

Ferns and Lycophytes as new challenges

Diversity and distribution of ferns and lycophytes in areas of restinga sandy coastal plain in south of Santa Catarina, Brazil

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Abstract

Ferns and lycophytes are plants often overlooked in most floristic inventories, leading to considerable gaps in the knowledge of their diversity and geographic distribution. To address this issue, we conducted a study aimed at reducing these gaps for the restingas of Santa Catarina, south Brazil. This involved conducting a series of field works in strategic sites within the municipality of Laguna, representing all three main restingas phytophysionomies (herbaceous/subshrubby, shrubby, and arboreal), across different abiotic conditions and conservation degrees. Two species of lycophytes (one family) and 31 ferns (14 families) were recorded in the restingas of Laguna, almost three-quarters of the diversity reported for the restingas of the state of Santa Catarina. Besides, 11 of these species are mentioned here for the first time for Santa Catarina restingas. These numbers were obtained through extensive field surveys, but considering the area of restinga remnants, some of which are still relatively unexplored, it is plausible that the diversity of ferns and lycophytes in Laguna may be even greater. These findings reinforce the need to carry out floristic surveys aimed at ferns and lycophytes in the different phytophysionomies of the restinga, because only with an increase of sampling effort, considering the environmental heterogeneity, it will be possible to better estimate the diversity of these and other plant groups. This study also provides important data for the management and conservation of the restingas, which are among the ecosystems historically most impacted by human activities.

Key words: biodiversity, coastal vegetation, floristics, pteridophytes, seedless vascular plants.

Resumo

Samambaias e licófitas geralmente são negligenciadas na maioria dos inventários florísticos. Consequentemente existem lacunas consideráveis no conhecimento sobre a diversidade e distribuição geográfica desses grupos. Neste artigo são apresentados os resultados de um estudo realizado com o objetivo de ajudar a reduzir as lacunas de conhecimento sobre esses grupos nas restingas de Santa Catarina, sul do Brasil. Para tal, foram realizadas coletas em áreas específicas do município de Laguna que representam as três principais fitofisionomias de restinga (herbácea/subarbusativa, arbustiva e arbórea) em variadas condições abióticas e graus de conservação. Foram registradas duas espécies de licófitas (uma família) e 31 samambaias (14 famílias) nas restingas de Laguna, englobando quase 75% da diversidade conhecida para as restingas de Santa Catarina. Além disso, 11 espécies são aqui citadas pela primeira vez para as restingas do estado. Esses resultados são produtos de um extensivo esforço de

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coleta, porém, considerando a área dos remanescentes de restingas, alguns ainda escassamente explorados, é plausível que a diversidade de licófitas e samambaias em Laguna pode ser ainda maior. Esses dados reforçam a importância de inventários florísticos com enfoque em samambaias e licófitas nas diferentes fitofisionomias das restingas, pois somente com um aumento do esforço de amostragem, considerando a heterogeneidade ambiental, será possível estimar mais acuradamente a diversidade para este e outros grupos de plantas. Este estudo também fornece dados para o manejo e a conservação das restingas, que estão entre os ambientes historicamente mais impactados por atividades humanas.

Palavras-chave: biodiversidade, vegetação costeira, florística, pteridófitas, plantas vasculares sem sementes.

Introduction

Lycophytes and ferns are seedless vascular plants encompassing ca. 12,000 species, the second richest group of plants after angiosperms (PPG I 2016). These plants play important ecological roles in nutrient cycling, ecosystem dynamics, and biomass production (Sharpe *et al.* 2010), and have been used as ecological indicators (*e.g.*, Pivello *et al.* 2018; Della & Falkenberg 2019a,b). Lycophytes and ferns, despite being globally distributed, have the greatest diversity in tropical and subtropical regions of the world, especially in mountain areas (Moran 2008; Suissa *et al.* 2021). The Atlantic Forest in South and Southeast Brazil is considered one of the centers of endemism for these groups, housing a total of 944 species, among which 408 are considered endemic (Tryon 1972; Souza *et al.* 2021).

The Brazilian Atlantic Forest is recognized as a biodiversity hotspot (Myers *et al.* 2000), encompassing the eastern coast of the country and featuring diverse forested habitats, including associated ecosystems like mangroves and restingas (IBGE 2012). Restingas represent a complex of plant communities established in areas of sandy quaternary deposits, which have accumulated particularly during marine regressions and transgressions (Lacerda *et al.* 1984). The vegetation of restingas is shaped by various edaphic and climatic factors, such as groundwater levels, wind and light intensity, temperature, salinity, and fertility, among others, resulting in a heterogeneous range of phytophysiognomies and high species richness (Hesp 1991; Magnago *et al.* 2012).

In South Brazil, the restingas of Santa Catarina state are classified into three main phytophysiognomies: herbaceous/subshrubby, shrubby, and arboreal (Falkenberg 1999). These communities may exhibit a horizontal structure, with a gradual increase in plant height and richness

from the shoreline to the inner parts of the continent, or they may present a mosaic pattern (Waechter 1985; Leite 1995). Over time, due to historical processes of colonization and urbanization in Brazil, restinga areas have been drastically reduced, leaving behind only remnants that are continuously affected by human activities. This situation poses a significant threat to the conservation of the native flora and fauna, including many endemic and threatened species (Lacerda *et al.* 1984; Morellato & Haddad 2000).

The inventories with the highest number of lycophytes and ferns in Santa Catarina restingas were conducted by Reitz (1961), Guimarães (2006), Korte *et al.* (2013), and Melo Júnior *et al.* (2018). However, it is important to note that these studies primarily focused on angiosperms. Specific floristic surveys targeting ferns and lycophytes in the restingas of Santa Catarina are scarce and limited to the works of Vieira Junior *et al.* (2019) and Carmes *et al.* (2020), which were carried out in the north and central portions of its coast, respectively.

Considering (I) the lack of studies focused on ferns and lycophytes in the south coast of Santa Catarina; (II) the south portion of the quaternary plain being the largest in the state, representing approximately 61% of the area (Veado 2016); and (III) this zone's role as a warm temperate biogeographic transition between northern tropical and southern cold temperate regions (Cordazzo & Seeliger 1988), we conducted a floristic survey of ferns and lycophytes in the municipality of Laguna. The vegetation of restinga in this area is still scarcely known (Reitz 1954, 1961). Our main goal was to contribute to the understanding and conservation of the plant biodiversity of restingas in South Brazil, while addressing Wallacean shortfalls (Hortal *et al.* 2015) in Brazilian ferns and lycophytes.

Material and Methods

Study area

This study was conducted in the municipality of Laguna, specifically in areas of restinga as defined by Falkenberg (1999) - terrestrial vegetation in areas composed of Quaternary sandy sediments. These restinga areas are located on the south-central coast of the state of Santa Catarina, Brazil (28°28'57"S, 48°46'51"W; Fig. 1) (Horn Filho *et al.* 2020). The climate of the region is classified as humid subtropical (Cfa type) according to the Köppen climate classification, characterized by an annual mean temperature of approximately 20 °C, an annual mean pluviosity of 1,373 mm, an annual mean relative humidity of 82%, and an annual mean wind velocity of 3.9 m/s (Wrege *et al.* 2012). Notably, about half of the city (approximately 170 km²) falls within the limits of the Right Whale Environmental Protection Area (Área de Proteção Ambiental Baleia Franca), which represents the largest federal conservation unit in Santa Catarina. This protected area includes both terrestrial and marine portions (ICMBio 2018).

Most of the terrestrial territory of Laguna is covered by Quaternary deposits of distinct ages, while the remaining area is represented by Precambrian crystalline rocks (Fig. 1) (Suguío *et al.* 1986; Caruso Junior *et al.* 2000; Veado 2016). The restingas of Laguna consist of herbaceous/subshrubby, shrubby, and arboreal phytophysionomies, forming a mosaic from the coast towards the interior of the city. The plant communities vary according to the specific climatic and edaphic conditions of each area.

Sampling and identification

Field trips were conducted between October 2020 and March 2023 using the botanical walk method (Filgueiras *et al.* 1994). We conducted surveys in six distinct areas of restinga, which encompassed all three types of phytophysionomies and varied in terrain characteristics, including levels of salinity, humidity, organic matter content, and sediment age. These areas also exhibited different degrees of conservation, with four of them located close to the coastline, experiencing greater marine influence (Mar Grosso, Gi, Gravatá, Cardoso, and Cigana), and the other two situated further from the coastline and near the Southern Lagoon Estuarine Complex of Santa Catarina (Caputera and Cabeçuda) (Fig. 1).

The ferns and lycophytes were collected and prepared following the procedures described by Bridson & Forman (1992). The samples were subsequently deposited at the Anita Garibaldi Herbarium (LAG; acronym according to Thiers, continuously updated). To gather information on past occurrences of ferns and lycophytes within the Laguna restingas, we conducted a thorough examination of the speciesLink (<<https://specieslink.net/>>) and JABOT (<<http://jabot.jbrj.gov.br/>>) web-based databases. Our focus was on specimens with available images, enabling us to verify their identification accurately.

Identifications were made using keys, descriptions, illustrations, and other data from the Flora e Funga do Brasil 2023 (continuously updated) and specialized literature (Labiak & Prado 1998; Salino 2000; Øllgaard & Windisch 2016; Miranda & Schwartsburd 2019; Robayo 2020; Sylvestre *et al.* 2022). To ensure accuracy, we also compared specimens to herbarium specimens certified by specialists. Currently accepted names of families, genera, and species follow the Flora e Funga do Brasil 2023 (continuously updated). For the preparation of an indented dichotomous key based on macro and micromorphological attributes, we adopted the terminology employed by Lellinger (2002).

The general distribution pattern of each species follows the classification of Labiak & Prado (1998) with adaptations: (1) pantropical - species that are widespread throughout the tropical regions of the world; (2) America - species distributed throughout the Americas, in tropical, subtropical, and/or temperate regions; (3) tropical America - species that are restricted to tropical and/or subtropical regions of the Americas, including southern USA; (4) species endemic to Brazil; (5) species endemic to southern and southeastern Brazil. Data on the distribution patterns were obtained from the Tropicos (<<https://tropicos.org/home/>>), Global Biodiversity Information Facility (<<https://www.gbif.org/>>), Plants of the World Online (<<https://powo.science.kew.org/>>), and Flora e Funga do Brasil 2023 (continuously updated) databases.

Information on the habit and habitat comes from our field observations, while the origin and phytogeographic domains are based on Prado & Sylvestre (2010) and Flora e Funga do Brasil 2023 (continuously updated). The classification of the aquatic macrophytes life forms followed the system proposed by Irgang & Gastal Junior

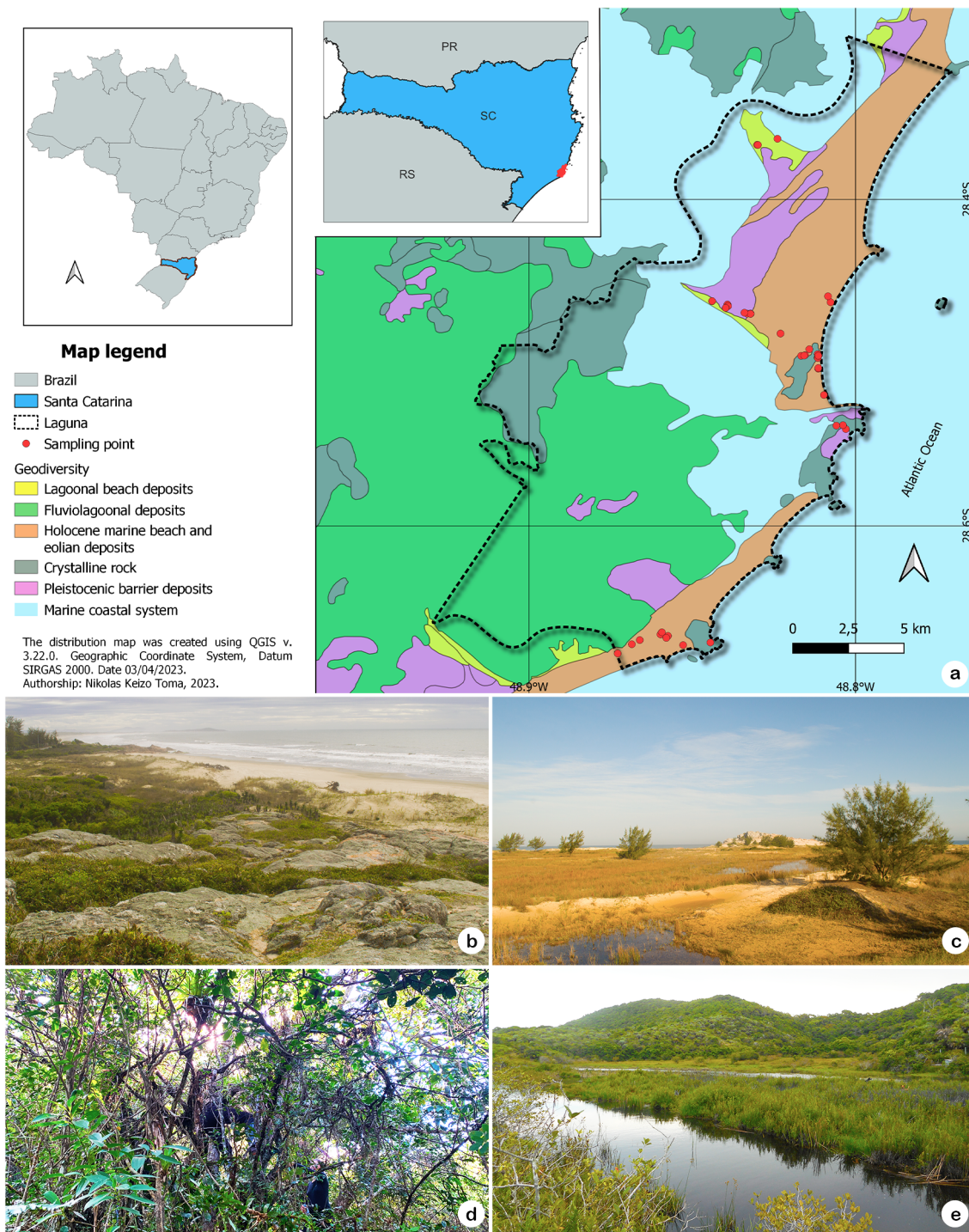


Figure 1 – a-e. Study area and examples of distinct restinga environments in Laguna, Santa Catarina – a. location of the study area and collection sites; b. herbaceous/subshrubby and shrubby phytophysionomies on dunes and rocky outcrops; c. herbaceous/subshrubby phytophysionomy on sandy plain near the sea; d. arboreal phytophysionomy (understory) on sandy plain near the lagoon; e. fresh water coastal lagoon with emergent macrophytes surrounded by shrubby and arboreal (dominated by *Butia catarinensis*) phytophysionomies on fixed dunes.

(1996), which includes amphibious species that colonize the interface between aquatic and terrestrial habitats, emergent species rooted in the bottom sediment, with emerging fronds, occurring in shallow areas and close to the shore, and free-floating species found in the deep and central zones of the water body, not rooted in the bottom, occurring on the surface of the water column.

The occurrence of the species in the phytophysiognomies of Santa Catarina follows Ziffer-Berger (2008), Gasper *et al.* (2012), Gasper & Salino (2015), Binfaré (2016), Miranda & Schwartsburd (2019), Vieira Junior *et al.* (2019), Carmes *et al.* (2020), and Flora e Funga do Brasil 2023 (continuously updated), following the classification proposed by Klein (1978). The distribution map was created using QGIS v. 3.22.0.

Results and Discussion

A total of 33 species were found in the restinga of Laguna, comprising 31 ferns and two lycophytes, distributed across 15 families and 25 genera. The richest family was Polypodiaceae, with eight species, followed by Pteridaceae with four species, and both Blechnaceae and Thelypteridaceae with three species each. Additionally, Anemiaceae, Ophioglossaceae, Lycopodiaceae, and Salviniaceae were represented by two species each, while Aspleniaceae, Cyatheaceae, Dennstaedtiaceae, Dryopteridaceae, Equisetaceae, Nephrolepidaceae, and Osmundaceae were each represented by one species [refer to Tabs. S1-S2 (available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>) and Figs. 2-7 for more details].

Key to the Ferns and Lycophytes of the restingas of Laguna

1. Plants with sporangia clustered in strobili 2
 2. Stem fistulous *Equisetum giganteum*
 - 2'. Stem not fistulous 3
 3. Plants erect, strobili pendulous at the apex of branches *Palhinhaea cernua*
 - 3'. Plants prostrate, strobili erect terminating in simple branches *Lycopodiella tupiana*
- 1'. Plants with sporangia clustered in sori, spikes, regularly distributed over the entire surface of fertile apical pinnae or limited to the basal pair of pinnae 4
 4. Plants with sporangia clustered in spikes, regularly distributed over the entire surface of fertile apical pinnae or limited to the basal pair of pinnae 5
 5. Plants with fused sporangia 6
 6. Laminae palmately lobed, usually > 30 cm in length; sporophores numerous, never solitary *Cheiroglossa palmata*
 - 6'. Laminae entire, usually < 15 cm in length; sporophores solitary *Ophioglossum nudicaule*
 - 5'. Plants with free sporangia 7
 7. Plants with sporangia regularly distributed over the entire surface of fertile apical pinnae, annulus rudimentary, lateral *Osmunda spectabilis*
 - 7'. Plants with sporangia limited to the basal pair of pinnae, annulus developed, apical 8
 8. Sterile laminae 1-pinnate *Anemia phyllitidis*
 - 8'. Sterile laminae 2-pinnate *Anemia raddiana*
- 4'. Plants with sporangia clustered in sori 9
 9. Plants free floating 10
 10. Laminae approximately 0.5 mm long, lobes unequal *Azolla caroliniana*
 - 10'. Laminae > 1 cm long, lobes equal *Salvinia herzogii*
 - 9'. Plants fixed, not floating 11
 11. Sporangia clustered in sori linear or acrostichoid 12
 12. Fronds dimorphic 13
 13. Sori acrostichoid *Acrostichum danaeifolium*
 - 13'. Sori linear *Lomariocycas schomburgkii*
 - 12'. Fronds monomorphic 14

14.	Plants epiphytic, laminae linear, usually < 1 cm wide.....	<i>Vittaria lineata</i>
14'.	Plants terrestrial or rupicolous, laminae pedate or pinnate, usually > 1 cm wide.....	15
15.	Fronds with laminae pedate	<i>Doryopteris pentagona</i>
15'.	Fronds with laminae pinnate	16
16.	Sori along the laminae margins.....	17
17.	Rhizomes short and compact, pinnae entire and linear	<i>Pteris vittata</i>
17'.	Rhizomes long-creeping, pinnae with free lobes between the segments	5.1. <i>Pteridium esculentum</i> subsp. <i>arachnoideum</i>
16'.	Sori near or along both sides of the costae.....	18
18.	Sori near the costae, parallel to the veins, not reaching the laminae margin	<i>Asplenium serra</i>
18'.	Sori along both sides of the costae	19
19.	Rhizomes long-creeping, pinnae articulate to rachises	<i>Telmatoblechnum serrulatum</i>
19'.	Rhizomes erect and forming caudex, pinnae continuous with the rachises	<i>Neoblechnum brasiliense</i>
11'.	Sporangia clustered in sori round or slightly elongated.....	20
20.	Laminae 2–3-pinnate.....	21
21.	Rhizomes forming caudex; rachis and petiole armed	<i>Cyathea atrovirens</i>
21'.	Rhizomes not forming caudex; rachis and petiole unarmed	22
22.	Rhizomes long-creeping, laminae 3-pinnate, usually glabrous; sori black in maturation	<i>Rumohra adiantiformis</i>
22'.	Rhizomes erect, decumbent or short-creeping, laminae 2-pinnate-pinnatifid, usually pilose; sori brown in maturation	<i>Macrothelypteris torresiana</i>
20'.	Laminae entire, lobed to 1-pinnate	23
23.	Fronds dimorphic	<i>Microgramma vacciniifolia</i>
23'.	Fronds monomorphic	24
24.	Indusium present	25
25.	Indusium lunulate	<i>Nephrolepis pectinata</i>
25'.	Indusium reniform.....	26
26.	Rhizomes short-creeping, with scales	<i>Christella hispidula</i>
26'.	Rhizomes long-creeping, usually scaleless	<i>Cyclosorus interruptus</i>
24'.	Indusium absent	27
27.	Laminae pectinate, petiole not sulcate	<i>Pecluma paradiseae</i>
27'.	Laminae entire, pinnate, pinnatisect, pinnatifid, petiole sulcate	28
28.	Immature sori densely covered by scales.....	29
29.	Plants epiphytic, rhizomes short-creeping, the abaxial surface of laminae covered by sparse scales.....	<i>Pleopeltis pleopeltifolia</i>
29'.	Plants terrestrial, rhizomes long-creeping, the abaxial surface of laminae densely covered by scales.....	<i>Pleopeltis lepidopteris</i>
28'.	Immature sori not covered by scales	30
30.	Laminae entire.....	<i>Campyloneurum atlanticum</i>
30'.	Laminae pinnate or pinnatisect.....	31
31.	Laminae pinnate, with white punctuations on the adaxial surface..	<i>Serpocaulon menisciifolium</i>
31'.	Laminae pinnatisect, without white punctuations on the adaxial surface	32
32.	Rhizomes whitened (pruinose).....	<i>Serpocaulon catharinae</i>
32'.	Rhizomes brown.....	<i>Serpocaulon latipes</i>

According to the Flora e Funga do Brasil 2023 (continuously updated), 486 species of ferns and lycophytes occur in Santa Catarina, 47 of these distributed along the restingas of the state, encompassing 19 families and 33 genera. In Laguna, we found approximately 70% of these species, 79% of the families, and 76% of the genera registered for the restingas of the state [Tabs. S1-S2 (available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>); Figs. 2-7]. The richness of ferns and lycophytes in Laguna is greater than that recorded in most studies carried out in the Santa Catarina restingas (Reitz 1961; Bresolin 1979; Cordazzo & Costa 1989; Danilevicz *et al.* 1990; Souza *et al.* 1991; Daniel 2006; Guimarães 2006; Klein *et al.* 2007; Hentschel 2008; Alves *et al.* 2011; Rampinelli 2011; Gasper *et al.* 2012; Korte *et al.* 2013; Binfaré 2016; Silva & Melo Júnior 2016; Melo Júnior *et al.* 2017, 2018; Carmes *et al.* 2020). These studies were mostly focused on angiosperms, therefore the number of ferns and lycophytes was underestimated.

Most of the floristic studies done in Santa Catarina were also restricted to a specific locality. Among these, so far, the highest diversity levels of ferns and lycophytes in the restingas of Santa Catarina have been recorded on the north coast, in Babitonga Bay (31 species, Melo Junior *et al.* 2018; 42 species, Vieira Junior *et al.* 2019). This region has the largest and most extensive areas of arboreal restinga in the state, where the environmental conditions, such as higher temperatures and humidity, and lower wind intensity, favor the occurrence of ferns and lycophytes. In Laguna, despite the environmental threats and limited remnants of arboreal restinga, we found a significant diversity of ferns and lycophytes, even surpassing those in the Babitonga Bay region. However, the anthropic pressure on these areas makes them highly susceptible to degradation (Marques *et al.* 2015).

Only two studies covered the entire coast of Santa Catarina. The oldest was performed by Reitz (1961), who listed 146 families and 956 species of vascular plants, including eight families and 26 species of ferns and lycophytes. The most recent study, conducted in four localities, was carried out by Korte *et al.* (2013) and listed 82 families and 225 species of vascular plants, including nine genera and 14 species of ferns and lycophytes. In Laguna, we found five of the species listed by Reitz (1961) and eight of those listed by Korte *et al.* (2013), namely *Cyathea atrovirens* (Fig. 3a-c), *Microgramma vacciniifolia* (Fig. 4n-o),

Neoblechnum brasiliense (Fig. 21-n), *Pecluma paradiseae* (Fig. 5a-c), *Pleopeltis lepidopteris* (Fig. 5d-e), *Pleopeltis pleopeltifolia* (Fig. 5f-h), *Rumohra adiantiformis* (Fig. 3f-g), and *Telmatoblechnum serrulatum* (Fig. 2o-q) (Tabs. S1-S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>).

Eleven species are here mentioned for the first time for the restingas of Santa Catarina: *Anemia raddiana* (Fig. 2c-e), *Azolla caroliniana* (Fig. 6l-n), *Campyloneurum atlanticum* (Fig. 4l-m), *Christella hispidula* (Fig. 7a-b), *Cyclosorus interruptus* (Fig. 7c-d), *Doryopteris pentagona* (Fig. 6d-e), *Lomariocycas schomburgkii* (Fig. 2i-k), *Nephrolepis pectinata* (Fig. 4a-b), *Pteris vittata* (Fig. 6f-h), *Salvinia herzogii* (Fig. 6o-q), and *Serpocaulon menisciifolium* (Fig. 5o-q) (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Of these, *Anemia raddiana*, *Lomariocycas schomburgkii*, *Nephrolepis pectinata*, *Doryopteris pentagona*, and *Christella hispidula* were previously known from areas of Dense Ombrophilous Forest, Mixed Ombrophilous Forest, and Seasonal Deciduous Forest; *Campyloneurum atlanticum*, *Serpocaulon menisciifolium*, and *Azolla caroliniana* from areas of Dense Ombrophilous Forest and Mixed Ombrophilous Forest; and *Cyclosorus interruptus* and *Pteris vittata* from the Dense Ombrophilous Forest (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>) (Flora e Funga do Brasil 2023, continuously updated). *Pteris vittata* probably was overlooked in previous floristic studies since it is a common naturalized species (Moro *et al.* 2012; Flora e Funga do Brasil 2023, continuously updated). Recording exotic species is important and necessary as they contribute to the understanding of spatial and temporal distribution patterns and provide information for invasive species management programs (Moro *et al.* 2012).

Some of the species cited above are commonly misidentified. *Christella hispidula* (Fig. 7a-b) is morphologically similar to the naturalized *C. dentata* (Forssk.) Brownsey & Jermy, differing mainly by the size of the trichomes on the abaxial surface of the costae, which are > 0.3 mm long and of varying sizes in *C. hispidula*, and ≤ 0.2 mm long and uniformly sized in *C. dentata* (Salino 2000; Flora e Funga do Brasil 2023, continuously updated). In our specimens, the trichomes have different sizes and can be larger than 0.6 mm long, matching the circumscription of *C. hispidula*.

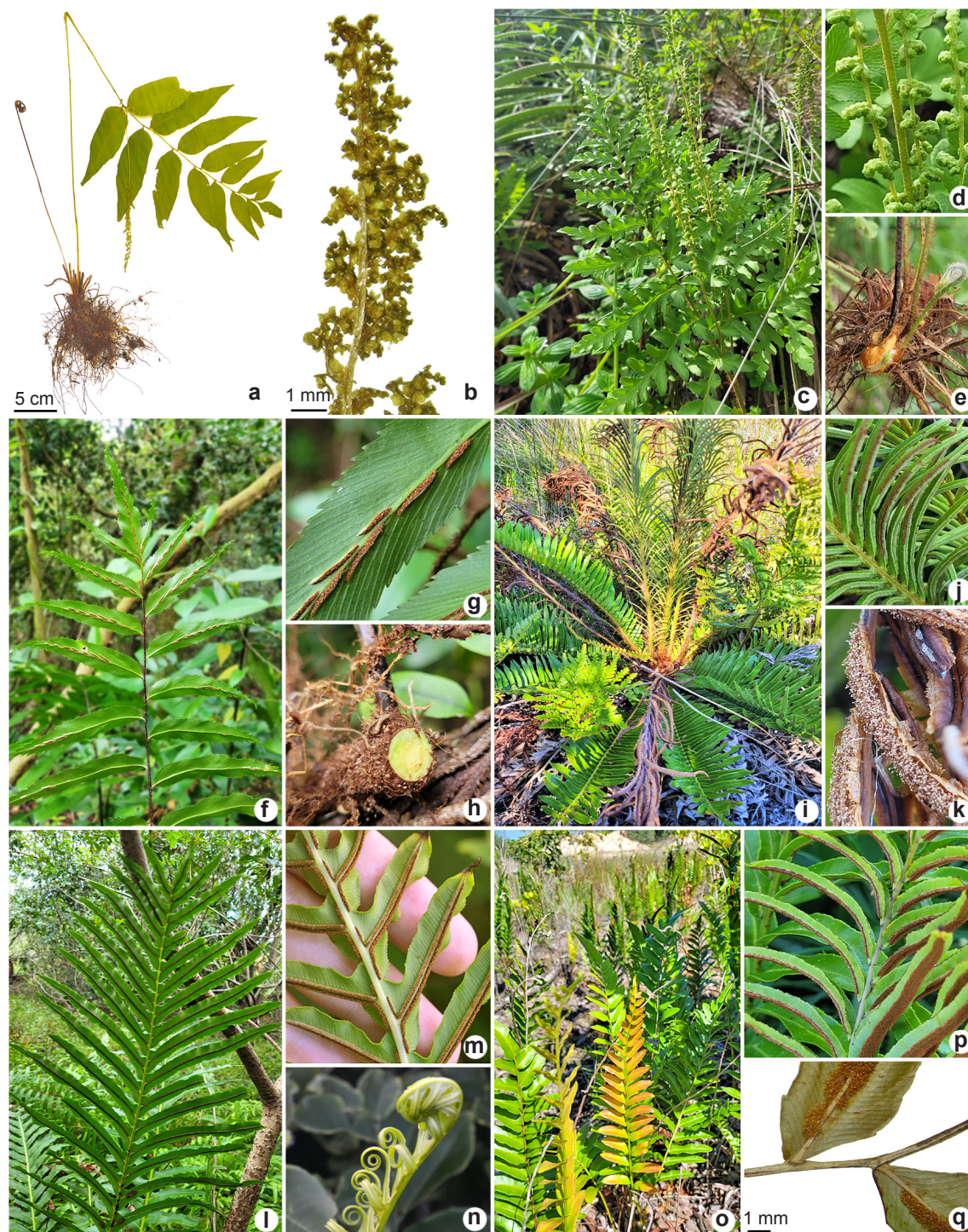


Figure 2 – a–q. Ferns recorded in Laguna, Santa Catarina – a–b. *Anemia phyllitidis* – a. habit, hemidimorphic laminae, petiole, and rhizome; b. fertile pinnae. c–e. *Anemia raddiana* – c. habit and hemidimorphic laminae; d. fertile pinnae; e. rhizome. f–h. *Asplenium serra* – f. abaxial frond; g. linear sori near the costae; h. rhizome. i–k. *Lomariocycas schomburgkii* – i. habit and dimorphic laminae; j. linear sori; k. frond scales. l–n. *Neoblechnum brasiliense* – l. abaxial laminae; m. linear sori; n. young leaf. o–q. *Telmatoblechnum serrulatum* – o. habit; p. linear sori; q. pinnae base.



Figure 3 – a-n. Ferns recorded in Laguna, Santa Catarina – a-c. *Cyathea atrovirens* – a. habit; b. rounded sori; c. petiole armed and scales. d-e. *Pteridium esculentum* subsp. *arachnoideum* – d. laminae apex; e. linear and marginal sori. f-g. *Rumohra adiantiformis* – f. habit and laminae; g. rounded black sori. h-j. *Equisetum giganteum* – h. habit; i. stem branches; j. strobilus. k-l. *Lycopodiella tupiana* – k. habit; l. immature strobilus. m-n. *Palhinhaea cernua* – m. habit; n. mature strobili.



Figure 4 – a-o. Ferns recorded in Laguna, Santa Catarina – a-b. *Nephrolepis pectinata* – a. laminiae; b. lunulate indusium. c-e. *Cheiroglossa palmata* – c. fertile frond; d. sporophores; e. fronds. f-h. *Ophioglossum nudicaule* – f. habit; g. sporophore; h. rhizome. i-k. *Osmunda spectabilis* – i. laminiae; j. venation; k. mature sporangia. l-m. *Campyloneurum atlanticum* – l. habit; m. adaxial frond. n-o. *Microgramma vacciniifolia* – n. habit, sterile frond; o. fertile frond.

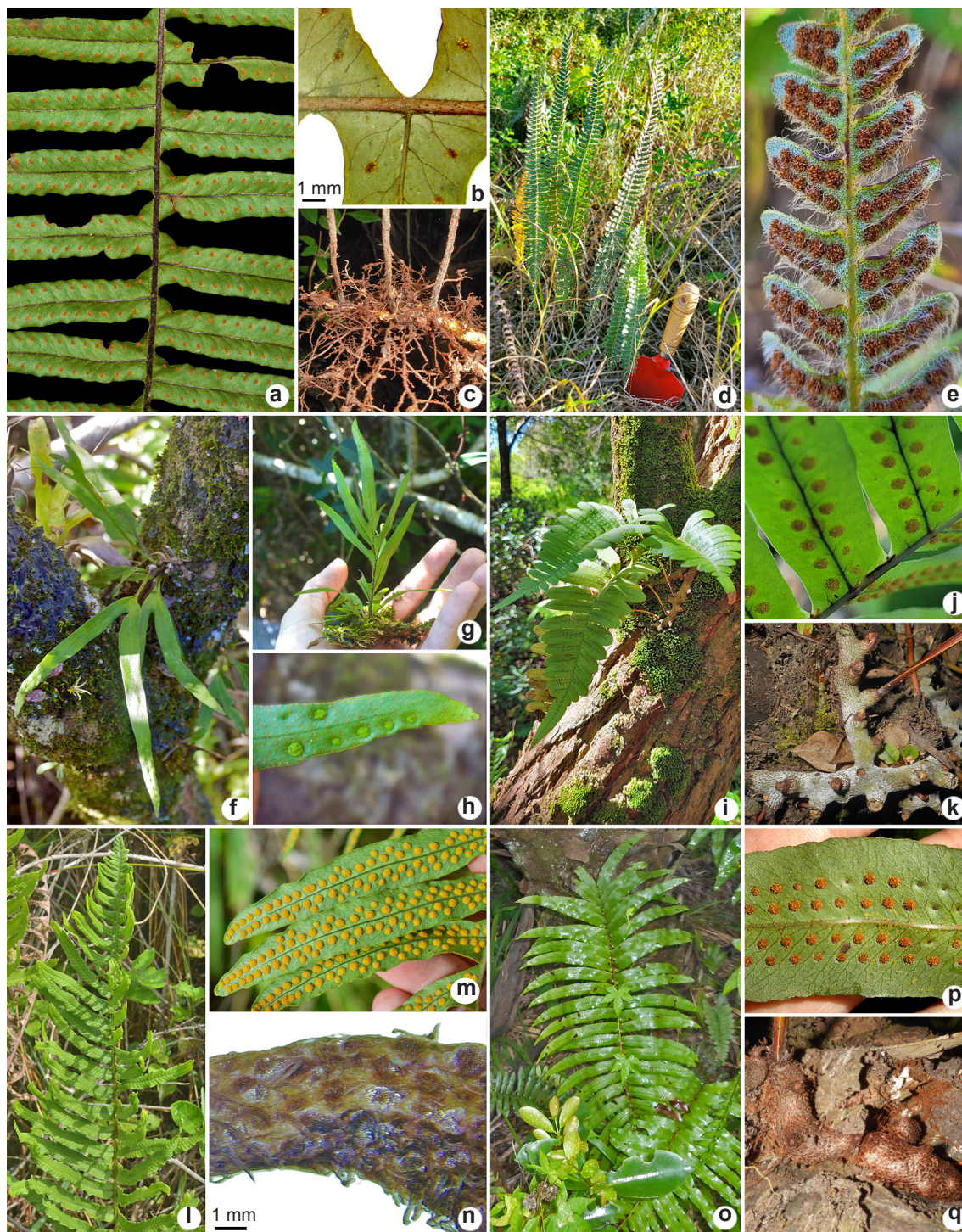


Figure 5 – a-q. Ferns recorded in Laguna, Santa Catarina – a-c. *Pecluma paradiseae* – a. abaxial fertile laminae; b. rounded sori and venation; c. rhizome. d-e. *Pleopeltis lepidopteris* – d. habit; e. rounded sori. f-h. *Pleopeltis pleopeltifolia* – f. habit; g. abaxial laminae; h. immature sori. i-k. *Serpocaulon catharinae* – i. habit; j. sori; k. rhizome. l-n. *Serpocaulon latipes* – l. laminae; m. rounded sori; n. rhizome scales. o-q. *Serpocaulon menisciifolium* – o. habit; p. rounded sori; q. rhizome.



Figure 6 – a-q. Ferns recorded in Laguna, Santa Catarina – a-c. *Acrostichum danaeifolium* – a. habit; b. sori; c. young laminae. d-e. *Doryopteris pentagona* – d. habit; e. linear sori. f-h. *Pteris vittata* – f. habit; g. linear sori; h. base of petioles scales. i-k. *Vittaria lineata* – i. habit; j. linear sori; k. rhizome and young leaves. l-n. *Azolla caroliniana* – l. habitat; m-n. habit. o-q. *Salvinia herzogii* – o. habitat; p. habit; q. sorophores.

One of our samples (*V. Dunzer et al.* 22) was made in the understory of an arboreal restinga, a habitat described for *C. hispidula*. However, the other (*A.O. Garcia & N.P. Vieira Junior* 77) was collected in an open area nearby a road, on the edge of a forest fragment with exotic tree elements, a more typical habitat of *C. dentata* (Salino 2000).

Salvinia herzogii (Fig. 6o-q) is commonly misidentified as *S. auriculata* Aubl., however, it can be separated from this and other morphologically closely related species by laminae apex highly incised and sorophore displayed in contracted spikes, with clustered sori (Miranda & Schwartsburd 2019; Flora e Funga do Brasil 2023, continuously updated).

Approximately 94% of the species recorded in Laguna are native to Brazil and two are naturalized, found in anthropized areas: *Macrothelypteris torresiana* (Fig. 7e-g), widely recorded in the southeastern and southern coastal region of Brazil (Gasper & Salino 2015), and *Pteris vittata* (Fig. 6f-h), commonly found on concrete surfaces in urban areas (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). These two plus other six species are pantropical, while the remaining 25 are restricted to the Americas, including two found in tropical, subtropical, and/or temperate regions, and 23 in Tropical America (which includes southern USA) (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Four species are endemic to Brazil: *Cyathea atrovirens* (Fig. 3a-c), *Pleopeltis lepidopteris* (Fig. 5d-e), *Pleopeltis pleopeltifolia* (Fig. 5f-h), and *Serpocaulon menisciifolium* (Fig. 5o-q) (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). The high proportion of South American species reinforces this as one of the richest regions in ferns and lycophytes in the world (Moran 2008). The Atlantic Forest in southeastern and southern Brazil is a prominent center of diversity and endemism of these plant groups (Tryon 1972; Suissa & Sundue 2020; Souza *et al.* 2021).

Three of the species recorded in Laguna are exclusive to the Atlantic Forest in Brazil - *Acrostichum danaeifolium* (Fig. 6a-c), *Campyloneurum atlanticum* (Fig. 4l-m), and *Pechluma paradiseae* (Fig. 5a-c) (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>) (Flora e Funga do Brasil 2023, continuously updated). Twenty-one species occur in more than three domains, and

nine occur in only two (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). *Pteridium esculentum* subsp. *arachnoideum* (Fig. 3d-e), *Ophioglossum nudicaule* (Fig. 4f-h), and *Cyclosorus interruptus* (Fig. 7c-d) are the only species distributed across all phytogeographic domains in Brazil (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Although the Pampa presents low diversity of ferns, approximately 73% of the species found in Laguna also occur in that domain (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). In recent years there has been a considerable increase in new occurrences for the Pampa, from 17 species (BFG 2018) to 119 (Flora e Funga do Brasil 2023, continuously updated). Thus, given that only a few studies on ferns and lycophytes have been done in the Pampa (Lehn *et al.* 2020; Silva *et al.* 2020), there must be a considerable gap in the knowledge about this group of plants in that domain. A smaller part of the diversity found in Laguna is shared with the Central Brazilian Savanna (18 spp.), the Amazon Rainforest (14), the Pantanal (eight), and the Caatinga (five) (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Part of the tropical species found in the region between central and south-central coast of Santa Catarina face a climatic barrier to their distribution further south. Similarly, some species adapted to colder climates have their northern distribution limit in this region (Reitz 1961). This probably explains the elevated number of species shared with the Pampa.

Regarding the distribution of the species in the phytogeographies, the highest diversity was found in the shrubby restinga with 17 species, but none of them are exclusive to shrubby areas (Tab. S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). The arboreal and herbaceous/subshrubby restingas had 13 and nine species, respectively, each with seven exclusive species (Tab. S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). These phytogeographies also presented the highest number of exclusive species on the north coast, in the Babitonga Bay region (Melo Junior *et al.* 2018).

In the restingas of Laguna, approximately 67% of the species were exclusively terrestrial (14 spp.) or epiphytic (five) or aquatic (two) or rupicolous (one), while the remaining were

found occupying two to four substrates (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). The predominance of terrestrial species was also observed in other areas of restinga in the states of Santa Catarina (Vieira Junior *et al.* 2019; Carmes *et al.* 2020) and Rio Grande do Sul (Gonzatti *et al.*

2016). Besides, it is a general pattern among the Brazilian ferns and lycophytes (Prado *et al.* 2015).

Along the gradient of phytophysiognomies, terrestrial species are distributed differently (Tabs. S1-S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Some of them occur exclusively in the



Figure 7 – a-g. Ferns recorded in Laguna, Santa Catarina – a-b. *Christella hispidula* – a. laminae apex; b. rounded sori. c-d. *Cyclosorus interruptus* – c. laminae apex; d. senescent rounded sori. e-g. *Macrothelypteris torresiana* – e. laminae; f. rounded sori; g. base of petioles scales.

shrubby and arboreal formations: *Anemia phyllitidis* (Fig. 2a-b), *Asplenium serra* (Fig. 2f-h), *Christella hispidula* (Fig. 7a-b), *Cyathea atrovirens* (Fig. 3a-c), *Doryopteris pentagona* (Fig. 6d-e), *Macrothelypteris torresiana* (Fig. 7e-g), *Nephrolepis pectinata* (Fig. 4a-b), *Neoblechnum brasiliense* (Fig. 2l-n), *Pecluma paradiseae* (Fig. 5a-c), and *Serpocaulon menisciifolium* (Fig. 5o-q) (Tab. S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Others also occur in open areas along the herbaceous/subshrubby and shrubby phytophysionomies, under high sunlight and wind intensity: *Acrostichum danaeifolium* (Fig. 6a-c), *Anemia raddiana* (Fig. 2c-e), *Cyclosorus interruptus* (Fig. 7c-d), *Equisetum giganteum* (Fig. 3h-j), *Lomariocycas schomburgkii* (Fig. 2i-k), *Ophioglossum nudicaule* (Fig. 4f-h), *Osmunda spectabilis* (Fig. 4i-k), *Palhinhaea cernua* (Fig. 3m-n), *Pleopeltis lepidopteris* (Fig. 5d-e), and *Pteridium esculentum* subsp. *arachnoideum* (Fig. 3d-e) (Tab. S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). However, only *Rumohra adiantiformis* (Fig. 3f-g), *Serpocaulon latipes* (Fig. 5l-n), and *Telmatoblechnum serrulatum* (Fig. 2o-q) occurred in all three phytophysionomies (Tab. S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Among these, only *Serpocaulon latipes* is exclusively terrestrial (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). *Rumohra adiantiformis*, commonly known as black-fern, presented varied habits and was observed in all habitats in the restingas of Laguna (Tabs. S1-S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). It can be considered one of the most common ferns in the Brazilian restingas due to its abundance and wide geographic distribution (Della & Falkenberg 2019b). Besides, it is also of ethnobotanical importance, representing an economic resource for the subsistence of families who live from its extraction (Baldauf *et al.* 2007; Marques 2013).

Most epiphytic species (75%) were associated with the endemic and endangered palm *Butia catarinensis* Noblick & Lorenzi (CONSEMA 2014; Elias *et al.* 2019), which is restricted to the restingas of Santa Catarina and Rio Grande do Sul (Flora e Funga do Brasil 2023, continuously updated) and constitutes large populations in

Laguna. Of these, *Cheiroglossa palmata* (Fig. 4c-e) and *Serpocaulon menisciifolium* (Fig. 5o-q) were found exclusively on stipes of *Butia catarinensis*. Despite its wide and odd geographic distribution, *Cheiroglossa palmata* is a rare and annual species (Chrysler 1941; Costa & Prado 2005). In the study area, only five individuals in different phenological stages were observed. It is noteworthy that this species is among the oldest collections of plants found in the *speciesLink* network for Laguna, made in 1889 by the German botanist Ernst Ule. We noticed that species such as *Cheiroglossa palmata*, *Microgramma vacciniifolia* (Fig. 4n-o), *Pleopeltis pleopeltifolia* (Fig. 5f-h), *Serpocaulon catharinae* (Fig. 5i-k), *Serpocaulon menisciifolium*, *Rumohra adiantiformis* (Fig. 3f-g), and *Vittaria lineata* (Fig. 6i-k) occur mostly in shrubby or arboreal phytophysionomies, but *Microgramma vacciniifolia* and *Rumohra adiantiformis* also occur as epiphytes in the herbaceous/subshrubby phytophysionomies (Tab. S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>) with a high concentration of *Butia catarinensis*.

The restinga in Laguna presents several natural aquatic environments, where 12 species belonging to eight families were found (Blechnaceae, Dryopteridaceae, Equisetaceae, Lycopodiaceae, Ophioglossaceae, Polypodiaceae, Pteridaceae, and Thelypteridaceae) (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Three of them are the only ones that tolerate brackish water (*Acrostichum danaeifolium* (Fig. 6a-c), *Equisetum giganteum* (Fig. 3h-j), and *Rumohra adiantiformis* (Fig. 3f-g) (Tab. S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). The remaining only occur in fresh water environments, including two free-floating [*Azolla caroliniana* (Fig. 6l-n) and *Salvinia herzogii* (Fig. 6o-q)] and seven amphibious to emergent species [(*Cyclosorus interruptus* (Fig. 7c-d), *Lycopodiella tupiana* (Fig. 3k-l), *Neoblechnum brasiliense* (Fig. 2l-n), *Ophioglossum nudicaule* (Fig. 4f-h), *Palhinhaea cernua* (Fig. 3m-n), *Pleopeltis lepidopteris* (Fig. 5d-e), and *Telmatoblechnum serrulatum* (Fig. 2o-q)] (Tabs. S1-S2, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). The macrophytes richness found in Laguna is higher than that recorded by Ferreira *et al.* (2017) in coastal lakes in Santa Catarina (four species and three families), and by Rolon *et al.* (2010) in natural and managed

wetlands in Rio Grande do Sul (nine species and six families). It is also higher than surveys carried out in other Brazilian regions (Moura Júnior *et al.* 2015; Moreira *et al.* 2017). However, compared to other regions the macrophytes diversity in Laguna is smaller, as found by Moura Júnior & Cotarelli (2019) in northeastern Brazil (19 species and six families), and by Pott & Pott (2000) in the Pantanal (13 species and six families).

In summary, our study contributes significantly to improve our understanding of the flora of the restingas of southern Brazil by recording 33 species of ferns and lycophytes in Laguna, 11 mentioned for the first time for the restingas of Santa Catarina (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.24418456.v1>>). Although possessing a subtropical climate and a predominance of herbaceous/subshrubby and shrubby phytophysiognomies, Laguna presents levels of diversity close or even higher than that reported for tropical areas on the north coast of the state, covered by large extensions of arboreal restingas. Some of the species found in Laguna are restricted to the Atlantic Forest, but most are shared with the Pampa rather than with other domains, which we hypothesize as a consequence of the tropical/subtropical climate barrier. We reinforce the importance of floristic surveys to continue to reduce knowledge gaps in the Brazilian diversity of ferns and lycophytes and to ensure the conservation of our flora.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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List of specimens examined

Camargo LMT 20 (12.2), 26 (10.2), 27 (6.1), 28 (12.4), 30 (12.7), 35 (13.1), 36 (3.2), 37 (3.3), 38 (8.1), 39 (15.2), 40 (1.1). **Dunzer VH** 15 (6.1), 21 (12.5), 22 (15.1), 23 (12.3), 24 (1.1). **Garcia AO** 8 (12.4), 9 (15.2), 15 (3.3), 20 (13.1), 21 (3.2), 76 (11.1), 77 (15.1), 78 (9.1), 79 (12.6), 80 (3.1), 81 (4.1), 82 (8.2), 83 (13.2), 84 (1.1), 85 (15.3), 86 (14.2), 87 (13.3), 88 (1.2), 89 (12.1), 90 (1.2), 91 (14.1), 92 (5.1). **Hatschbach G** 29394 (7.1), 40972 (6.1). **Rocha LCF** 175 (12.4), 182 (10.1). **Silva C** 1536 (12.6), 1537 (12.8), 1538 (12.7), 1542 (3.3), 1547 (13.4), 1567 (7.1). **Snak C** 1403 (13.4), 1480 (10.1). **Ule E** 300 (10.1). **Wegener MK** 30 (6.1), 134 (12.2).

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