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PHYLOGENETIC TRENDS IN NEOTROPICAL AQUATIC PLANTS ASSEMBLIES

TENDENCIAS FILOGENÉTICAS EN ENSAMBLAJES DE PLANTAS ACUÁTICAS NEOTROPICALES

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ABSTRACT

The phylogenetic assembly rule has received particular attention in its application in biological assemblies, and the present study aims to apply the use of this concept in studies of Neotropical plants associated with aquatic environments. Thus, species information was compiled from the scientific database Scopus, including information for 2813 aquatic and border spermatophytes and their types of dispersal syndromes from 76 assemblages distributed across the Neotropical. We constructed phylogenetic trees for the Neotropical region and for each province separately to define the structure of the ancestral relationships of the species in those assemblies by calculating the phylogenetic metrics of the singularities of each component of diversity and conducting multiple regressions of each phylogenetic diversity metric against environmental variables that represent the hypothesis of determinant contemporary processes. The phylogenetic structure was maintained within the context of species observed in the biogeographical provinces. The multiple regressions indicated no relationship between environmental variables and the predictor's richness and phylogenetic diversity. It was found that most of these species disperse by anemochory and endozoochory, which can be important historical indicators for explaining the phylogenetic pattern displayed. More phylogenetic structure occurred in arid regions as opposed to the most phylogenetically aggregated species occurring in humid tropical zones. It was concluded that the Neotropical floras were dominated by non-random assembly rules, with a tendency to be composed of the same clades, independent of geographic distances; however, they demonstrated a tendency to form assemblies themselves into more congeneric or co-familiar forms rather than random associations. This phenomenon may be related to the types of dispersal syndromes of ancestral lineages. The Neotropical aquatic and border Spermatophyte were dominated by non-random assembly rules,

with a tendency to be composed of the same clades, independent of geographic distances. This phenomenon may be related to the types of dispersal of ancestral lineages.

Keywords: Biogeography – Dispersal – Hydrophytes

RESUMEN

La regla del ensamblaje filogenético ha recibido especial atención en su aplicación en ensamblajes biológicos, y el presente estudio pretende aplicar el uso de este concepto en estudios de plantas Neotropicales asociadas a ambientes acuáticos. Por lo tanto, la información de las especies se compiló de la base de datos científica Scopus, incluida la información de 2813 espermatofitas acuáticas y de borde, y sus tipos de síndromes de dispersión de 76 ensamblajes distribuidos a lo largo del Neotrópico. Construimos árboles filogenéticos para la región Neotropical y para cada provincia por separado para definir la estructura de las relaciones ancestrales de las especies en esos ensamblajes calculando las métricas filogenéticas de las singularidades de cada componente de diversidad y realizando regresiones múltiples de cada métrica de diversidad filogenética contra variables ambientales que representan la hipótesis de procesos contemporáneos determinantes. La estructura filogenética se mantuvo dentro del contexto de las especies observadas en las provincias biogeográficas. Las regresiones múltiples no indicaron relación entre las variables ambientales y los predictores de riqueza y diversidad filogenética. Se encontró que la mayoría de estas especies se dispersan por anemocoria y endozoocoria, las cuales pueden ser importantes indicadores históricos para explicar el patrón filogenético mostrado. La estructura filogenética ocurrió en regiones áridas en oposición a las especies más estrechamente relacionadas desde un punto de vista filogenético que ocurren en zonas tropicales húmedas. Se concluyó que la flora neotropical estuvo dominada por reglas de ensamblaje no aleatorias, con tendencia a estar compuestas por los mismos clados, independientemente de las distancias geográficas; sin embargo, demostraron una tendencia a formar ensamblajes en formas más congenéricas o cofamiliares en lugar de asociaciones aleatorias. Este fenómeno puede estar relacionado con los tipos de síndromes de dispersión de los linajes ancestrales. Las espermatofitas acuáticas y de borde neotropicales estuvieron dominadas por reglas de ensamblaje no aleatorias, con tendencia a estar compuestas por los mismos clados, independientemente de las distancias geográficas. Este fenómeno puede estar relacionado con los tipos de dispersión de los linajes ancestrales.

Palabras clave: Biogeografía – Dispersión – Hidrófitas

INTRODUCTION

Biogeographic provinces are defined by the phytophysiognomies of the dominant plant species and by environmental characteristics such as temperature, rainfall, and, in some cases, altitude (Posadas *et al.,* 2006). These regionalizations occur because their diversities demonstrate non-random internal distribution patterns (Chazdon *et al.,* 2003). The development of new tools and the accumulation of technical observations have allowed scientists to examine these patterns, particularly at macro-ecological scales (Nagaligum *et al.,* 2015).

Some biogeographic provinces are considered diversity hotspots, given the wealth of species found in these locations (Marchese, 2015). According to Maestre *et al.* (2009), the distribution of species richness responds to stress gradients associated with variation in abiotic conditions (e.g., temperature), resource scarcity (e.g., semiarid zones), or location (e.g., the altitude of mountain ranges) and, these factors determine the diversity patterns of biotic assemblages, especially for terrestrial plants, not to mention that richness is not distributed homogeneously within a province (Vamosi *et al.,* 2009).

However, species richness considers only one taxonomic parameter (Willig *et al.,* 2003; Wiens, 2011; Prevedello *et al.*, 2018). With the development of phylogeny studies, other measures of phylogenetic diversity have come under consideration, and species assemblages can currently be thought of in terms of hierarchical components linked by ancestral relationships (Webb *et al.,* 2002). These metrics can provide estimates of evolutionary history in a given geographic region (Donoghue, 2008). This analysis can outcome in a better understanding of biodiversity patterns (Vamosi *et al.,* 2009) by applying evolutionary principles to better understand assemblies.

Phylogenetic studies of spermatophyte assemblies are relatively recent and they have been concentrated on upland forests (Chazdon *et al.,* 2003; Cavender-Bares *et al.,* 2006; Santos *et al.,* 2010; Arroyo-Rodríguez *et al.,* 2012). There is also phylogenetic information on plants in seasonally flooded forests (Fine & Kembel, 2011). These local/regional studies using environmental variables at small scales cannot, however, contribute to macro-ecological perspectives of assemblies phylogenies, reinforcing the need to conduct studies that will allow the understanding of biodiversity at a large spatial scale.

Phylogenetic assemblies' studies have not yet been applied in plants associated with aquatic environments, swampy areas and aquatic body borders (category *lato sensu*) despite the fact that these assemblages are significant and of relevant importance to freshwater environments (Chambers *et al.,* 2008; Padial *et al.,* 2008).

The understanding of factors that structure aquatic spermatophyte assemblies is still based on water quality standards (Penning *et al.,* 2008; Goswami *et al.,* 2010) and seasonal/functional groups (Sarr *et al.,* 2001; Gandullo & Faggi, 2005) but it is not clear how the effects of latitudinal "stress gradients" act on this group in terms of its diversity and phylogenetic structure (Bini *et al.*, 2006; Jarzyna *et al.*, 2021).

The present study analysed the structures of phylogenetic diversity, richness, and dispersal syndromes of Neotropical "*lato sensu*" spermatophytes assemblies based on the hypothesis that different floras should be phylogenetically distributed in different phytogeographical provinces, sensu Cabrera & Willink (1980). Theoretically, these aquatic and border spermatophyta assemblies should respond to temperature (acting at the regional scale), precipitation, and/or altitudinal gradients (acting on local heterogeneity); these issues are better understood for terrestrial vegetation, but there is still a gap in knowledge for assemblages.

Within this context, based on the phylogenetic metrics associated with the above-mentioned environmental variables that act on each of the floras associated with aquatic or paludosos aquatic bodies, we expected that 1) phylogenetic diversity decreases with increasing latitude; 2) assemblies are more aggregated phylogenetically than would be expected by chance among provinces, including within dry tropical or high-altitude climatic zones since assemblies with more severe ecological conditions are expected to be more aggregated (Webb *et al.,* 2002); and 3) historical biogeographic processes should best explain the distribution of the diversity of aquatic spermatophytes.

MATERIAL AND METHODS

Study Area

The Neotropical region extends from Mexico (including the Baja California peninsula and southern Florida) through Central America (including all of the Caribbean islands) to South America and includes tropical, temperate, and altitudinal provinces. Cabrera & Willink (1980) proposed subdivisions of biodiversity zones within the various regions of the Neotropics, defining 28 distinct phytogeographical provinces. In this study, analysed 14 of such provinces were analysed using floristic digital databases available online. These provinces were still sectorized in dry, humid and high-altitude areas, according to Kottek *et al.* (2006).

Data collection and organization

This work is based on floristic and phytosociological studies of aquatic bodies and swampy freshwater environments the Neotropical spermatophytes available online (raw data can be requested from the corresponding author). A search was conducted in the SCOPUS (©Elsevier, the Netherlands) database for original papers with the words "aquatic flora", "aquatic macrophytes", "aquatic plants", "floral surveys", "checklist of plant species" and using papers in English, Spanish, Portuguese, and French. In addition to using the keywords, the boolean search engine "and" was used to relate the keywords to each other. Thus, 76 papers were found to perform this analysis (Fig 1). The following information was extracted: (1) predictor environmental variables (mean annual rainfall, mean annual temperature and altitude) and (2) plant species and life forms. Dispersal syndromes were identified based on diaspores observed in herbarium material or described in the literature.

Many articles were identified that included plant growth associated with aquatic- swampy environments, but only those with floristic collection or phytosociology methodologies were selected and only one ecosystem was analyzed. Articles that had regional collection plans or more than one aquatic body were disregarded. No review articles of a single botanical family were also considered. We have only opted to use publications until the year 2014, even so, it is possible that some research has not been included in our analyzes. The raw data used in this study can be made available to interested researchers via the corresponding author's e-mail.

We consider *lato sensu* aquatic plants as being the plants that occur within the aquatic body and in the lake shore, better known as "amphibians" and which correspond to

a vegetative component that is extremely representative in the analyzed ecosystems (Machado-Filho *et al.,* 2014). Some more authors do not consider this floristic component as aquatic, but following the more traditional concepts (Sculthorpe, 1967), we will consider this component in our analyzes. The most important to note, is that in most floristic surveys on these taxa, it considers amphibian plants as part of the assembly.

The floras were identified according to their locations in the biogeographic provinces delimited by Cabrera & Willink (1980). These assemblies were considered "isolated island habitats", that is, ecosystems resulting from the gradual association of successful species, in terms of dispersal, with a natural surrounding matrix (Bosiacka & Pieńkowski., 2012).

Botanical family names were updated using the Angiosperm Phylogeny Group (APG IV, 2016), and the genera/species names were verified based on The Plant List (2013) to standardize the species pools, correct synonyms, and adopt the current designations for each taxon.

Phylogenetic and assemblies analyses

The phylogenetic diversity for each province was analysed based on the phylogeny of the species. The phylogenetic tree was made using Phylomatic, version 3 (Webb & Donoghue, 2005). The most recent version available (R20120829) of the phylogenetic tree of the Metaphyta was used in the Newick format. The lengths of the branches of the generated phylogenetic tree were adjusted by Bladj tools using the Phylocom software (Webb *et al.,* 2008) to coincide with the estimated ages of the Spermatophytes as described by Renner (2009) and Bell *et al.* (2010). The assemblies and the phylogenetic diversity (PD) metric were randomized 999 times using the Phylocom software, which generates a theoretical null model (Webb *et al.,* 2008).

The taxonomy taxa "cf", "aff" or "sp", identified only at the genus level, were included in the phylogenetic analysis plus letters "a", "b", "c", etc. When the same genus presented more than one unidentified species. This consideration is important concerning the phylogenetic weight of the genus in the assembly, which is indicative of exact confirmation of the taxon.

Phylogenetic diversity distances (mean pairwise distance, MPD; mean nearest taxon distance, MNTD) and metrics of the phylogenetic structure (net relatedness index; nearest taxon index, NTI) (Webb *et al.,* 2008) for each of the 76 assemblies locations identified in the

studies were calculated in addition to the richness of those assemblies. With these data, multiple regressions were used to evaluate the effects of environmental variables (rainfall, temperature, and altitude) on the species richness of an assemblies and on the indices of phylogenetic diversity.

Ethic aspects: Not applicable, as only secondary data from scientific articles published in journals was analysed.

RESULTS

We recorded 2813 species of plants associated with aquatic environments, paludal and aquatic body borders distributed in 1006 genera, 171 families, and 44 orders. Most species were eudicotyledons (1766 spp.), followed by monocotyledons (988 spp.), basal angiosperms (57 spp.), and gymnosperms (2 spp.), which were rare (raw data can be requested from the author for correspondence). The most abundant orders of plants associated with aquatic environments were Asterales, Myrtales, Santalales, and Fabales, which together contributed approximately 50% of the eudicotyledons; Poales contributed more than 60% of the monocotyledons; and Nymphaeales contributed approximately 50% of the basal angiosperms. Among the gymnosperms, only two orders and two families were recorded (Araucaliales – Araucariaceae and Cupressales – Cupressaceae).

Most of the species examined belong to the plant families Poaceae (330 spp.), Asteraceae (288 spp.), Cyperaceae (260 spp.), and Fabaceae (163 spp.). These families were also the most representative in terms of the number of genera and species. These families, of course, are not exclusively aquatic, and the species considered were treated as amphibious or aquatic *latu sensu*. The plants considered aquatic macrophytes *stricto sensu* were smaller in number (10% of the total number of families observed) compared to the amphibious species. The commons genera were *Cyperus* (212 spp.), *Eleocharis* (186 spp.), *Ludwigia* (158 spp.), *Persicaria* (109 spp.), *Utricularia* (85 spp.), *Paspalum* (85 spp.), *Juncus* (74 spp.), *Eichhornia* (69 spp.), *Panicum* (67 spp.), *Hydrocotyle* (65 spp.), *Rhynchospora* (59 spp.), and *Ipomoea* (51 spp.), representing 43.2% of the total. Approximately 7% of the families were represented by a monospecific genus or a single species; and the most representative species in the assemblies were *Eichhornia crassipes* (Mart.) Solms, *Pistia stratiotes* L., *Persicaria hydropiperoides* (Michx.) Small, *Hydrocotyle ranunculoides* L.f., *Typha domingensis* Pers., and *Eclipta prostrata* (L.) L.

Anemochory was the predominant dispersal syndrome in most of the assemblies, followed by endozoochory, autochory, hydrochory, and ectozoochory (Fig 2). Only the Yungas and Subantártica provinces showed endozoochory as the most representative dispersal syndrome.

The linear models (Fig 3) indicated that richness was not explained by the environmental variables and that the phylogenetic metrics were likewise only weakly explained by those variables. The regressions indicate more significant relationships between mean temperatures and MPD (R^2=0.07; $p<0.01$), NRI (R^2=0.09; $p<0.01$), MNTD (R^2=0.09; $p<0.01$), and NTI (R^2=0.13; $p<0.001$), while the mean altitude above sea level was most related to NRI (R^2=0.10; $p<0.01$), MNTD (R^2=0.11; $p<0.01$), and NTI (R^2=0.28 $p<0.01$); but not significant with MPD.

The highest MPD (Table 2) was observed for the Caribe province (263.55), while the lowest value was reported for the Altoandina province (237.75); when the province closest to the Yungas (251.17) was considered, it could be seen that phylogenetic diversity decreased with increasing altitude. Species richness differed among the biogeographic provinces, with values of 51 (Yungas) to 151 species (Pacífica). Despite the considerable differences

between the provinces, they showed similar MPD values because this metric compares the floristic compositions of the areas, considering co-occurring plant groups.

Table 2 shows positive NRI values for the provinces Altoandina, Yungas, Pampeana, southern desert, Pacífica, Subantártica (provinces with subtropical or tropical altitudinal climates), Amazonia, Atlántica (tropical humid climates), and Sabana (tropical dry climate), indicating a tendency for phylogenetic grouping in relation to the set of continental species. The Caatinga, Cerrado, Xorófila (dry tropical climate) and Paranaense (subtropical climate) provinces have more phylogenetically diverse assemblages of plants associated with aquatic environments, as indicated by their negative NRI values.

The MNTDs indicated that the Subantarctic province and the assemblies associated with the east coast of South America (Amazonia, Atlántica, Caatinga, Cerrado, Paranaense, and Pampeana), when grouping the flora of Brazil, demonstrated lower numbers of species per genus. As the distances between their closest relatives were therefore lower compared to the other provinces (which demonstrated many species associated with the same genus), these Brazilian floras were considered more diverse.

Table 1. Environmental variables of each biogeographical province analysed in this study. Annual temperature (Temp.), rainfall (Rain.), and altitude (Alt.). Environmental variables of each biogeographical province analysed in this study. Annual temperature (Temp.), rainfall (Rain.), and altitude (Alt.).

Area	Province	Temp. (°C) (Mean)	Rain. (mm) (Mean)	Alt. (m) (Mean)
Altitude areas	Alto andina	12.6	576.5	3013.6
	Yungas	10.3	1363.9	3017
Humid areas	Amazonia	28.1	2212.6	886
	Atlántica	21.1	1636.7	24.9
	Caribe	25	1400	220
	Pampeana	19.7	1284.1	176.9
	Paranaense	20.7	1241.3	749.7
	Subantártica	12.9	1598.7	619.6
Dry areas	Caatinga	25.3	614.7	420.6
	Cerrado	23.4	1300.5	297.0
	Del desierto	18.7	790.2	886
	Pacífica	16.1	414.4	1305
	Sabana	21	1200	200
	Xerófila	20.9	1083.3	1382

Table 2. Number of species (S) and phylogenetic metrics of aquatic plant assemblages in 14 biogeographic provinces across the Neotropics. MPD = mean pairwise distance; MNTD = mean nearest neighbour distance; NRI = net relatedness index; NTI = nearest taxon index.

Number of species (S) and phylogenetic metrics of aquatic plant assemblages in 14 biogeographic provinces across the Neotropics. MPD = mean pairwise distance; MNTD = mean nearest neighbour distance; NRI = net relatedness index; NTI = nearest taxon index.

Area	Province	S	MPD	NRI	MNTD	NTI
Altitude	Altoandina	177	237.7	4.22	57.1	0.82
	Yungas	154	251.2	1.25	70.2	0.57
Humid Area	Amazonia	492	250.7	0.28	49.4	1.18
	Atlántica	484	250.8	0.34	44.2	1.31
	Caribe	58	263.5	0.99	90.8	0.11
	Pampeana	721	250.9	2.22	32.9	2.39
	Paranaense	877	251.09	-0.49	50.7	1.08
	Subantártica	466	250.9	1.75	31.8	1.86
Dry Area	Caatinga	361	250.9	-0.27	48.6	1.06
	Cerrado	570	251.0	-1.21	42.3	1.39
	Del Desierto	478	250.9	2.25	57.9	0.79
	Pacífica	303	251.2	1.18	69.4	0.58
	Sabana	113	251.2	0.02	122.1	1.78
	Xerófila	410	250.9	-2.20	52.2	11.87

The floras associated with the provinces located in North America (Xerophila), Central America (Caribe), and in the provinces under the influence of the Andes Mountains (Altoandina, Del Desierto, Pacífica, and Yungas) showed MNTDs varying from 51-100 million years (only the Sabana province showed an MNTD above 100 million years [122.11 m.y.]), indicating floras with greater distances between their closest relatives, that is, fewer numbers of species associated with each genus. All NTI values were positive, showing that the assemblies found within the provinces demonstrated assemblage rules with more co-generic taxa than expected by chance.

DISCUSSION

The results showed that environmental variables presented little (temperature and altitude) or no (rainfall) influence on the species richness and phylogenetic diversity of the local assemblies of Neotropical plants associated with aquatic environments. The MPD indicated a slight association with temperature, although it did not support the equator-pole diversity gradient proposed by Willig

et al. (2003) and Maestre *et al.* (2009). Phylogenetic diversity likewise varied very little at the spatial scale, principally because the floristic compositions of these assemblages tended to be closer phylogenetically.

The results confirmed the expectation that the assemblies found within high altitude, tropical humid, or sub-humid climatic zones would demonstrate plant diversities that tended to be more aggregated phylogenetically than expected by chance. The floras of dry-hot tropical environments, on the other hand, exhibited assemblages that were more phylogenetically diverse than expected by chance. This characteristic places the dry zones as more fragile ecosystems considering to the loss of species since any change in their phylogenetic structure alters the established relationships, including ecological niches with other organisms.

This situation establishes an interesting paradox: how can a set of assemblies, that demonstrate similar mean phylogenetic diversities, be composed, at the same time, of both more aggregated and more phylogenetically dispersed individual assemblies? The response appears to be that while the same genera co-occur in these assemblies,
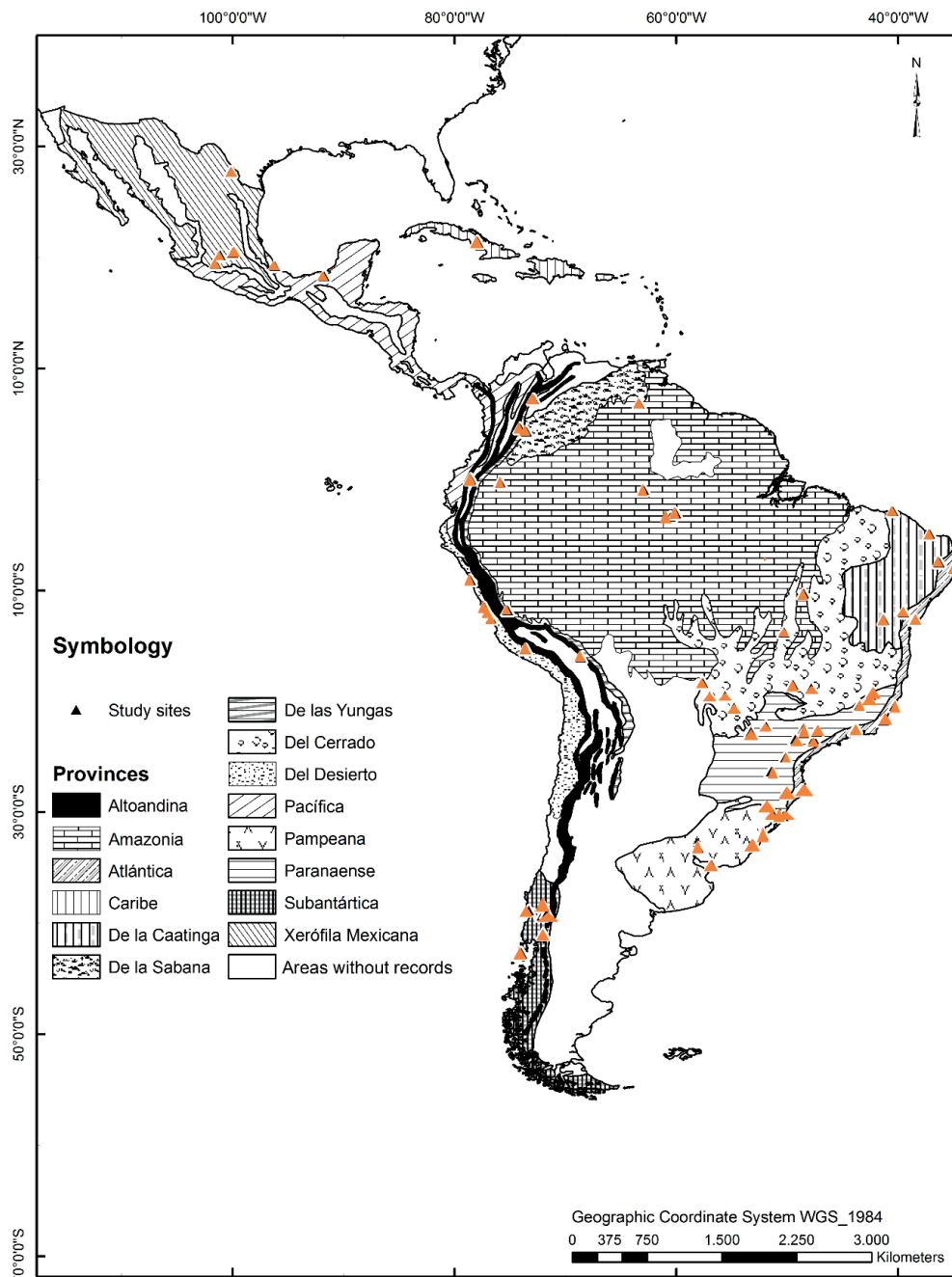
Figure 1. Locations of sampling sites by biogeographic provinces (sensu Cabrera & Willink, 1980) analysed in this article.

their component numbers of species can vary greatly. The distances between the branches in the phylogenetic trees of more aggregated assemblies are smaller than those in more dispersed assemblies (Webb *et al.,* 2002).

This process of favouring distinct lineages of plants associated with aquatic environments in dry environments is likely related to historical factors, such as those resulting from the most recent glaciations. The climatic changes

of the Pleistocene era allowed the expansion of lineages well-adapted to dry areas, where the most successful species were successful in competition (Burnham & Graham 1999), principally in South America, where the Pleistocene Arc hypothesis has been used to explain the distributions of different floras in dry zones (Neves *et al.,* 2015).

Figure 2. Percentages of dispersion syndromes of the species by biogeographic provinces.
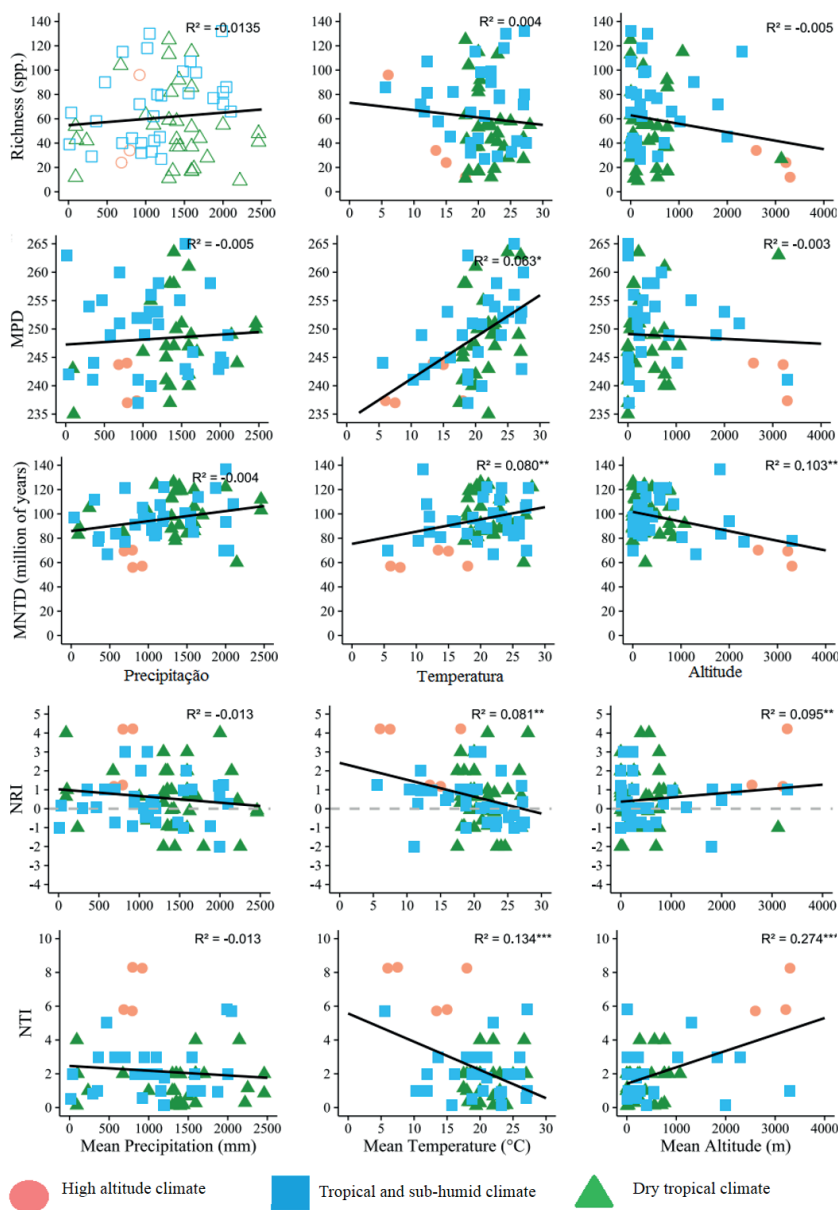

Figure 3. Linear regressions using the richness and phylogenetic diversity metrics (MPD; NRI; MNTD, and NTI) with environmental variables. Mean of temperature, mean of rainfall and mean of altitude. (Note: * = P<0.01; ** = P<0.001).

The Pleistocene Arc model theory indicates that a diagonal band connecting the Caatinga to the Chaco could have been an important floristic corridor for this region during the Pleistocene, and with the global changes in the Holocene, only species better adapted to the new environmental filters could continue to co-occur (Silva *et al.*, 2022). Evidences of this phenomenon are reflected in the flora of aquatic plants found in the provinces - which demonstrate good adjustments with the Pleistocene Arc model - with the results of the NRI metric of this study, indicating the occurrence of clades with different lineages adapted to dry regions in the Caatinga, Cerrado, and the biogeographical provinces of Paranaense.

The finding that the floras of hot-dry tropical zones tend towards phylogenetic dispersal in their assembly rules suggests that these aquatic spermatophyte assemblies must have been exposed to two ecological processes: (1) they tend to be exceptions to the rule established in the "competition by kinship hypothesis", where species that are more closely related tend to compete for the same resources (Darwin, 1859) and, with the evolution of this process, the existence of a relationship of facilitation by distantly related species develops because species that are less evolutionarily related do not compete as strongly for the same resources as those that are more closely related (Valiente-Banuet & Verdu, 2007). These processes are difficult to quantify, but, in theory, they explain "magnetic dispersion", that is, the phylogenetic distances among the taxa (Cahill *et al.,* 2007).

Altitude was the environmental variable that stood out in relation to the others. Although only two of the provinces represented high altitude regions (Altoandina and Yungas), the phylogenetic diversity was observed to decrease as altitude increased, while the numbers of species per genus tended to increase, indicating more phylogenetic aggregation than the other provinces. This result may indicate that these flowers are governed by the logic of the "U" diversity hypothesis presented by Rahbek (2005) and Werenkrauft & Rugiero (2011), who propose that the altitude gradients exert an influence on plants in general, Imposing, The higher altitude, the less the phytodiversity. However, this hypothesis will need to be investigated further.

The MNTD indicated that vicariant processes must have formed the diversity structures of Neotropical plants associated with aquatic environments during the evolution of their lineages. The rising of the Andes Mountains, which isolated the southwestern sub-Antarctic region of South America from the Brazilian region on the Atlantic coast, generated conditions for the

expansion of endemism (Antonelli & Sanmartín, 2011; Hughes *et al.,* 2013), with elevated species ratios per genus.

The results also indicate a case of "phylogenetic signal" with the presence of repeated co-occurring clades in the ecosystems analysed, as suggested by the MPD metric and confirmed by the NTI analyses. This leads us to believe that even though additional environmental variables were not considered (such as water quality, the conservation status of the area, soil types, or the sizes of water bodies), they must not have significant influences on the structure of those assemblages.

The floristic compositions of the assemblies analysed here demonstrated clades that were well-distributed in the pool of regional species. Even the so-called "bio-indicators" of eutrophication, such as *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae), *Egeria densa* Planch. (Hidrocharitaceae)*,* and *Pistia stratiotes* L. (Araceae), did not demonstrate greater than normal growth as constituent parts of well-represented lineages in those ecosystems. It is worth noting that these bio-indicator species are treated as "problems" only when they are excessively abundant—not when they are simply present.

As was noted earlier, the Neotropical aquatic spermatophyte clades are recurrent, independent of environmental conditions or geographic distances. One possible explanation for this phenomenon may be related to the successful dispersal of their ancestral taxa. This corroborates the hypothesis put forward by Donoghue (2008) suggesting that traditional explanations based on environmental correlations must yield more space for historical factors, principally when considering widely distributed groups such as plants associated with aquatic environments.

In theory, only enormous dispersal events could have resulted in widely distant assemblies having such similar phylogenetic characteristics. Intuitively, the Andean barrier represents an insurmountable obstacle that should result in distinct differentiation of the eastern and western floras, although it appears to have only influenced the appearance of more phylogenetically aggregated floras. As such, these taxa must have been dispersed before the rise of this orographic barrier, and when one examines the phylogenetic tree constructed for the regional pool of species, it can be seen that most of the genera (84% of the total) appeared before the vicariant processes generated by the appearance of the Andes. The genera that appeared after this geological event are overwhelmingly composed of anemochoric species.

The principal dispersal syndromes of these taxa within the regional pool of anemochoric and endozoochoric species can be seen in Figure 2. Our results indicate that these autechological factors must have been preserved from ancestral species, converging in different strains, and using their ecological advantages to facilitate the wide dispersion of these groups. The wide geographic distribution of these anemochoric clades is supported by the fact that their diaspores are very light and demonstrate adaptations for floating on the winds (Skarpaas *et al.,* 2006) as well as small cross-sectional areas that facilitate their aerial transport (Nathan & Kabul, 2005). The conditions of the endozoochoric species are supported by the routes of migratory birds (Santamaría, 2002), considering that these routes must certainly have been changed along the evolutionary histories of those water bodies and those birds (Green *et al.,* 2002; Santamaría & Klaassen, 2002; Charalambidou & Santamaría, 2002).

From the standpoint of the phylogenies of the assemblies, the lists of the Neotropical aquatic spermatophyte species "*lato sensu*" demonstrated levels of phylogenetic diversity that varied very little among the different biogeographic provinces examined.

It was observed that temperature and altitude were demonstrably related to the structures of the assemblies analysed here and to a notably higher degree than rainfall; regions with tropical altitudinal climates tended to demonstrate phylogenetic aggregation of their taxa, in contrast to hot and dry tropical regions, which demonstrate phylogenetic dispersal of their taxa. It was not possible to confirm the hypothesis of "stress gradients" in the equator-pole direction for plants associated with aquatic environments, in a macroecological perspective, but altitudinal changes supported the "U gradient" hypothesis, which appears to require more investigation, besides presenting floristic groups more phylogenetically dispersed, in relation to chance, in dry areas, indicating more fragile ecosystems for species loss, from the point of view of conservation biology.

Terminal taxa (genera) and large groups (families/orders) are largely uniformly distributed within the regional phylogenetic pool, and the results indicated a tendency for the co-occurrence of the same groups in these aquatic ecosystems. The floristic lists indicated that variation was greater at the specific level (with Brazil being the most biodiverse region), while the same taxa are widely recurrent at the generic and family/order levels.

This study suggests an extensive regional competitive exclusion of other taxa or a persistent phylogenetic signal of allopatric speciation in all of the clades. This hypothesis indicates that the extinction of species in these habitat sites may occur randomly throughout the phylogenetic trees, although with concurrent processes of substitution involving those same existing clades, as those taxa are more closely related to existing taxa than expected by chance alone.

Nonetheless, additional studies will be needed to focus on the detection of limits for the loss of species of plants associated with aquatic environments where the phylogenetic structure of diversity could potentially be altered in ways that would compromise ecosystem functioning in those habitat sites and the evolution of the Neotropical floras in these emergent and dynamic environments.

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