness) differs between aquatic and terrestrial conditions, and (ii) between seasons—rainy and dry. A total of 60 AMF species, distributed in 10 families and 17 genera, were found, with a difference in AMF composition between conditions (terrestrial and aquatic) and seasons (dry and rainy). The absolute species richness differed between conditions, seasons, and interactions. The aquatic/rainy season, which retrieved the most significant number of species, had the highest absolute richness and number of glomerospores and differed significantly from the terrestrial/rainy season. The results suggest that a shallow oligotrophic lake harbors a high AMF richness. In addition, this environment has a distinct AMF community from the adjacent coastal sand plain vegetation and is affected by seasonality.

Keywords: AMF communities; coastal sandy plain vegetation (*restinga*); diversity; Glomeromycota; lentic ecosystems; oligotrophic; seasonality

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1. Introduction

Arbuscular Mycorrhizal Fungi (AMF) is a basal lineage that belongs to the phylum Glomeromycota [1–3]. With exception of *Geosiphon pyriformis*, the Glomeromycotean fungi form endomycorrhizal mutualistic symbiosis with the roots of most land plants [4–6]. In this symbiosis, AMF plays a functional role to the hosts by foraging for water and nutrients in the soil, especially phosphorus, while plant partners provide photosynthates for fungal nutrition [7]. In addition, they confer higher plant tolerance to abiotic stress conditions such as salinity, water scarcity, and heavy metals [8–11].

Approximately 350 AMF species have been described [3,12]. Nevertheless, molecular inventories indicate the occurrence of several Operational Taxonomic Units (OTUs) that do not belong to known taxa [13–15]. However, studies on AMF diversity, distribution, and function were conducted mainly in terrestrial environments [16]. Although historically less studied, aquatic ecosystems have already proved to be a habitat for AMF [17–19], especially lentic ecosystems [20]. They lead the species richness documented for the aquatic condition [20] and have already revealed themselves as potential shelters for new taxa [21,22].

Coastal lagoons that occupy about 13% of the world's coastline are examples of generally shallow lentic systems separated from the sea by deposition barriers [23]. Due to their position at the interface between land and sea, coastal lagoons can play an important role in regulating nutrients and materials exported from their watersheds [24], besides providing critical habitat for macro and microorganisms and support for recreational activities. They are sensitive to changes in temperature and nutrient loading in their surroundings [25]. In addition, they are among the ecosystems most threatened by natural and anthropogenic influences, especially in the Neotropics [26,27]. Coastal lagoons that do not have a direct connection to the ocean are called closed lagoons [23]. Interdune coastal lagoons are those formed from the upwelling of the water table under a strong influence of the dune system where the sandy coastal plain ecosystem typically occurs [28].

Brazilian sandy coastal plains vegetation (called *restingas*) covers about 79% of the Brazilian coast and represents a transition between marine and continental environments [29]. Its vegetation composition varies from arboreal and shrubby to herbaceous types [30,31]. In addition, it is adapted to stressful environmental factors such as high temperature, luminosity, salinity, strong winds, salt deposition, and low availability of nutrients in the soil [32–34]. Under these conditions, the association with AMF is an essential adaptive strategy [35]. Taxonomic and ecological studies have already been conducted in Brazilian *restingas*, investigating the relationship of AMF communities with mining activity [36,37], vegetation [38,39], seasonality and soil chemical attributes [40].

Brazil has a sizeable hydrographic dimension and an expressive richness of aquatic macrophytes [41,42]. However, it has been only three reports of AMF in submerged areas. First, Marins et al. [43] investigated the occurrence of AMF in a lotic environment based on the morphological approach. Ortiz-Vera et al. [44] detected high diversity of several phyla of the kingdom Fungi in a polluted lotic environment (including unidentified taxa of Glomeromycota) based on environmental sequences. Finally, Queiroz et al. [45] reported 10 new global records of AMF species, under lentic and lotic conditions, in northeastern Brazil. Thus, the AMF community that mainly inhabits the lentic areas of Brazil remains underexplored.

Few studies on the submerged condition have investigated AMF communities or evaluated the influence of environmental variables on them, e.g., [19,22,46–48]. In terrestrial environments, AMF community dynamics are seasonally influenced [49–51]. However, there is no evidence to show a seasonal influence on the occurrence of AMF in aquatic sediments in tropical environments. The variation in the occurrence dynamics of AMF communities between the underlying aquatic and terrestrial conditions is even less known.

The present study aimed to characterize the occurrence and structure of the AMF community in a terrestrial-aquatic transition area in an oligotrophic shallow lake impacted by anthropogenic action. To fulfill this aim, we collected soil samples in two seasons from a lagoon within Atlantic Forest biome to test (i) whether AMF community structure (composition, richness, diversity, dominance and evenness) differ between aquatic and terrestrial conditions, and (ii) between rainy and dry seasons.

2. Materials and Methods

2.1. Study Area

The study was carried out in the municipality of Nísia Floresta, state of Rio Grande do Norte, Brazil, in the Bonfim-Guaraíras Environmental Protection Area, Figure 1a.

The sampled area comprised an aquatic-terrestrial gradient (Figure 1c). The aquatic part is represented by interdune coastal lagoon, freshwater and oligotrophic (Alcaçuz Lagoon 5°59′40.1″ S, 35°08′39.0″ W) (Figure 1b), where macrophyte families such as Alismataceae, Cyperaceae, Eriocaulaceae, Lentibulariaceae, Mayacaceae, Melastomataceae and Xyridaceae are found [52]. The terrestrial part is a *restinga* vegetation 10 m apart from the lagoon, characterized by herbaceous and shrubby plant species with a predominance of the Chrysobalanaceae, Cyperaceae, Fabaceae, Poaceae and Rubiaceae families [31,53,54]. The Alcaçuz Lagoon is part of the water circuit, a tourist route of great appeal on the coast of

the Rio Grande do Norte State [55], receiving thousands of tourists throughout the year. The region's climate is tropically warm and humid (group As) according to the Köppen classification, with an annual average temperature of 25.8 °C [56]. The rainy season mainly occurs between May and July, and the dry season between September and December. The chemical attributes of aquatic sediment and terrestrial soil are presented in Table S1 in the Supplementary Material.

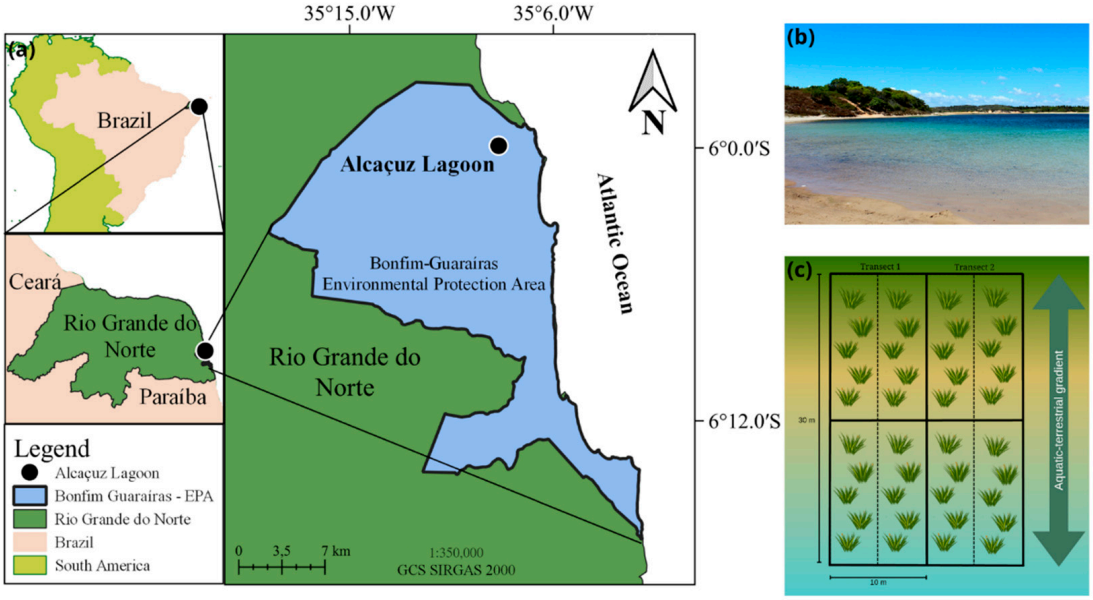

Figure 1. A location map of the Alcaçuz Lagoon, in the Bonfim-Guaraíras Environmental Protection area, Rio Grande do Norte State, Brazil (**a**), and draw of the methodology adopted to collect sediment and soil samples (**b**,**c**).

2.2. Sediment Collection and Sampling

Sediment sampling was carried out in the same area in October/2015 and May/2016 during the dry and rainy seasons. Collection efforts were to sample soil and sediments from the same host plant in both environments. Two transects (30 m) transverse to the lagoon line, 10 m apart, were arranged from the lagoon shore to the sandbar (Figure 1c). This design was made to contemplate host plants growing in aquatic and terrestrial conditions. Four plots were included in each transect (Figure 1c). Five rhizospheric soils samples (0–30 cm depth) were taken for each of them, totaling 40 samples for each period and condition.

2.3. Extraction and Identification of Glomerospores

Glomerospores and glomerocarps were extracted from 50 g soil and sediment samples in three replicates, using the wet sieving method [57] and water and sucrose (50%) centrifugation [58] for separation and counting of glomerospores under microscopy. Glomerospores were separated by morphotypes based on size, color, and shape and were fixed on slides containing polyvinyl alcohol–acid–glycerol (PVLG) [59] and a mixture of PVLG and Melzer's reagent (1:1 *v/v*). Glomerospores were examined to determine their morphological features, such as phenotype and histochemical characteristics of spore wall layers.

Species identification was performed through the following procedures. First, viable glomerospores were separated from those not viable during slide mounting [60]. Subsequently, several spores of each morphotype were mounted together during spore preparation to improve comparison as previously described by Błaszkowski [61] and Błaszkowski et al. [62]. In addition, species were identified using Schenck and Pérez [63], Błaszkowski [61], and other supplementary materials, such as descriptions on the website INVAM (https://invam.ku.edu/species-descriptions, accessed on 16 May 2016). The characters used to identify the species were (i) spore development (if acaulosporoid, di-

versisporoid, entrophosporoid, glomoid, gigasporoid, kuklosporoid, racocetroid or scutellosporoid) following papers [64–66], (ii) the number of spore wall structures and phenetic and histochemical features of each spore wall layer, (iii) Melzer's reaction of the spore wall layers, (iv) the color and thickness of spore wall layers, and (v) the color and shape of glomerospores, and (vi) shape, organization and color of glomerocarps. We accepted the arguments presented by Sieverding et al. [67] and used the generic name *Rhizoglomus* Sieverd., G.A. Silva and Oehl instead of *Rhizophagus* P.A. Dang following recent papers [3,62,68–70].

2.4. Ecological and Statistical Analysis of AMF Communities

The AMF communities were evaluated for relative abundance (RA), frequency of occurrence (FO), absolute richness (S), diversity (H), dominance (C), and evenness (J). RA was calculated by the number of glomerospores of each species/total number of glomerospores found ($\times$100). For FO, the number of samples in which each species occurred/total number of samples ($\times$100) was considered, and according to FO, the species were analyzed as dominant (FO > 50%), very common (30% < FO $\leq$ 50%), common (10% < FO $\leq$ 30%) or rare (FO $\leq$ 10%). S was calculated considering the total number of species in each sample (50 g of soil). Diversity was measured by the Shannon-Weaver index, considering H = $-\Sigma$ (Xi/Xo) $\times$ log(Xi/Xo), where Xi is the number of spores of each species and Xo the total number of spores of all species [71]. The dominance was measured by the Simpson index with C = [ni (ni $-$ 1)/N (N $-$ 1)], where ni is the number of spores of each species and N is the total number of species [72]. The equation obtains the evenness by the Pielou index: J = H/Log(S), where H is the Shannon diversity and S is the total number of species [73]. The Shannon-Weaver and Simpson indices were obtained from the "diversity" function in the "vegan" package [74]. For the glomerospore number (NG), the number of glomerospores recovered in each sample (50 g of soil) was considered.

An Exploratory Analysis Protocol (EDA) was used, according to Zuur et al. [75]. The analyses were made to verify outliers, homoscedasticity, and normality. First, the outliers were detected from the Cleveland Dot plot charts. All analyzes were performed in the software R version 4.0.3 [76]. For EDA, we use the HighstAtlibv11 script [75]. The selection of the best fit for the data distribution (absolute richness (S), diversity (H), dominance (C), equitability (J), and the number of glomerospores (NG)) was performed using the "descdist" function in the "fitdistrplus" package [77]. The H, C, and J indexes were adjusted to the Gaussian distribution. The S and NG parameters were better adjusted to the negative binomial distribution. The model residues premises of normality and homoscedasticity were observed using the Shapiro Wilk and Levene tests with the functions "shapiro.test" and "leveneTest" in the "car" package [78], respectively. Principal Component Analysis (PCA) was applied to AMF abundance data to reduce multivariate dimensions [79]. The first three principal components were extracted to visualize the relationship between species and conditions/seasons (aquatic/rainy, aquatic/dry, terrestrial/rainy, and terrestrial/dry). In the analysis, the function "PCA" was used in the "FactoMineR" package [80]. The PCA visualization was obtained using the function "fviz_pca_biplot" in the "factoextra" package [81]. Subsequently, we tested the effect of conditions/periods on the AMF abundance matrix with permutational multivariate analysis of variance (PERMANOVA). For this, the abundance data were converted into a Bray-Curtis dissimilarity matrix (4999 permutations), and the test was performed using the "adonis" function in the "vegan" package [74]. Later to the permanova, the multiple comparison test was made using the function "pairwise.perm.manova" in the package "RVAideMemoire" [82]. We used the "iNEXT" package [83] to obtain rarefaction and extrapolation curves for AMF species richness (Hill number q = 0). This procedure was based on the number of sampling units, with a 95% confidence interval set to 999 replications of bootstrap resampling [84].

Linear and Generalized Linear Models (LM and GLM) were used to analyze the interaction between conditions/periods with ecological indices. The functions "lm" [76] and "glm.nb" were used in the "MASS" package [85]. The explanatory variables (interaction between conditions/periods) and the diversity indices (response variables) were obtained

using the "Anova" function of the "car" package [78]. The "emmeans" function in the "emmeans" package [86] was used to perform multiple posteriori comparisons applying Tukey's correction.

3. Results

3.1. AMF Communities

A total of 60 AMF species were found, classified in 10 families—Glomeraceae (38.3%), Acaulosporaceae (21.6%), Dentiscutataceae (15%), Racocetraceae (6.6%), Ambisporaceae (5%), Entrophosporaceae (3.3%), Gigasporaceae (3.3%), Scutellosporaceae (3.3%), Diversisporaceae (1.6%) and Paraglomeraceae (1.6%)—and 17 genera—*Acaulospora* (21.6%), *Glomus* (18.3%), *Rhizoglomus* (11.6%), *Fuscutata* (10%), *Ambispora* (5%), *Dentiscutata* (5%), *Racocetra* (5%), *Claroideoglomus* (3.3%), *Gigaspora* (3.3%), *Scutellospora* (3.3%), *Septoglomus* (3.3%), *Cetraspora* (1.6%), *Oehlia* (1.6%), *Redeckera* (1.6%), *Sclerocystis* (1.6%), *Simiglomus* (1.6%) and *Paraglomus* (1.6%). Of this total, 50 species occurred in the aquatic condition, 42 and 33 in the rainy and dry seasons, respectively. Additionally, 33 species were identified in the terrestrial condition, 20 and 28 in the rainy and dry seasons, respectively. Furthermore, 25 species were shared by aquatic and terrestrial conditions. Nine species were recovered from both conditions and seasons (Table 1). Figures illustrating AMF species identified in the aquatic-terrestrial gradient samples are available in supplementary files (Figure S1).

Table 1. AMF species in an aquatic-terrestrial gradient and their respective relative abundances (RA%) and frequencies of occurrence (FO%) in an interdune oligotrophic lagoon of coastal *restinga* in Brazil.

Families/*Species*	**RA (A/R)**	**RA (A/D)**	**RA (T/R)**	**RA (T/D)**	**FO (A/R)**	**FO (A/D)**	**FO (T/R)**	**FO (T/D)**
Ambisporaceae								
Ambispora appendicula (Spain, Sieverd., N.C. Schenck) C. Walker	6.86	3.52	2.21	14.97	65	21.05	40	45
Ambispora gerdemannii (S.L. Rose, B.A. Daniels & Trappe) C. Walker, Vestberg & A. Schüssler	0.71	-	0.4	-	15	-	5	-
Ambispora sp.	1.78	0.23	-	0.94	25	5.26	-	10
Acaulosporaceae								
Acaulospora denticulata Sieverd. & S. Toro	0.12	-	-	-	5	-	-	-
Acaulospora foveata Trappe & Janos	0.24	0.23	-	-	5	5.26	-	-
Acaulospora herrerae Furrazola, B.T. Goto, G.A. Silva, Sieverd. & Oehl	-	-	-	0.13	-	-	-	5
Acaulospora ignota Błaszk., Góralska, Chwat & B.T. Goto	-	0.23	-	-	-	5.26	-	-
Acaulospora morrowiae Spain & N.C. Schenck	1.07	0.23	-	-	45	5.26	-	-
Acaulospora spinosa C. Walker & Trappe	0.24	-	-	-	10	-	-	-
Acaulospora spinulifera Oehl, V.M. Santos, J.S. Pontes & G.A. Silva	-	0.23	-	-	-	5.26	-	-
Acaulospora tuberculata Janos & Trappe	17.63	30.05	67.67	17.51	75	63.16	40	55
Acaulospora cf. *colossica*	-	0.47	0.2	-	-	10.53	5	-
Acaulospora cf. *cavernata*	0.59	0.23	-	4.14	15	5.26	-	25
Acaulospora cf. *herrerae*	-	-	0.2	-	-	-	5	-
Acaulospora cf. *morrowiae*	3.91	1.64	1.41	1.20	15	21.05	20	5
Acaulospora sp.	0.59	0.7	1	0.27	5	15.79	15	10
Dentiscutataceae								
Dentiscutata cf. *cerradensis*	-	-	-	0.13	-	-	-	5
Dentiscutata cf. *scutata*	-	-	-	0.27	-	-	-	5
Dentiscutata sp.	0.12	0.23	-	-	5	5.26	-	-
Fuscutata aurea Oehl, C.M. Mello & G.A. Silva	0.47	-	0.6	1.34	10	-	10	20
Fuscutata heterogama Oehl, F.A. de Souza, L.C. Maia & Sieverd.	5.33	2.35	4.02	1.87	35	10.53	30	25
Fuscutata rubra (Stürmer & J.B. Morton) Oehl, F.A. de Souza & Sieverd.	0.12	-	-	18.45	5	-	-	25
Fuscutata cf. *aurea*	0.47	0.23	-	-	5	5.26	-	-
Fuscutata cf. *rubra*	1.07	-	-	-	5	-	-	-
Fuscutata sp.	0.47	0.23	-	-	10	5.26	-	-
Diversisporaceae								
Redeckera fulva (Berk. & Broome) C. Walker & A. Schüssler	0.24	0.47	-	-	10	5.26	-	-

Table 1. *Cont.*

Families/*Species*	RA (A/R)	RA (A/D)	RA (T/R)	RA (T/D)	FO (A/R)	FO (A/D)	FO (T/R)	FO (T/D)
Entrophosporaceae								
Claroideoglomus etunicatum (W.N. Becker & Gerd.) C. Walker & A. Schüssler	-	-	-	0.27	-	-	-	5
Claroideoglomus cf. *etunicatum*	0.12	-	-	-	5	-	-	-
Gigasporaceae								
Gigaspora cf. *gigantea*	0.12	-	0.4	-	5	-	5	-
Gigaspora sp.	7.93	11.5	15.46	15.68	55	68.42	80	65
Glomeraceae								
Glomus glomerulatum Sieverd.	2.49	6.34	0.2	0.53	10	10.53	5	5
Glomus spinuliferum Sieverd. & Oehl	0.12	-	-	0.40	5	-	-	5
Glomus trufemii B.T. Goto, G.A. Silva & Oehl	34.67	5.4	-	-	35	36.84	-	-
Glomus cf. *ambisporum*	-	-	-	0.13	-	-	-	5
Glomus cf. *badium*	-	0.47	-	0.13	-	5.26	-	5
Glomus cf. *brohultii*	-	-	0.8	0.13	-	-	15	5
Glomus cf. *glomerulatum*	0.12	-	-	-	5	-	-	-
Glomus cf. *trufemii* 1	4.73	1.64	0.4	4.81	25	15.79	5	10
Glomus cf. *trufemii* 2	-	22.77	-	9.63	-	31.58	-	35
Glomus sp. 1	0.95	0.23	-	-	20	5.26	-	-
Glomus sp. 2	-	-	-	0.13	-	-	-	5
Oehlia diaphana (J.B. Morton & C. Walker) Błaszk., Kozłowska & Dalpé	-	-	0.2	-	-	-	5	-
Rhizoglomus clarum (T.H. Nicolson & N.C. Schenck) Sieverd., G.A. Silva & Oehl	-	1.17	0.4	0.53	-	10.3	10	15
Rhizoglomus manihotis (R.H. Howeler, Sieverd. & N.C. Schenck) Sieverd., G.A. Silva & Oehl	0.71	1.88	-	-	15	21.05	-	-
Rhizoglomus microaggregatum (Koske, Gemma & P.D. Olexia) Sieverd., G.A. Silva & Oehl	0.12	-	-	0.13	5	-	-	5
Rhizoglomus cf. *aggregatum*	0.47	-	-	-	10	-	-	-
Rhizoglomus cf. *clarum*	0.83	0.23	-	1.47	10	5.26	-	10
Rhizoglomus cf. *intraradices*	0.47	0.47	-	-	5	5.26	-	-
Rhizoglomus cf. *invermaium*	0.59	0.7	-	2.27	5	5.26	-	10
Sclerocystis sinuosa Gerd. & B.K. Bakshi	0.12	-	-	-	5	-	-	-
Septoglomus cf. *titan*	0.12	-	-	-	5	-	-	-
Septoglomus sp.	0.12	-	1.2	-	5	-	30	-
Simiglomus sp.	-	-	0.4	-	-	-	5	-
Paraglomeraceae								
Paraglomus occultum (C. Walker) J.B. Morton & D. Redecker	-	0.47	-	-	-	5.26	-	-
Racocetraceae								
Cetraspora gilmorei (Trappe & Gerd.) Oehl, F.A. de Souza & Sieverd.	-	0.47	-	-	-	5.26	-	-
Racocetra gregaria (N.C. Schenck & T.H. Nicolson) Oehl, F.A. de Souza & Sieverd.	0.83	3.05	2.61	2.41	20	31.58	30	30
Racocetra cf. *tropicana*	0.47	-	-	-	5	-	-	-
Racocetra sp.	0.36	0.23	-	0.13	10	5.26	-	5
Scutellosporaceae								
Scutellospora sp. 1	0.24	-	-	-	5	-	-	-
Scutellospora sp. 2	1.3	1.64	0.2	-	10	5.26	5	-

(A/R)—aquatic condition and rainy season; (A/D)—aquatic condition and dry season; (T/R)—terrestrial condition and rainy season; (T/D)—terrestrial condition and dry season.

In Principal Component Analysis, five components explained 74% of the overall variance (Table S2 in the Supplementary Material). The first three axes showed that *Acaulospora tuberculata*, *Gigaspora* sp. and *Glomus* cf. *trufemii* 2 were most heavily related to conditions and seasons (Figure 2a,b). *Acaulospora tuberculata* was strongly related to the aquatic/rainy season. *Gigaspora* sp. showed a higher relationship with the terrestrial/rainy season. *Glomus* cf. *trufemii* 2 was more related to the dry season in aquatic and terrestrial conditions.

All conditions and seasons analyzed presented a high number of rare species (67% in A/R, 58% in A/D, 55% in T/R and 64% in T/D), few dominant species (7% in A/R, 6% in A/D, 5% in T/R and 7% in T/D), and other species distributed as very common or common. *Gigaspora* sp. was the only species classified as dominant in all interactions analyzed (Table 1). However, the high FO in the terrestrial/rainy season contributed to its higher response in this interaction (Figure 2a,b).

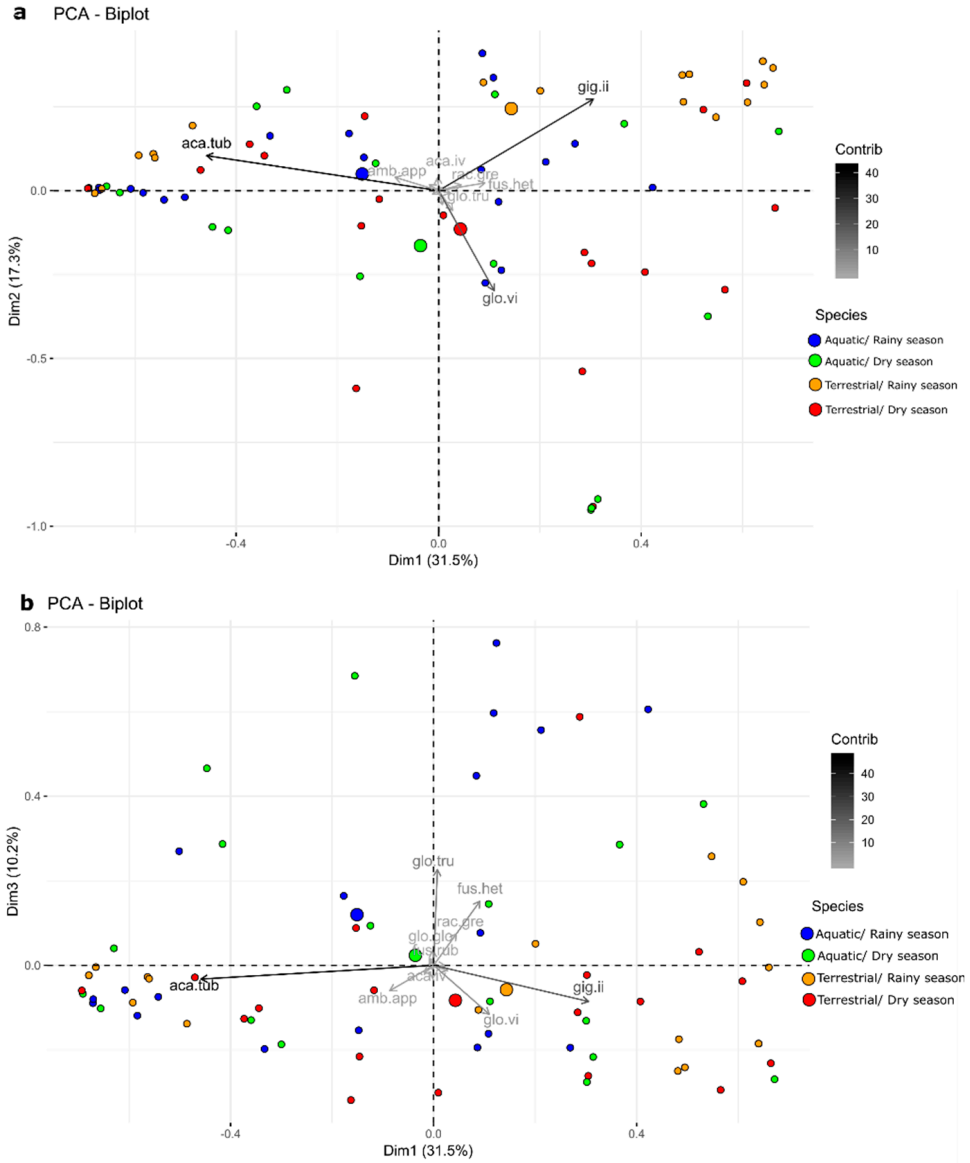

Figure 2. Principal Component Analysis of AMF species related to aquatic/terrestrial conditions and rainy/dry periods. Species—aca.tub: *Acaulospora tuberculata*, amb.app: *Ambispora appendicula*, fus.het: *Fuscutata heterogama*, gig.ii: *Gigaspora* sp., glo.tru: *Glomus trufemii*, glo.glo: *Glomus glomerulatum*, fus.rub: *Fuscutata rubra*, rac.gre: *Racocetra gregaria*, glo.vi: *Glomus* cf. *trufemii* 2, aca.iv: *Acaulospora* cf. *morrowiae*. In (**a**) we have PC1 with PC2 and (**b**) PC1 with PC3. In both PCA graphics, the larger dots indicate the centroids of conditions and periods.

The composition of AMF species was related to environments and seasons (PERMANOVA F = 3.13; $p < 0.01$). The differences correspond to the interactions between aquatic/dry season and terrestrial/rainy season ($p = 0.012$) and between aquatic/rainy season and terrestrial/rainy season ($p = 0.018$).

For aquatic condition, sample-size-based rarefaction curves did not approach an asymptote, and the estimated total richness greatly exceeded the observed species richness. The shape of curves suggested that a more significant proportion of the AMF richness was captured in the terrestrial condition, although no curve reached the saturation platform (Figure 3).

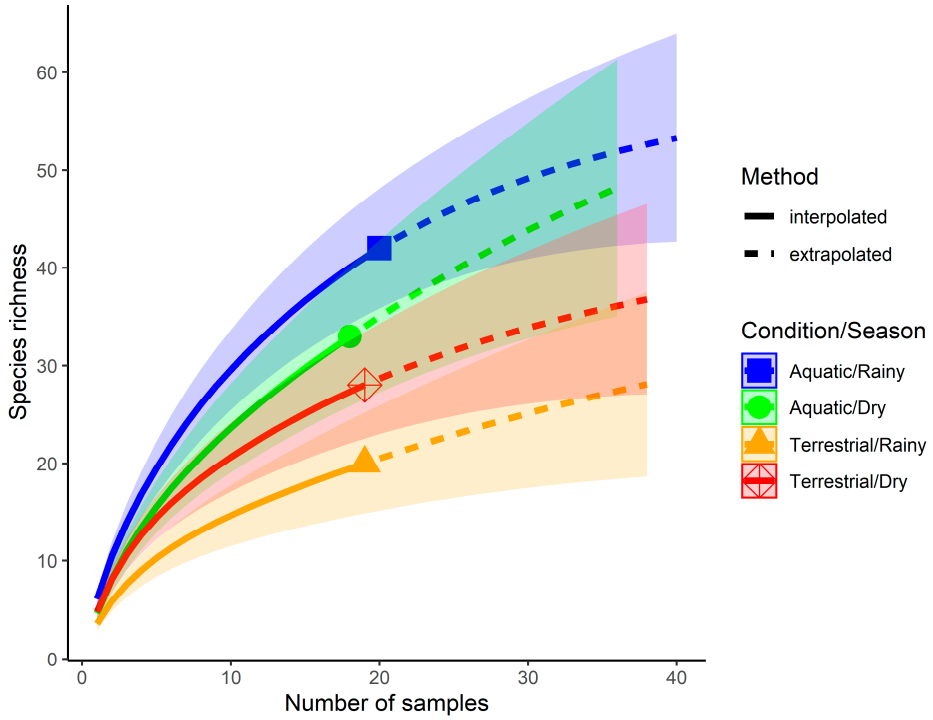

Figure 3. The sample-size-based rarefaction curves showing interpolated (continuous lines) and extrapolated (dashed lines) AMF species richness in aquatic/terrestrial and rainy/dry season conditions. The shaded areas represent a 95% confidence interval obtained using a bootstrap method based on 999 replications.

3.2. Ecological Indices

The absolute species richness (S) differed between conditions, seasons, and interactions (Table 2). The aquatic/rainy season, from which were retrieved the largest number of species (Table 1), had the highest absolute richness and differed significantly from the terrestrial/rainy season (Table S3 in the Supplementary Material, Figure 4a). The lowest richness was found for terrestrial/rainy season. Shannon's diversity (H), Simpson's dominance (C), and Pielou's equitability (J) indices did not show significant differences between conditions, seasons, and interactions (Table 2, Figure 4b–d).

Table 2. Linear (LM) and Generalized Linear (GLM) models exploring differences in richness (S), diversity (H), dominance (C) and evenness (J) in relation to condition (aquatic/terrestrial), seasonality (rainy/dry) and interactions (condition/season).

Response	Sum Sq	Df	F Values	Pr (>F)
S				
Condition	8.286	1	7.7657	0.006825 **
Season	4.735	1	4.4377	0.038690 *
Condition: Season	5.654	1	5.2989	0.024275 *
Residuals	75.753	71	-	-
H				
(Intercept)	29.6915	1	82.9543	1.316×10^{-13} ***
Condition	0.5620	1	1.5701	0.2143
Season	0.0006	1	0.0016	0.9677
Residuals	25.7707	72	-	-

Table 2. *Cont.*

Response	Sum Sq	Df	F Values	Pr (>F)
C				
(Intercept)	5.9945	1	87.1474	5.655×10^{-14} ***
Condition	0.2200	1	3.1984	0.07798
Season	0.0709	1	1.0312	0.31333
Condition: Season	0.2107	1	3.0632	0.08440
Residuals	4.8838	71	-	-
J				
(Intercept)	10.8885	1	132.4999	$<2 \times 10^{-16}$ ***
Condition	0.0059	1	0.0714	0.7900
Season	0.0030	1	0.0361	0.8498
Residuals	5.9168	72	-	-

Sum Sq: Sum of squares; Df: Degrees of freedom; *p*-value for F statistics. Signif. codes: 0—***—0.001 —**—0.01—*—0.05—.—0.1— —1. Significant when $p < 0.05$.

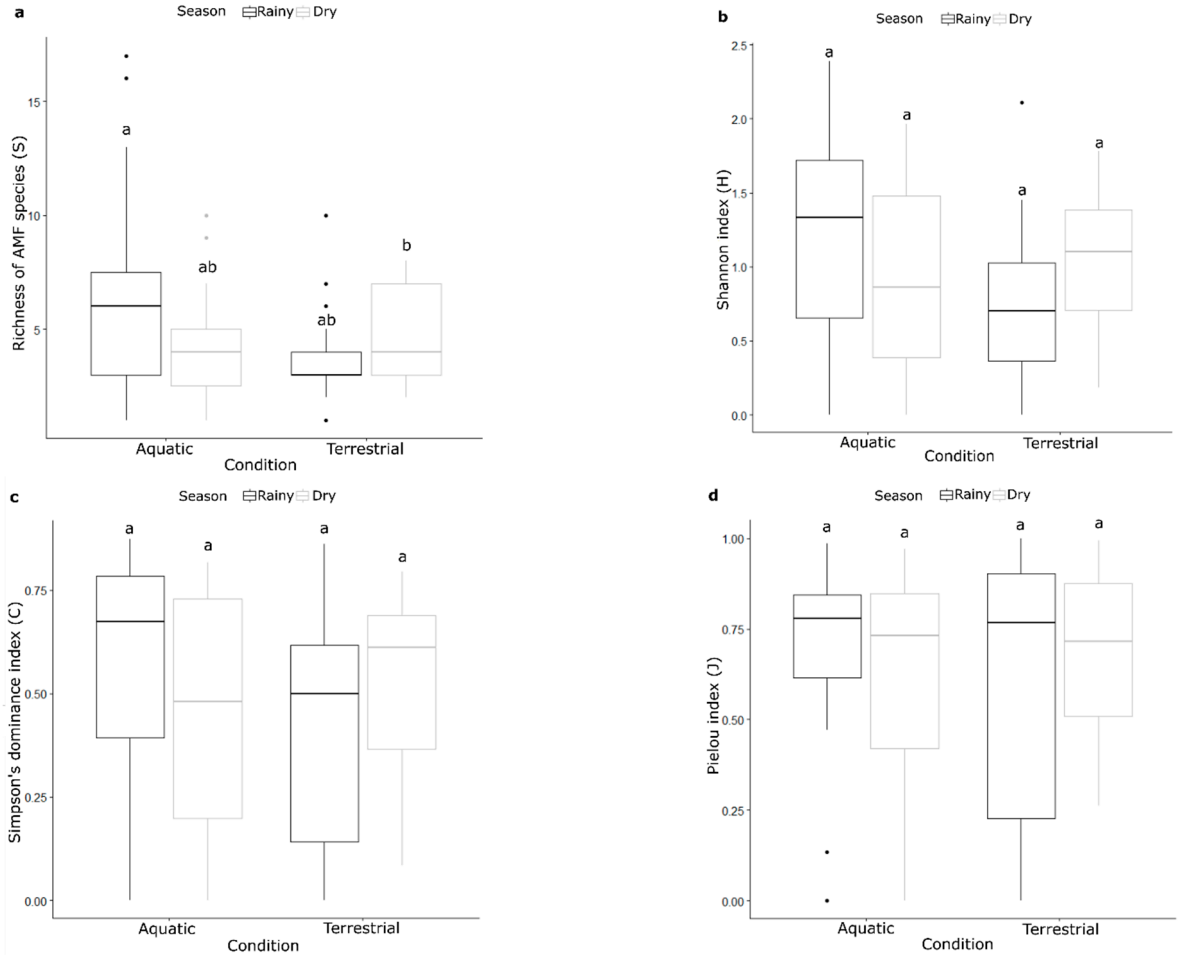

Figure 4. Species richness (**a**), Shannon diversity (**b**), Simpson dominance (**c**) and Pielou equitability (**d**) for AMF communities in aquatic/terrestrial and rainy/dry season conditions. Boxplots with different letters differ statistically by ANOVA ($p < 0.05$).

3.3. Glomerospore Number

Most glomerospores were detected in the aquatic/rainy interaction (Figure 5). In contrast, the terrestrial/rainy presented the lowest number of glomerospores recovered. There was a significant difference in the glomerospores number between conditions and

interactions (Table 3), being terrestrial/rainy different from the other interactions (Figure 5, Table S3 in the Supplementary Material).

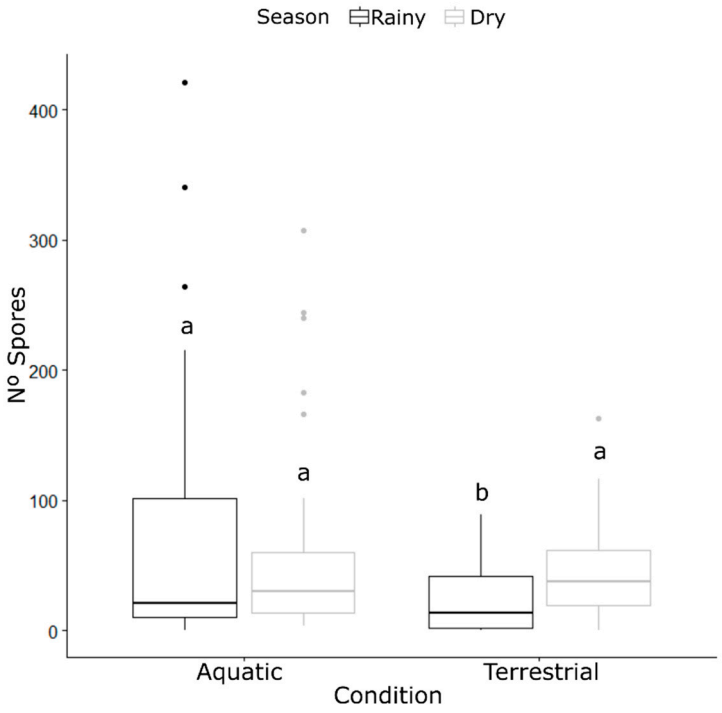

Figure 5. The number of glomerospores recovered in aquatic/terrestrial and rainy/dry season conditions. Boxplots with different letters differ statistically by ANOVA ($p < 0.05$).

Table 3. Generalized Linear Models (GLM) exploring differences in number of glomerospores (NG) in relation to condition (aquatic/terrestrial), seasonality (rainy/dry) and interactions (condition/season).

NG	Df	Chisq	Pr (>Chisq)
(Intercept)	1	816.9725	$<2.2 \times 10^{-16}$ ***
Condition	1	22.5457	2.052×10^{-6} ***
Season	1	1.0576	0.303753
Condition: Season	1	8.3396	0.003879 **

Df: Degrees of freedom; *p*-value for Chi-square statistics. Signif. codes: 0—***—0.001—**—0.01—*—0.05—.—0.1——1. Significant when $p < 0.05$.

4. Discussion

We report a high species richness of glomeromycotan fungi found in sediments collected from a shallow oligotrophic lake in the tropical region of Brazil. The 50 species found represent 14.3% of the known glomeromycotan species, while in the terrestrial vegetation nearby we found 33 species. For Brazil 153 glomeromycotan species were reported occurring in the Atlantic Rainforest biome and our results represent 40% of this total [87].

That result surprised us because aquatic environments have been shown to be less rich in glomeromycotan species in both temperate and tropical conditions [20], despite the Atlantic Forest being widely recognized as a biome that harbors high AMF richness [31,35–38,87]. For instance, a study of the AMF diversity in *restinga* and sand dunes areas in Brazilian Northeast reported a total of 34 species, of which 29 were identified in field samples and five after trap culturing [37]. In another study, the patterns of AMF distribution on mainland and islands in six sites along the Brazilian coastal sand plain ecosystem (*restinga*) reported a total of 53 species, ranging from 9 to 25 species per site [88]. A study from another environment carried out on five habitats of high-altitude (Brazilian rupestrian fields) reported 49 AMF species in total, with a variation of 19 to 33 species

per habitat [89]. In a semiarid habitat from Northwest Brazil 47 AMF species occurred on six sites (natural and agricultural), where the richness ranged from 25 to 44 species per site [90]. On the other hand, coastal dune vegetations in other countries harbor a limited species richness of 31, 20, 14 and 7 subjected to different conditions [91–94], even using high-throughput sequencing technology in sand dunes of Australia and New Zealand, Hanlon [95] detected 16 species belong to five genera, and Johansen et al. [96] detected 22 species in seven genera, respectively.

It is evident that aquatic sediments in such conditions have a high potential to harbor a diversified AMF community. The high richness of Glomeraceae and Acaulosporaceae families, and their respective genera *Glomus* and *Acaulospora*, was maintained for two conditions and seasons. These families and genera are the most numerous of the phylum Glomeromycota [2,3]. They are known to produce glomerospores and mycelium that allow for rapid colonization [97–99]. Furthermore, it has tolerance to several stressful environmental conditions [51,100,101], which explains the high richness and abundance in different terrestrial [89,102–104] and aquatic [20,105] conditions worldwide.

Acaulospora tuberculata is among Brazilian biomes' most widely distributed AMF species [87]. In the present study, *A. tuberculata* was recovered in both conditions and seasons (Table 2). However, despite this generalist feature, the species was strongly related to the condition and seasonality, with greater weight in the aquatic/rainy interaction (Figure 2a,b). The predominance of this species and other *Acaulospora* species is commonly observed in studies of *restinga* and sea dunes [31,38,88,106]. It can be attributed to the high infectivity rate and ability to regenerate from hyphae and spores [107]. The species *Glomus* cf. *trufemii* 2 had a higher relationship in the dry period in both the aquatic and terrestrial environments (Figure 2a). This may be due to the different strategies of colonization and production of glomerospores in the Glomeraceae [15,70,108]. The high number of *Acaulospora* and *Glomus* phylotypes recovered from macrophyte root fragments in oligotrophic lakes [109] suggests that the high infectivity of these groups can also occur in aquatic ecosystems.

Gigasporales species are widely distributed in the neotropics [110] and invest in the massive production of extraradical mycelium [111], which are essential for soil aggregation and nutrient acquisition [112,113]. In addition, species of the Gigasporales are commonly found in *restinga* in the dry and rainy seasons [37] and dunes ecosystems [38]. This is due to the high sand content of the *restinga* soil, which makes it unstable, and a high prevalence of macroporous and weak aggregate stability as such in sand dunes, favoring the development of large spore-forming fungi such as gigasporoids [114]. This condition might explain the high abundance and frequency of occurrence of *Gigaspora* sp. (Table 2), especially in the terrestrial environment during the rainy season (Figure 2a,b). Records of Gigasporales in aquatic sediments are still limited [20], but two new records (*Dentiscutata hawaiiensis* and *Intraornatospora intraornata*) obtained from river sediments were recently improved in Brazil [45].

Other species are not related to condition and seasonality. Such species could be generalist or rare since they did not show a correlation between environment and seasonality. Dark arrows (Figure 2a,b) represent the three species with the highest contribution percentage (*A. tuberculata*, *Gigaspora* sp., and *Glomus* cf. *trufemii* 2), responding to the environment and condition type. Thus, these differences may reflect the preference of these fungi for each type of environment and seasonality.

Although the statistical difference in species richness was found between conditions, seasons, and interactions (Figure 4a), this parameter was high in all situations studied. Furthermore, the extrapolated rarefaction curves suggested that the species richness, especially in the aquatic condition, may be even higher. AMF constitutes an important adaptation in stressful abiotic conditions such as *restinga*, where high temperatures, strong winds, salinity and low nutrients availability in soil limit the establishment and maintenance of vegetation [36,115,116], and high richness has already been reported in previous investigations [37,40]. These fungi are also thought to play a key role for aquatic macrophytes that

live in nutritionally poor sediments such as oligotrophic lakes, and greater richness has been recovered from these lakes to the detriment of mesotrophic and eutrophic [22,117].

However, the richness and number of glomerospores for the aquatic condition superior to the terrestrial condition was unexpected (Figures 4a and 5). The known AMF diversity in aquatic ecosystems is limited, and the most significant number of taxa ever reported based on spore morphology was 28 by D'Souza and Rodrigues [105] in India, followed by Marins et al. [43]. They reported 27 species in the Brazilian river-floodplain. In contrast, environmental DNA sequencing in different aquatic habitats has shown high numbers of phylotypes and OTUs belonging to Glomeromycota [22,109,118,119], demonstrating the potential of these little-explored ecosystems to harbor AMF.

The seasonal fluctuations in the colonization (hyphae, vesicles, and arbuscules), richness and sporulation are already known [49,120,121]. Corroborating our results, higher richness in the terrestrial condition has generally been found in the dry season and may be associated with higher sporulation detected in this period [51,122,123]. However, the dry season in the Alcaçuz Lagoon does not affect the availability of water to the macrophytes as compared to the adjacent dry land vegetation. The biggest change caused by the seasonality is this lagoon is nutrient content, turbidimetry and temperature. These three parameters are known to affect the photosynthetic capacity and the growing rate of the macrophytes [124], which might affect the sporulation rate. Another factor that can change between the dry and rainy seasons is the redox potential. Beck-Nielsen and Madsen [125] verified that occurrence of AMF colonization in aquatic macrophytes in lakes and streams was related with the redox potential in sediments with non-colonized and colonized species ranged, respectively, from 54 to 280 mV and 250 to 530 mV, indicating that the redox potential of the sediment might play a role in the development of AMF in aquatic systems.

The studies of seasonal dynamics in flooded areas evaluated how colonization is affected by periods of higher flooding, with some studies detecting a decrease in colonization [118,126]. Others revealed that flooding might not be a limiting factor for the association [127,128]. Fabian et al. [129] investigated the seasonal influence on species richness in wetlands and found an increase in the rainy season, a result similar to that found by us. During the rainy season, the rains may have contributed to the glomerospores transfer from the edge to the lake's interior (hydrochory), promoting higher richness and spore number in this condition and period. Despite hydrochory being a dispersal mechanism in fungi, only 43% of AMF species were shared between terrestrial and aquatic areas and there were statistical differences in species composition between aquatic/rainy and terrestrial/rainy interactions. In addition, the highest richness was found in the aquatic environment. These results suggest that the high diversity in sediment may not simply be due to the flow from the terrestrial environment, and that a species occurrence dynamic is probably determined by the contrasting characteristics of these two ecosystems.

The Shannon-Weaver diversity observed for the terrestrial condition was lower than already recorded in other *restingas* in northeastern Brazil [37,38], who reported 4.04 and 3.19, respectively. However, the flooded condition has a high diversity compared to the few studies evaluating the structure of AMF communities through ecological indices. Sidhoum et al. [130] evaluated different flooded environments subjected to anthropogenic disturbances and obtained variation in Shannon-Weaver from 1.41 to 1.72. Through environmental molecular analysis, Wirsel [131] found the highest diversity, ranging from 1.99 to 2.41 in different flooded sites and seasons. In contrast, Wang et al. [118] also obtained low diversity of 0.4 to 1.3 along a hydrological gradient using molecular tools.

Molecular inventories indicate the occurrence of several operational taxonomic units that do not belong to known taxa mostly in the coastal sand dunes that harbor new species [15] even in ranking taxa as genus and family [132].

The Alcaçuz Lagoon, represented by a shallow oligotrophic lake, located in the Neotropical zone, harbors a high richness of AMF, with the distinction between fungal communities due to condition (terrestrial and aquatic) and season (dry and rainy). Species

such as *Acaulospora tuberculata* and *Glomus* cf. *trufemii* 2, respond better to the aquatic condition and present distinct population dynamics according to seasonality.

The present study provides robust evidence of the potential of aquatic environments to harbor high species richness of glomeromycotan fungi, even in a single site and absence of molecular tools to assess the diversity of these organisms. We hope that our findings motivate the scientific community to develop more AMF inventories and to investigate population dynamics, dispersal strategies, occurrence and importance of mycotrophism in aquatic plants (macrophytes). Environmental sequence approaches are necessary in other inventories to recognize AMF assembly not yet detected by morphological tools colonizing both sediments and roots of plant species growing in these conditions.

This sort of basic research is essential to attempt to bridge the gaps existing in the role of AMF occurrence and function in aquatic ecosystems and thenceforward to delimit future strategies for the preservation or restoration, especially for aquatic ecosystems threatened by anthropic pressure, such as the lagoon studied here.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14121046/s1, Table S1: Chemical attributes of sediment from aquatic-terrestrial Alcaçuz Lagoon gradient in the coastal zone of Rio Grande do Norte, Brazil; Table S2: Percent variance explained by each of the five principal components; Table S3: Multiple posteriori comparisons of species richness and glomerospore number in interactions between conditions/periods applying Tukey's correction. Figure S1: Arbuscular mycorrhizal fungi obtained from a tropical shallow lake in Rio Grande do Norte, Brazil.

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