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Running title: Ferns and Lycophytes in Rio Grande do Norte State, Brazil

ABSTRACT

Brazil, with its vast territory and climatic diversity, harbors a rich biodiversity of plants, including ferns and lycophytes. However, these groups remain understudied in northeastern Brazil, particularly in the state of Rio Grande do Norte. This study provides a comprehensive floristic survey of spore-bearing vascular plants in Rio Grande do Norte, documenting 334 records encompassing 64 species across 23 families. Fourteen species are recorded for the first time in the state. Collection gaps and sampling biases were identified, revealing ecological and distribution patterns. The analysis highlights a significant concentration of sampling effort in the Atlantic Forest and Caatinga, influenced notably by seasonality and water availability. This study underscores the need for conservation efforts targeting fern and lycophyte species and identifies critical areas for future research.

Keywords: Atlantic Forest, biodiversity, Caatinga, floristic survey, sampling bias

Introduction

Brazil stands out in the neotropical region for its vast continental extent, encompassing diverse climatic zones, vegetation, and a vast richness of plant species (Ribeiro *et al.* 2009, BFG 2022, Flora and Funga of Brazil 2024). However, this immense territorial expanse has led to significant biases in floristic knowledge, highlighting the need for efforts to address gaps related to taxonomic groups such as ferns and lycophytes, as well as underexplored regions like northeastern Brazil (Ribeiro *et al.* 2009, Almeida & Salino 2016, Oliveira *et al.* 2017, Santiago *et al.* 2023).

Ferns and lycophytes are two groups of spore-bearing vascular plants that share certain characteristics, such as a life cycle divided into two independent phases: the sporophytic and gametophytic phases (Haufler *et al.* 2016). Despite these similarities, they represent distinct monophyletic lineages and should be studied separately (PPG I 2016, Lehtonen *et al.* 2017, Almeida 2023). Another shared trait is their strong dependence on environmental factors, particularly humidity and topographic heterogeneity. Favorable environmental conditions are crucial for the proper development of the gametophytic phase—where sexual reproduction occurs—and, consequently, the establishment of the sporophytic phase (Sharpe *et al.* 2010, Weigand *et al.* 2020).

The remarkable richness of ferns and lycophytes in Brazil, currently comprising 1,412 documented species (Flora and Funga of Brazil 2024), reflects the country's overall high plant diversity. This megadiversity results from the interplay of climatic and edaphic factors (Ribeiro *et al.* 2009, BFG 2022). A notable example is the Atlantic Forest domain, which is home to 945 species of ferns and lycophytes, including 357 endemics (Flora and Funga of Brazil 2024). Although these plants typically depend on water for reproduction and development, some species have adapted successfully to semi-arid climates, demonstrating remarkable ecological flexibility (Moran & Smith 2001, Page 2002, Santiago *et al.* 2023).

Northeastern Brazil encompasses three main phytogeographic domains (IBGE 2019). The extensive semi-arid drylands of the Caatinga cover more than half of the region. The Atlantic Forest occupies the northern and eastern parts, comprising primarily coastal forests and enclaves within the Caatinga known as *Brejos de Altitude* (Velloso *et al.* 2002, Silva & Casteleti 2005). Additionally, a small portion of the Cerrado is found in the states of Maranhão and Ceará (Moro *et al.* 2015, IBGE 2019). The region hosts 553 species of ferns and lycophytes (Flora and Funga of Brazil 2024). However, it also includes states with the lowest species richness for these groups in

Brazil, such as Piauí (56 species), Sergipe (50 species), and Rio Grande do Norte (34 species) (Flora and Funga of Brazil 2024).

In Rio Grande do Norte, the flora of certain plant groups is relatively well-documented, including Apocynaceae (Sousa Junior & Jardim 2021), Bromeliaceae (Tomaz & Versieux 2019), Lamiaceae (Soares *et al.* 2017), and Fabaceae - Papilionoideae (São-Mateus *et al.* 2013). Floristic surveys have also been conducted in various areas (Almeida Jr. & Zickel 2012, Oliveira *et al.* 2012, Ribeiro *et al.* 2014), including a study on ferns and lycophytes in an altitude wetland in the state (Silvestre *et al.* 2019).

Floristic inventories frequently highlight the issues of collection gaps and limited sampling efforts in the state (Versieux *et al.* 2017, Soares *et al.* 2017). Rio Grande do Norte has the lowest recorded richness of ferns and lycophytes among Brazilian states, with only 34 species documented (Flora and Funga of Brazil 2024). The few remaining Atlantic Forest fragments in the state (Capobianco 2001) suggest the limited availability of suitable habitats for the establishment of ferns and lycophytes. However, the currently low number of recorded species may also be attributed to the lack of compiled collection data and systematic studies in the region (Sylvestre 2003, Santiago 2013).

Thus, the objective of this study was to 1) provide a checklist of ferns and lycophytes in the state of Rio Grande do Norte based on herbarium specimens, new collections, and literature and 2) analyze distribution patterns, collection gaps, and sampling biases.

Material and Methods

Study site

The state of Rio Grande do Norte covers an area of 52,608.60 km² in northeastern Brazil (Fig. 1), featuring various geological formations and relief types. According to Pfaltzgraf & Torres (2010), the coastline consists mainly of the Barreiras Group formations, characterized by dune deposits, coastal plateaus, and some lacustrine complexes. Moving inland, extensive fluvial plains transition into two primary geological formations: a vast sedimentary plain with karstic features in the north and a crystalline area with more pronounced relief in the south, marked by inselbergs and plateaus (Pfaltzgraf & Torres 2010). The climate in the state is classified into two types according to the Köppen classification (Alvares *et al.* 2013). The eastern coastal and Agreste regions have a tropical wet climate with dry summers (As), while the more inland and northern coastal regions have a hot semi-arid climate (Bsh), characterized by low latitudes and altitudes (Alvares *et al.* 2013). The vegetation of Rio Grande do Norte reflects its geological variation and the differing climatic conditions across the state. The coastal vegetation falls within the Atlantic Forest domain, covering 9% of the state's territory and featuring formations such as Restinga, which ranges from herbaceous to arboreal types, as well as fragments of Semi-deciduous and Deciduous Seasonal Forests (Serviço Florestal Brasileiro 2018). This forested vegetation follows an East-West precipitation gradient until it transitions into the predominant Caatinga domain. The Caatinga vegetation displays flora and structural characteristics corresponding to the crystalline and sedimentary geological formations found in the interior of the state (Moro *et al.* 2016, Serviço Florestal Brasileiro 2018).

The checklist of ferns and lycophytes in Rio Grande do Norte was compiled by analyzing specimens from the IPA, HST, PEUFR, RN, and UFRN herbaria (acronyms follow Thiers 2024), alongside a literature review of relevant records (Santiago 2006, Xavier *et al.* 2012, Silvestre *et al.* 2019). Between September 2017 and November

2022, field expeditions were conducted in coastal lacustrine complexes and forest fragments to collect additional specimens. The collection of ferns and lycophytes from the MOSS herbarium was not analyzed due to its current unavailability, following a misplacement incident during a loan return process (MOSS herbarium curation, personal communication). However, digital records of the collection remain accessible via the Splink platform (https://specieslink.net/search), and the geographic information from these records was utilized to discuss species distribution in Rio Grande do Norte.

Taxonomic classification follows PPG I (2016), with all scientific names and identifications verified through the Flora and Funga of Brazil (2024) and specialized literature (Kramer 1957, Johnson 1986, Hovenkamp & Miyamoto 2005, Cárdenas *et al.* 2016, Gasper *et al.* 2016, Góes-Neto 2016, Mickel 2016, Øllgaard & Windisch 2016, Weigand & Lehnert 2016, Viveros *et al.* 2018, Bohn *et al.* 2019, Prado & Hirai 2020). The conservation status of the species was assessed based on the List of Threatened Species of the Fauna and Flora of Brazil (MMA Ordinance No. 148/2022) (BRASIL 2022).

Life forms were classified following the frameworks of Raunkiaer (1934) and Müller-Dombois & Ellenberg (1974) as follows: epiphytes (species growing on other plants), geophytes (species with growth organs below the soil surface, often with rhizomes), hemicryptophytes (species with growth organs at soil level, typical of grasslands), hydrophytes (floating aquatic species), and lianas (climbing species). Environmental preferences were categorized according to the Technical Manual of Brazilian Vegetation (IBGE 2012). Light preferences were classified as heliophytes (species thriving in full sun), semi-sciophytes (species favoring environments with low light incidence), and sciophytes (species preferring shaded environments). Substrate preferences were classified as corticolous (species growing on the trunks of woody plants), floating (species with lower parts submerged but not sessile), marshy (species in saturated soil environments), riparian (species in gallery forests along streams), ruderal (species with no substrate preference, commonly found in disturbed areas), rupicolous (species in rocky environments with sediment accumulation), and terrestrial (species favoring non-saturated soils). Environmental preferences for each species were determined through field observations and references to specialized literature.

Geographic data were obtained from the repositories Reflora (http://reflora.jbrj.gov.br/) and speciesLink (https://specieslink.net/search) to create distribution maps and analyze species richness, sampling effort, and potential gaps or biases in the data. Records identified only at the genus level or lacking complete location information were excluded from the analysis.

For the assessment of species richness and sampling effort, a grid of 0.125° x 0.125° was applied, comprising 337 grid cells, offering a suitable resolution for analyzing species distribution within the state. Potential sampling biases were evaluated by comparing collection records with randomly generated points across the state. The random points matched the number of collection records and were used to calculate the shortest geographic distances to roads and water bodies (rivers, lakes, and ponds) for both data sets (collected records and random points). Spatial analyses and map creation were conducted using QGIS 3.30.1 (QGIS 2023), while statistical tests for bias detection were performed using the Mann-Whitney U test in R v. 4.2.1 (R Core Team 2022) via RStudio v. 2023.03.1+446 (Posit Team 2023). Distribution maps were finalized in QGIS 3.16.

Results

We identified 334 records corresponding to 64 species, including six lycophytes from three families and five genera, and 58 ferns from 20 families and 37 genera (Table 1). Among these, 12 species were recorded exclusively in the literature: *Adiantum pulverulentum*, *Anemia hirta*, *Asplenium formosum*, *Campyloneurum nitidum*, *Ctenitis submarginalis*, *Cyathea pungens*, *Danaea nodosa*, *Diplazium plantaginifolium*, *Doryopteris sagittifolia*, *Meniscium serratum*, *Neoblechnum brasiliense*, and *Pteris biaurita* (Santiago 2006, P. S. M. Sarmento, pers. comm.) (Table 1). The families with the highest species richness were Pteridaceae (12 species) and Anemiaceae (six species), with the most represented genera being *Anemia* (five species), followed by *Adiantum*, *Doryopteris*, *Marsilea*, *Nephrolepis*, and *Salvinia* (three species each) (Table 1). Three recorded species—*Macrothelypteris torresiana*, *Nephrolepis brownii*, and *Pteris vittata*—are non-native but naturalized in Brazil (Table 1; Flora and Funga of Brasil 2024).

Twenty-one species were identified as new records for Rio Grande do Norte according to the Flora and Funga of Brazil (2024). Six of these were previously reported in the literature: *Adiantum raddianum*, *Anemia dentata*, *Blechnum occidentale*, and *Christella hispidula* (Silvestre *et al.* 2019), as well as *Marsilea deflexa* and *Selaginella erythropus* (Xavier *et al.* 2012). The remaining 15 species, supported by voucher specimens, represent new occurrences for the state: *Anemia ferruginea*, *A. hirsuta*, *A. tomentosa*, *Asplenium scandicinum*, *Azolla filiculoides*, *Cyathea phalerata*, *Doryopteris collina*, *Lindsaea stricta*, *Lycopodiella* cf. *longipes*, *Nephrolepis brownii*, *Palhinhaea cernua*, *Pseudolycopodiella meridionalis*, *Pteris vittata*, *Selaginella oblongifolia*, and *Salvinia radula* (Table 1). No voucher specimens or references in the literature were found for five species listed as occurring in Rio Grande do Norte in the Flora and Funga of Brazil (2024): *Ctenitis fenestralis* (C.Chr.) Copel., *Megalastrum canescens* (Kunze ex Mett.) A.R.Sm. & R.C.Moran, *M. retrorsum* R.C.Moran et al., *Vandenboschia rupestris* (Raddi) Ebihara, and *Phlebodium pseudoaureum* (Cav.) Lellinger. These species occurrences in Rio Grande do Norte may have been mistakenly recorded.

The most common life form identified was hemicryptophyte, comprising 46 species, followed by epiphytes, with six species, and geophytes, with five species. In terms of ecological preferences, 43 species exhibit low tolerance to direct sunlight, including 23 sciophytes and 20 semi-sciophytes. Regarding substrate preferences, 27 species are terrestrial, 13 are marsh-dwelling, and 12 are rupicolous. Notably, seven species occur in both terrestrial and rupicolous habitats (*Anemia dentata*, *A. oblongifolia*, *Cyclodium meniscioides*, *Adiantum deflectens*, *A. raddianum*, *Doryopteris concolor*, and *Selaginella convoluta*), while one species, *Microgramma geminata*, is found in both corticolous and rupicolous habitats.

A total of 103 specimens, representing 28 species of lycophytes and ferns, were collected within protected areas (PAs). Of these, 59 specimens (20 species) came from PAs designated for sustainable use of natural resources, while 44 specimens (eight species) were recorded in integral protection PAs. Regarding conservation status, one species is classified as endangered (*Isoetes luetzelburgii*) and another as vulnerable (*Anemia dentata*). The remaining species are either of least concern or have not been assessed. In Rio Grande do Norte, *Isoetes luetzelburgii* is restricted to the Seridó Ecological Station. Although more broadly distributed across Brazil, *Anemia dentata* is underrepresented in well-sampled regions. In northeastern Brazil, its records are in currently degraded habitats, affected by frequent fires and ongoing deforestation (Messina & Moraes 2012, evaluated as the synonym *A. mirabilis* Brade).

Out of the 337 grid cells analyzed, only 78 (23%) contained records of ferns and lycophytes (Fig. 1a-c). These records are concentrated along the state's eastern coastline, primarily in the Atlantic Forest and transitional zones with the Caatinga (Fig. 1a-c). Additionally, occurrences in this region are often associated with water bodies, such as rivers, streams, and ponds (Fig. 1a). The most frequently collected species in the area are *Telmatoblechnum serrulatum* (25 records across 15 grid cells), *Microgramma vacciniifolia* (24 records across eight grid cells), and *Ceratopteris thalictroides* (18 records across 14 grid cells) (Fig. 1b).

Species occurrences in more inland regions of the state, within the Caatinga domain, are primarily associated with rocky outcrops and hills (Fig. 1a). The most common species in this domain are *Selaginella convoluta* (23 records across 13 grid cells), *Adiantum deflectens* (15 records across 10 grid cells), and *Doryopteris concolor* (nine records across seven grid cells) (Fig. 1b). *Salvinia auriculata* is the most frequently collected and widely distributed species, with 26 records across 17 grid cells, occurring in both domains (Fig. 1b).

Grid cells with higher species richness, ranging from 10 to 13 species, correspond to areas with the highest concentration of collections, varying from 16 to 23 records per grid cell. These include grid cell 8 (12 species, 18 collections), 58 (13 species, 23 collections), 71 (11 species, 21 collections), 75 (13 species, 16 collections), and 77 (10 species, 16 collections) (Fig. 1b-c). Grid cells 8 and 58 are situated within the Caatinga domain, while grid cells 71, 75, and 77 are located within the Atlantic Forest domain, the latter forming a north-south alignment near the coastline. The environments in these areas are characterized by high humidity and proximity to water bodies, including the highland wet forests of Portalegre (cell 8), the Bonfim lacustrine complex (cell 71), and forest fragments of the Atlantic Forest and riparian forests (cells 58, 75, and 77).

In addition to the distance between the grid cells with the highest species richness, the environmental conditions of these cells are also distinct, resulting in unique floras that share few species. Grid cell 8 corresponds to a high-altitude wetland, where species such as *Adiantum deflectens*, *Anemia dentata*, *Blechnum occidentale*, *Christella hispidula*, *Cyclodium meniscioides*, *Doryopteris concolor*, *Lygodium venustum*, *Macrothelypteris torresiana*, *Pityrogramma calomelanos*, *Pteridium esculentum*, and *Selaginella erythropus* are found (Table 1, Figure 1b). Grid cell 58 features an environment characterized by forest fragments, water bodies, and flooded areas, supporting species such as *Acrostichum danaeifolium*, *Ceratopteris thalictroides*, *Cyclosorus interruptus*, *Dicranopteris flexuosa*, *Lindsaea stricta*, *Lygodium volubile*, *Marsilea minuta*, *Palhinhaea cernua*, *Phlebodium decumanum*, *Pseudolycopodiella meridionalis*, *Pteris vitata*, and *Telmatoblechnum serrulatum* (Table 1, Figure 1b). Meanwhile, grid cell 75 is characterized as a remnant of the Atlantic Forest with riparian vegetation, harboring species such as *Cyathea phalerata*, *Cyclodium meniscioides*, *Dicranopteris flexuosa*, *Lindsaea lancea*, *L. stricta*, *Lygodium venustum*, *L. volubile*, *Metaxya parkeri*, *Microgramma vacciniifolia*, *Phlebodium decumanum*, *Salpichlaena volubilis*, and *Telmatoblechnum serrulatum* (Table 1, Figure 1b).

The bias analysis revealed that collections are significantly closer to highways and access roads than expected under a null model of random sampling ($p = 0.01386$). However, no bias was detected concerning proximity to water bodies ($p = 0.3928$).

DISCUSSION

Currently, only 34 species of ferns and lycophytes are recorded for Rio Grande do Norte, according to the Flora and Funga of Brazil (2024), five of which lack herbarium specimens for vouchering. This study contributed 24 vouchered species to the list, representing an 83% increase in species richness. Despite this significant addition, Rio Grande do Norte remains one of the states with the lowest species richness and collection efforts in Brazil, ranking just behind Paraíba (with 78 species) and ahead of Sergipe and Piauí, which have 46 and 56 species, respectively (Flora and Funga of Brazil 2024).

Among the richest fern families, Pteridaceae stands out due to its cosmopolitan distribution, remarkable diversity of life forms, and adaptations to xeric environments (Tryon & Tryon 1982). This family is frequently identified as one of the most species-rich in various inventories of the Atlantic Forest, particularly within the Pernambuco center of endemism (Pereira *et al.* 2011, Lourenço & Xavier 2013, Silvestre & Xavier 2013, Santiago *et al.* 2014). In these studies, other families with high species richness that closely resemble the diversity observed in the coastal region of Rio Grande do Norte (within the Atlantic Forest domain) include Dryopteridaceae, Polypodiaceae, and Thelypteridaceae (Table 1).

Anemiaceae, the second richest family, and the genus *Anemia*, the richest genus in Rio Grande do Norte (RN), are primarily distributed within the Caatinga phytogeographic domain. Only one species, *Anemia hirta*, has been cited for the Atlantic Forest (Santiago 2006, Table 1). According to Xavier *et al.* (2012), *Anemia* is the richest genus in the northeastern semi-arid region, where its species exhibit poikilohydry—a xeromorphic adaptation that allows their fronds to curl during dry periods, reducing desiccation (Mickel 2016).

The non-native naturalized species recorded in the state are known to be invasive and capable of rapidly colonizing diverse environments (Prado & Windisch 2000, Salino & Semir 2002, Hovenkamp & Miyamoto 2005). *Nephrolepis brownii* and *P. vittata* are commonly observed in urban areas, where small populations establish themselves on concrete surfaces. In contrast, *M. torresiana* thrives in areas with higher soil moisture, forming dense naturalized species. Further data are needed to assess whether they pose a significant threat to native species.

The dominance of hemicryptophytes aligns with patterns observed in various studies across the different phytogeographic domains of Brazil (Table 1) (Silva *et al.* 2011, Gonzatti *et al.* 2014, Kreutz *et al.* 2016, Lehn *et al.* 2020). This life form supports species persistence during unfavorable periods by protecting the growth buds through surrounding soil deposition and the individuals' vegetative remains (Kornás 1985, Gonzatti *et al.* 2014).

The predominance of species with low or moderate light tolerance in Rio Grande do Norte (RN) may be linked to the types of forests in which they are predominantly found, including Seasonal Deciduous and Semideciduous Forests, Restinga woody formations in the Atlantic Forest, and microhabitats associated with forested savanna-steppe formations in the Caatinga (Table 1) (Cestaro 2002, IBGE 2012, Silvestre *et al.* 2019). Studies on ferns and lycophytes in neighboring states support the prevalence of species in these forest typologies (Xavier *et al.* 2012; Lourenço & Xavier 2013, Silvestre & Xavier 2013, Andrade *et al.* 2018, Silvestre *et al.* 2019). These forests allow greater light penetration in the understory, creating diverse microhabitats that contribute to the richness of fern and lycophyte species in these environments (Inácio & Jarenkow 2008). This characteristic may also explain the predominance of terrestrial over corticolous species in the state (Table 1), a pattern consistent with studies of the northeastern Atlantic Forest (Lourenço & Xavier 2013, Silvestre & Xavier 2013, Andrade *et al.* 2018, Santiago *et al.* 2014, Silvestre *et al.* 2019). The increased light incidence in the understory acts as a filter, promoting the establishment of specific or better-adapted life forms (Holttum 1938, Gonzatti *et al.* 2014).

Another critical environmental factor for ferns and lycophytes in the state is their preference for humid and flooded environments, with 12 marsh species associated with water bodies such as rivers, streams, and lagoons (Table 1). The coastal region of RN is characterized by significant water availability, a feature also observed in floristic surveys in Paraíba, the neighboring state, where high species richness is recorded near streams within forests (Lourenço & Xavier 2013, Silvestre & Xavier 2013, Santiago *et al.* 2014). This preference for flooded environments is further evidenced by the high number of collections of species such as *Salvinia auriculata* (26 records) and *Telmatoblechnum serrulatum* (25 records), which are frequently associated with rivers and lagoons.

Due to the association of fern and lycophyte communities with flooded environments and water bodies, seasonality and light incidence are important and limiting factors in the richness patterns observed. Seasonality, particularly in riparian environments, is a determinant factor for the establishment and growth of these species, acting as a selective filter (Kreutz *et al.* 2016). Additionally, the ecological succession of aquatic macrophytes in these habitats, where populations are frequently replaced due to competition, must also be considered (Kufner *et al.* 2011, Moura Jr. *et al.* 2011). In Rio Grande do Norte, two cases illustrate the influence of seasonality on species records: *Ceratopteris thalictroides*, a new occurrence for the Caatinga, was collected in an intermittent river (UFRN1928), while *Isoetes luetzelburgii*, endemic to the Caatinga and classified as endangered, was recorded in an ephemeral lagoon (UFRN3666, UPCB49067). According to Pereira *et al.* (2018), the corms of *I. luetzelburgii* can withstand up to 18 months of drought and regenerate under favorable conditions.

Based on ecological observations, species distribution records, and field data, it is possible to identify patterns of favorable environments for the establishment and maintenance of ferns and lycophytes in Rio Grande do Norte. Species richness and occurrence in the state are primarily associated with water bodies and are influenced by seasonality across the phytogeographic domains. Notably, species diversity in perennial rivers differs from that in intermittent rivers. These patterns can be categorized as follows: (I) intermittent riverbeds and floodplains, (II) intermittent lagoons and seasonally flooded fields, (III) ephemeral stream margins and outcrops, (IV) perennial lagoons, river and stream margins, (V) perennial stream margins within forests, (VI) and banks and forest edges.

Intermittent riverbeds and floodplains (I)—These habitats provide greater soil moisture availability during unfavorable periods, supporting the development of species with adaptations for succession or persistence during the rainy season. These environments also have strong sunlight exposure, which further influences species composition. Common species in these habitats include *Acrostichum danaeifolium*, *Ceratopteris thalictroides*, and *Marsilea minuta*.

Intermittent lagoons and seasonally flooded fields (II)—Some lagoons in the state are intermittent, providing water availability for a large part of the year. Similarly, seasonally flooded fields and radial springs exhibit comparable floristic compositions. These environments are exposed to direct sunlight, with dominant species including *Lindsaea stricta*, *Palhinhaea cernua*, and *Pseudolycopodiella meridionalis*.

Environmental patterns I and II include species with morphological and reproductive adaptations to withstand unfavorable water conditions. For instance, the genera *Azolla*, *Marsilea*, and *Salvinia* are distinguished by the presence of sporocarps, which ensure population continuity during rainy periods. Additionally, some species, such as *Cyclosorus interruptus* and *Telmatoblechnum serrulatum*, possess leathery leaf blades—a morphological trait that enhances resistance to desiccation (Read & Sanson 2003). This adaptation to minimize water loss is also considered a likely survival strategy for *Acrostichum danaeifolium* (Fonini *et al.* 2017).

Ephemeral stream margins and outcrops (III)—On the margins of ephemeral streams, as well as on slopes with significant rainwater runoff, ravines with steep terrain, and shaded rocky outcrops, suitable habitats exist for the development of ferns and lycophytes in the Caatinga. Common species in these environments include *Adiantum deflectens*, *Doryopteris concolor*, and *Selaginella convoluta*. This pattern corresponds to environments in the Caatinga that support fern and lycophyte species adapted to the semi-arid climate. Such habitats, characterized by moist and shaded microhabitats like rock crevices, shaded ravines, springs, and temporarily flooded areas, have been described as typical of the semi-arid region by Xavier *et al.* (2012). Similarly, Silvestre *et al.* (2019) highlight shaded and highly humid environments in the highland wet forests of Rio Grande do Norte. However, the floristic composition of these high-altitude areas differs significantly from that of the surrounding semi-arid matrix due to distinct topographical conditions.

Perennial lagoons, river and stream margins (IV)—Riparian forests of perennial rivers, streams, and lagoons provide favorable habitats for species such as *Cyclosorus interruptus* and *Macrothelypteris torresiana*, which thrive in shaded conditions. In areas with higher light incidence, species like *Ceratopteris thalictroides* and *Telmatoblechnum serrulatum* are commonly found. This pattern refers to riparian vegetation, with variation based on light exposure. In moist, shaded environments under tree canopies, such as perennial rivers and streams, a distinct floristic community develops compared to areas with higher sunlight exposure, like lagoons.

Perennial stream margins within forests (V)—The margins of small streams within forests are highly shaded and humid environments, creating ideal conditions for species with greater environmental sensitivity. Common species in these habitats include *Lindsaea lancea*, *Metaxya parkeri*, and *Salpichlaena volubilis*. This pattern also involves riparian forests but specifically describes highly shaded environments removed from edge effects in forest fragments. These conditions allow for the establishment of species sensitive to environmental variations, such as those in Dryopteridaceae (Santiago 2006).

Banks and forest edges (VI)— In embankments, slopes, and forest edges, which are generally exposed to direct sunlight, species more tolerant to anthropogenic disturbances are prevalent. Frequently observed in these environments are *Dicranopteris flexuosa*, *Lygodium* spp., and *Pteridium esculentum*. These species often have fronds with a leathery texture, an adaptation to the conditions of these habitats. Pattern VI describes environments with low water availability, typically under direct sunlight and often influenced by anthropogenic disturbances. In these conditions, the success of fern and lycophyte species is limited, favoring the establishment of species adapted to such challenging habitats.

Regarding protected areas, 20 fern and lycophyte species were recorded in sustainable-use conservation units (UCs), compared to only eight in fully protected UCs. The latter have stricter regulations for preservation and conservation within their territory; thus, the species of ferns and lycophytes tend to be better protected in integral protection PAs than those in sustainable use PAs (Heringer *et al.* 2019). However, most species in these groups remain vulnerable to anthropic habitat changes since the majority occur outside any protected area in the Rio Grande do Norte.

The occurrences of ferns and lycophytes in Rio Grande do Norte align with the richness patterns observed by Soares *et al.* (2017), who analyzed the distribution of the Lamiaceae family in the state. Their study identified three major areas of high species richness: the East Coast, the Seridó region, and the West region. These areas are also considered priority zones for conservation. The Seridó and West regions share similar characteristics in terms of vegetation, topography, and geological formations. Notably, the steep topography in these regions contributes to the preservation of natural areas within the Caatinga domain (Pfaltzgraff & Torres 2010, Pereira Neto & Silva 2012, Soares *et al.* 2017).

The disparity in species richness and collection efforts for ferns and lycophytes in the central and northern regions of Rio Grande do Norte may be attributed to two primary factors. The first is natural: the region's geological formation is predominantly sedimentary and karstic, characterized by a poorly developed fluvial network and well-drained soils, which act as a natural filter limiting the establishment of herbaceous flora (Pfaltzgraff & Torres 2010, Moro *et al.* 2016). The second factor is anthropogenic: agricultural and livestock activities have significantly reduced natural areas, further compounded by the low sampling effort typically observed across all botanical groups in the region (Soares *et al.* 2017).

Given the observed distribution of fern and lycophyte species in Rio Grande do Norte and the established occurrence patterns, identifying rare species in the state remains challenging. Nearly one-third of the species (20 species, 31.7%) have only one or two records and exhibit disjunct distributions within the state (Figs. 1a–b). This limited number of records per species is likely due to the scarcity of systematic studies focusing on these lineages in the state. Additionally, specialists in other botanical groups often lack the habit or interest in collecting ferns and lycophytes, contributing to underestimating their richness. However, several regions in RN present favorable environments for the development of ferns and lycophytes, which warrant further study. These include the mountainous region in the extreme west of the state, such as the Serra de João do Vale in Jucurutu, the Serra das Araras spanning the municipalities of Cerro Corá, Currais Novos, and São Tomé, as well as the permanent preservation areas of the coastal watershed on the eastern side of the state.

CONCLUSION

This study highlights the importance of further exploring the diversity of ferns and lycophytes in Rio Grande do Norte state. Despite the significant increase in the number of recorded species compared to previous data, the state remains one of the least documented in Brazil. The new records and the analysis of distribution patterns contribute to a better understanding of the environmental factors that influence the occurrence of these plant groups. Notably, the preferential association with water bodies and humid environments across the phytogeographic domains of the state emerges as a crucial factor for fern and lycophyte distribution. Additionally, the study underscores the importance of protected areas, particularly those with stricter regulations, for the conservation of these plant groups.

AUTHORS' CONTRIBUTIONS

Maurício Borges do Nascimento: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft. Augusto César Pessôa Santiago: Data curation, Formal Analysis, Validation, Visualization, Writing – original draft, Writing – review & editing. Fernanda Antunes Carvalho: Conceptualization, Methodology, Validation, Visualization, Writing –

original draft, Writing – review & editing. Thaís Elias Almeida: Conceptualization, Formal Analysis, Investigation, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing.

CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest of a personal, scientific, commercial, political, or financial nature in the submitted manuscript.

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Figure legends

FIGURE 1. Maps of records, richness, and sampling effort of ferns and lycophytes in Rio Grande do Norte. A – Map showing the physical characteristics, phytogeographic domains, and species records in the state. B – Map displaying the number of species per grid cell. Numbers within cells indicate grid IDs. C. Map showing the number of collections per grid cell; numbers within cells indicate grid IDs. Each grid cell corresponds to 0.175 x 0.175 degrees of latitude and longitude.

FIGURE 2. Habitat diversity in the study area. A – Temporary pond, Floresta Nacional de Nísia Floresta (FLONA Nísia Floresta), Nísia Floresta municipality. B – Floodplain, Escola Agrícola de Jundiaí (EAJ - UFRN), Macaíba municipality. C – Gallery forest, Mata Estrela, Baía Formosa municipality. D – Intermittent riverbed, Macaíba municipality. E – Seasonal lagoon, Área de Proteção Ambiental Bonfim-Guaraíras, Nísia Floresta municipality. F – Population of *Telmatoblechnum serrulatum* on the margin of the perennial Veríssimo lagoon, Rio do Fogo municipality. G – Riparian forest, Macaíba municipality (Photo: V.P. Moreira). H – Population of *Selaginella convoluta* in a ravine, Estação Ecológica do Seridó (ESEC Seridó), Serra Negra do Norte municipality. I – Rocky outcrop, Brejinho municipality (Photo: V.P. Moreira).

TABLE 1. List of Fern and Lycophyte species and their ecological aspects in the state of Rio Grande do Norte, Brazil. Life forms. E = epiphyte, G = geophytes, HM = hemicryptophyte, HD = hydrophyte, L = liana. Light preferences. Heli – heliophytes, Scio = sciophytes, Semi = semi-sciophytes. Substrate preferences. Cort = corticolous, Float = floating, Mars = marshy, Rip = riparian, Rud = ruderal, Rup = rupicolous, Terr

= terrestrial. Conservation status: EN = endangered; VU = vulnerable, LC – low concern, NE = not evaluated. * New records for Rio Grande do Norte state, Brazil.

Taxa	**Life form**	**Light preferences**	**Substrate preferences**	**Conservation status**	**Voucher**
LYCOPHYTES					
ISOETACEAE					
Isoetes luetzelburgii U.Weber	HM	Heli	Mars	EN	UFRN3666
LYCOPODIACEAE					
Lycopodiella cf. *longipes* (Grev. & Hooker) Holub	HM	Heli	Mars	NE	UFRN13454
Palhinhaea cernua (L.) Franco & Vasc. *	HM	Heli	Mars	NE	UFRN24148
Pseudolycopodiella meridionalis (Underw. & Lloyd) Holub *	HM	Heli	Mars	NE	UFRN26382
SELAGINELLACEAE					
Selaginella convoluta (Arn.) Spring	HM	Semi	Terr/Rup	LC	UFRN26776
Selaginella erythropus (Mart.) Spring	HM	Scio	Terr	NE	RN936
FERNS					
ANEMIACEAE					
Anemia dentata Gardner	HM	Semi	Terr/Rup	VU	UFRN7656

Anemia ferruginea Humb. & Bonpl. ex Kunth *	HM	Scio	Terr	NE	R30508
Anemia hirsuta (L.) Sw. *	HM	Semi	Terr	NE	UFRN9066
Anemia hirta (L.) Sw.	HM	Scio	Terr	NE	Santiago (2006)
Anemia oblongifolia (Cav.) Sw.	HM	Semi	Terr/Rup	NE	RN950
Anemia tomentosa (Sav.) Sw. *	HM	Heli	Terr	NE	UFRN26890
ASPLENIACEAE					
Asplenium formosum Willd.	E	Scio	Cort	NE	Santiago (2006)
Asplenium scandicinum Kaulf. *	E	Semi	Cort	NE	IPA29369
ATHYRIACEAE					
Diplazium plantaginifolium (L.) Urb.	HM	Scio	Terr	NE	Santiago (2006)
BLECHNACEAE					
Blechnum occidentale L.	HM	Scio	Terr	NE	RN941
Neoblechnum brasiliense (Desv.) Gasper & V.A.O.Dittrich	HM	Scio	Rup	NE	Santiago (2006)
Salpichlaena volubilis (Kaulf.) J.Sm.	L	Scio	Terr	NE	UFRN18606

Telmatoblechnum serrulatum (Rich.) Perrie, D.J.Ohlsen & Brownsey	G	Heli	Mars	NE	RN4061
CYATHEACEAE					
Cyathea phalerata Mart. *	HM	Scio	Terr	NE	UFRN18607
Cyathea pungens (Willd.) Domin	HM	Scio	Terr	LC	Santiago (2006)
DENNSTAEDTIACEAE					
Pteridium esculentum subsp. *arachnoideum* (Kaulf.) Thomson	G	Heli	Terr	NE	RN4276
DRYOPTERIDACEAE					
Ctenitis submarginalis (Langsd. & Fisch.) Ching	HM	Scio	Rip	NE	Santiago (2006)
Cyclodium meniscioides (Willd.) C.Presl	HM	Scio	Terr/Rup	NE	UFRN18609
Elaphoglossum langsdorffii (Hook. & Grev.) T.Moore	HM	Semi	Rup	LC	IPA29368
Rumohra adiantiformis (G.Forst.) Ching	HM	Scio	Terr	NE	RN3489
GLEICHENIACEAE					
Dicranopteris flexuosa (Schrad.) Underw.	G	Semi	Terr	NE	RN3627
LINDSAEACEAE					
Lindsaea lancea (L.) Bedd.	HM	Scio	Rip	NE	RN4277

Lindsaea stricta (Sw.) Dryand. *	HM	Heli	Mars	NE	RN2697
LYGODIACEAE					
Lygodium venustum Sw.	L	Semi	Terr	NE	RN4069
Lygodium volubile Sw.	L	Semi	Terr	NE	RN4083
MARATTIACEAE					
Danaea nodosa (L.) Sm.	HM	Scio	Rip	NE	Santiago (2006)
MARSILEACEAE					
Marsilea deflexa A.Braun	HM	Heli	Mars	NE	MOSS2420
Marsilea minuta L.	HM	Heli	Mars	NE	UFRN26032
METAXYACEAE					
Metaxya parkeri (Hook. & Grev.) J.Sm.	HM	Scio	Rip	NE	UFRN18611
NEPHROLEPIDACEAE					
Nephrolepis biserrata (Sw.) Schott	HM	Heli	Rud	NE	MOSS4349
Nephrolepis brownii (Desv.) Hovenkamp & Miyam. *	HM	Heli	Rud	NE	UFRN7834
Nephrolepis exaltata (L.) Schott	HM	Heli	Rud	NE	MOSS4638
POLYPODIACEAE					
Campyloneurum nitidum C.Presl	E	Scio	Cort	NE	Santiago (2006)

Microgramma geminata (Schrad.) R.M.Tryon & A.F.Tryon	E	Semi	Cort/Rup	NE	UFRN22199
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	E	Semi	Cort	NE	UFRN26387
Phlebodium decumanum (Willd.) J.Sm.	E	Semi	Cort	NE	UFRN26379
PSILOTACEAE					
Psilotum nudum (L.) P.Beauv.	HM	Semi	Rud	NE	UFRN27533
PTERIDACEAE					
Acrostichum aureum L.	HM	Heli	Mars	NE	RN4745
Acrostichum danaeifolium Langsd. & Fisch.	HM	Heli	Mars	NE	UFRN9189
Adiantum deflectens Mart.	HM	Semi	Terr/Rup	NE	RN938
Adiantum pulverulentum L.	HM	Scio	Terr	NE	Santiago (2006)
Adiantum raddianum C.Presl	HM	Scio	Terr/Rup	NE	RN937
Ceratopteris thalictroides (L.) Brongn.	HM	Heli	Mars	NE	UFRN24146
Doryopteris collina (Raddi) J.Sm. *	HM	Semi	Rup	NE	UFRN14551

Doryopteris concolor (Langsd. & Fisch.) Kuhn & Decken	HM	Semi	Terr/Rup	NE	UFRN7656
Doryopteris sagittifolia (Raddi) J.Sm.	HM	Scio	Terr	NE	Santiago (2006)
Pityrogramma calomelanos (L.) Link	HM	Semi	Terr	NE	UFRN18598
Pteris biaurita L.	HM	Scio	Terr	NE	Santiago (2006)
Pteris vittata L. *	HM	Heli	Rud	NE	UFRN26220
SALVINIACEAE					
Azolla filiculoides Lam *	HD	Heli	Float	NE	UFRN13907
Salvinia auriculata Aubl.	HD	Heli	Float	NE	UFRN26386
Salvinia oblongifolia Mart. *	HD	Heli	Float	NE	HSTM14339
Salvinia radula Baker *	HD	Heli	Float	NE	UFRN26384
SCHIZAEACEAE					
Actinostachys pennula (Sw.) Hook.	HM	Semi	Terr	NE	RN3305
THELYPTERIDACEAE					
Christella hispidula (Decne.) Holttum	HM	Scio	Rup	NE	RN944
Cyclosorus interruptus (Willd.) H.Itô	G	Semi	Mars	NE	RN2682

Macrothelypteris torresiana (Gaudich.) Ching	G	Semi	Mars	NE	RN939
Meniscium serratum Cav.	HM	Scio	Rip	NE	Santiago 2006