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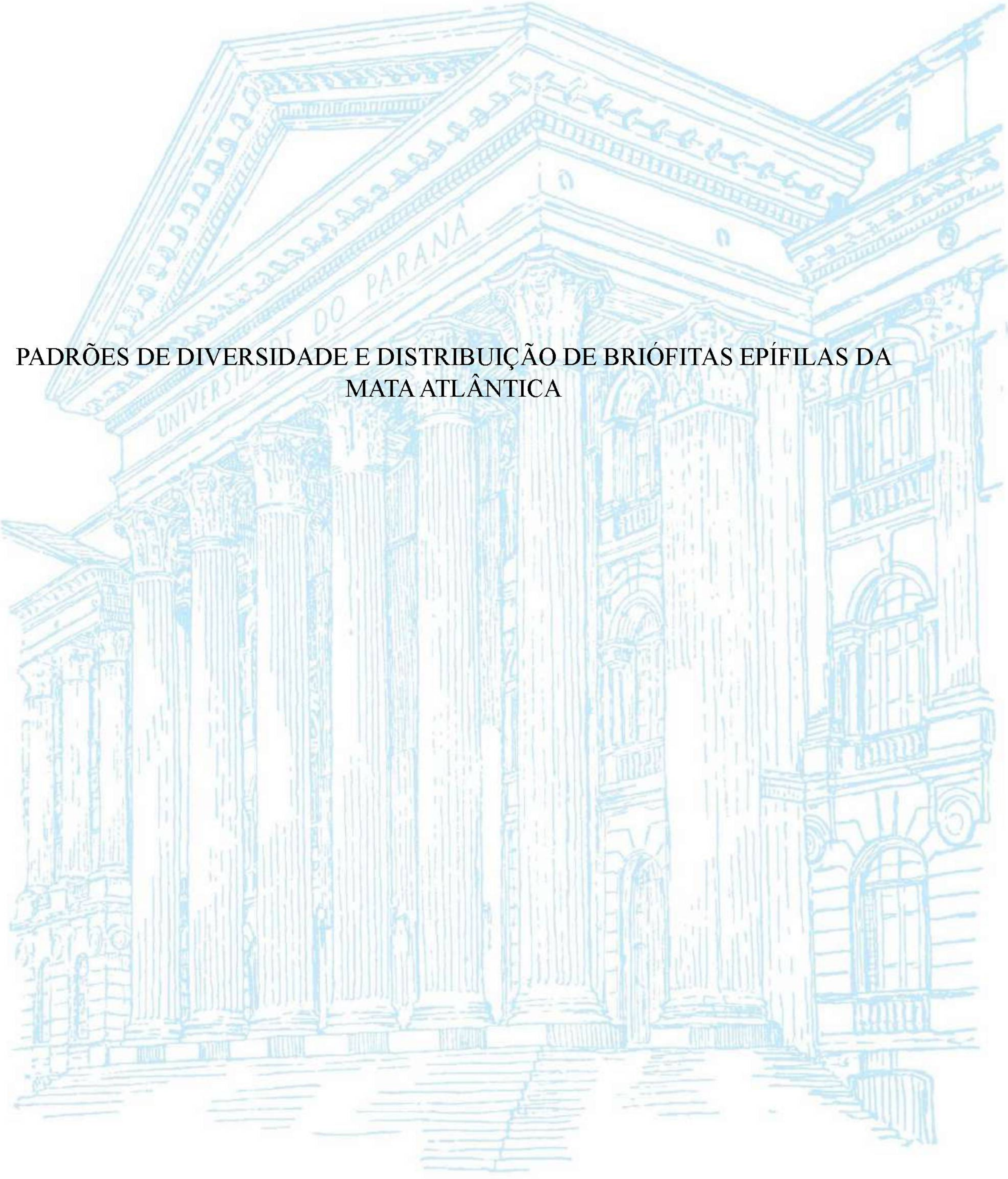

PADRÕES DE DIVERSIDADE E DISTRIBUIÇÃO DE BRIÓFITAS EPÍFILAS DA MATA ATLÂNTICA

CURITIBA

2025

ANTONIA TAINARA SOUSA DA SILVA

PADRÕES DE DIVERSIDADE E DISTRIBUIÇÃO DE BRIÓFITAS EPÍFILAS DA MATA ATLÂNTICA

Tese apresentada ao Programa de Pós-Graduação em Botânica, no Setor de Ciências Biológicas, da Universidade Federal do Paraná como requisito parcial à obtenção do título de Doutora em Botânica.

Orientador: Prof. Dr. Victor Pereira Zwiener

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação BOTÂNICA da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **ANTONIA TAINARA SOUSA DA SILVA**, intitulada: **Padrões de diversidade e distribuição de briófitas epífilas da Mata Atlântica**, sob orientação do Prof. Dr. VICTOR PEREIRA ZWIENER, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutora está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 28 de Março de 2025.

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"A maior ameaça ao nosso planeta é a crença de que alguém o salvará."

– Robert Swan

RESUMO

As briófitas epífilas são um grupo vegetal que se desenvolve sobre as folhas de outras plantas, cujo sobrevivência e manutenção de suas populações e comunidades dependem diretamente das condições ambientais de temperatura e umidade do ar, bem como de características do substrato como a textura e a idade do forófito. Embora esteja bem estabelecido que as briófitas epífilas atingem sua maior diversidade e abundância em regiões de florestas tropicais úmidas, o conhecimento sobre os padrões de distribuição da diversidade deste grupo vegetal ainda possui significativas lacunas que dificultam a tomada de ações para o estabelecimento de medidas conservacionistas efetivas. Essas lacunas de conhecimento estão relacionadas às incertezas sobre a distribuição, taxonomia, evolução e dinâmica das espécies. Diante disso, a presente tese teve como objetivo entender os aspectos ecológicos (interações bióticas e abióticas) que influenciam os padrões de diversidade e distribuição de briófitas epífilas na Mata Atlântica. Para tanto, a tese está dividida em três capítulos: o primeiro no qual fornecemos informações sobre os padrões de distribuição das briófitas epífilas, identificação de regiões que apresentam lacunas de conhecimento, dados sobre forófitos e avaliação do atual estado de conservação das briófitas epífilas na Mata Atlântica. No segundo capítulo, buscamos entender como a incorporação de fatores bióticos, especificamente forófitos, influenciam a performance de modelos de nicho ecológico em comparação com modelos ajustados somente com variáveis bioclimáticas. E, finalmente, o terceiro capítulo que trata da influência dos forófitos na predição dos impactos das mudanças climáticas futuras nas espécies de briófitas epífilas. Os resultados deste trabalho contribuem para a ampliação do conhecimento sobre os padrões de diversidade, distribuição e conservação das briófitas epífilas da Mata Atlântica, verificando a influência das interações com o forófito e variáveis climáticas, para compreender como as mudanças no clima afetarão a distribuição desses táxons.

Palavras-chave: Briófitas epífilas; Mata Atlântica; Forófitos; Modelagem de Nicho Ecológico; Conservação.

ABSTRACT

Epiphyllous bryophytes are a group of plants that grow on the leaves of other plants and depend directly on temperature, humidity, and substrate characteristics, such as texture and host age. The lack of knowledge about this group hinders conservation efforts and raises global concern among researchers who seek to expand knowledge about biodiversity. These knowledge gaps are related to uncertainties about species distribution, taxonomy, evolution, and dynamics. In light of this, the present thesis aimed to understand the ecological aspects (biotic and abiotic interactions) that influence the patterns of diversity and distribution of epiphyllous bryophytes in the Atlantic Forest. To this end, the thesis is divided into three chapters: the first, in which we provide information on the distribution patterns of epiphyllous bryophytes, identifying regions that represent knowledge gaps, data on hosts, and an assessment of the current conservation status of epiphyllous bryophytes in the Atlantic Forest. In the second chapter, we explore how the incorporation of biotic factors, specifically hosts, influences the performance of ecological niche models in comparison with models adjusted only with bioclimatic variables. Finally, the third chapter addresses the influence of hosts in predicting the impacts of future climate change on epiphyllous bryophyte species. The results of this work contribute to expanding knowledge on the patterns of diversity, distribution, and conservation of epiphyllous bryophytes in the Atlantic Forest, examining the influence of interactions with hosts and climatic variables to understand how climate change will affect the distribution of these taxa.

Keywords: Epiphyllous bryophytes; Atlantic Forest; Hosts; Ecological Niche Modeling; Conservation.

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1. INTRODUÇÃO GERAL

A epifilia se caracteriza como uma forma de epifitismo da maior especificidade, pois apenas uma parte específica do vegetal será colonizada, no caso a folha de indíviduos vivos (Vanderpoorten e Goffinet, 2009). Entre os organismos que demonstram essa relação estão as briófitas, um grupo de plantas criptógamas de pequeno porte caracterizado pela ausência de vasos condutores especializados e com ampla distribuição geográfica (Goffinet e Shaw, 2009). No Brasil, a maior diversidade do grupo é encontrada na Mata Atlântica, um bioma com grande diversidade de ecossistemas, de substratos e com ampla variedade de microclimas, sendo, ainda, considerado um *hotspot* da diversidade (Gradstein, 1997; Flora e Funga do Brasil, 2022; MMA, 2006; Henry-Silva, 2005; Almeida, 2016). Os representantes do grupo são encontrados nos mais diversos tipos de substratos, como: troncos de árvores vivas ou em decomposição, húmus, superfífice de folhas, rochas, solos e substratos artificiais (Costa e Luizi-Ponzo, 2010) .

Briófitas epífilas ocorrem exlusivamente em ambientes de ecossistemas de florestas tropicais, sendo consideradas as mais sensíveis e especializadas entre todo o grupo de briófitas (Richards, 1984). A distribuição dessas espécies no ambiente, assim como de outros organismos, é determinada pela combinação de uma série de fatores abióticos e bióticos incluíndo padrões de movimento e dispersão das espécies, conforme proposto no diagrama de BAM (Soberón e Peterson, 2005). Os mecanismos abióticos referem-se às variáveis do ambiente como temperatura e precipitação, os quais podem limitar ou facilitar a dispersão de determinadas espécies. No caso das briófitas epifilas, que se estabelecem sobre as folhas de outras plantas e dependem diretamente da umidade atmosférica (Gradstein, 1997), esse fator pode ser crucial para a sobrevivência das espécies. Além da dependência direta com o microclima, a colonização das briófitas epífilas, bem como a manutenção de suas populações, é fortemente influenciada por características do substrato como a textura da folha e a idade do forófito (Vanden Berghen, 1973; Frahm, 1990).

Dentro do nicho epífilo, as briófitas podem ser subdivididas em dois grupos de acordo com a especificidade do substrato: as epífilas exclusivas, que colonizam unicamente folhas vivas, e as epífilas facultativas, que podem ocorrer tanto sobre folhas vivas como em outros tipos de substratos (Pócs, 1997). As briófitas epífilas exclusivas são representadas, em sua maioria, por espécies de hepáticas, principalmente representantes da família Lejeuneaceae, as quais possuem características morfológicas que lhe garantem boa aderência ao substrato (Gradstein, 1995). Poucos exemplos de musgos epífilos são descritos na literatura, entre os quais se destacam táxons dos gêneros *Crossomitrium* Müll. Hal., *Syrrhopodon* M.Fleisch (Lücking e Lücking, 1996; Sipman, 1997) e *Phyllophyllum*, este último que no Brasil ocorre exclusivamente em substrato epífilo (Flora e Fungado Brasil, 2022).

Em às interações entre briófitas epífilas e seus forófitos, em um estudo realizado em ambiente de floresta tal Uniyal (1999) registrou a preferência de briófitas por folhas de árvores jovens. No trabalho desenvolvido por Orbán (1997) foi descrita a especificidade de espécies do gênero *Syrrhopodon* em colonizar a região mediana e a margem foliar. A maioria dos estudos com briófitas epífilas da Mata Atlântica estão voltados a descrever os táxons e seu nicho epífilo, não disponibilizando síntese em relação aos forófitos em que as espécies são

encontradas (Silva e Pôrto, 2015; Oliveira e Oliveira, 2016; Yano et al., 2019; Visnadi, 2019; Borella et al., 2019). Relaciona-se essas dificuldades no desenvolvimento de trabalhos sobre as interações do grupo com as plantas vasculares, a metodologia de coleta empregada (Frahm, 2003) que normalmente não contempla o registro da espécie de forófito colonizado pela briófita epífila. Essa ausência de informação dificulta a realização de análises que correlacione a especificidade entre o forófito e a espécie de briófita, bem como a compreensão da amplitude do nicho da comunidade em estudo.

A deficiência de conhecimento em torno do grupo dificulta a tomada de ações conservacionistas e gera preocupação global entre os pesquisadores que buscam ampliar o conhecimento sobre a biodiversidade (Tydecks et al., 2018; Hortal et al., 2015). Essas lacunas estão relacionadas às incertezas e deficiências de conhecimento na distribuição, taxonomia, evolução e dinâmica de espécies (Cardoso et al., 2011; Diniz-Filho et al., 2013) e são definidas como Lacuna Linneana (déficits na taxonomia e filogenia), Lacuna Wallaceana (déficits na distribuição geográfica), Lacuna Prestoniana (déficits sobre a abundância e dinâmica populacional), Lacuna Darwiana (déficits sobre a evolução e informações filogenéticas), Lacuna Raunkiaerana (déficits sobre as características funcionais e funções ecológicas), Lacuna Hutchinsoniana (déficits sobre as tolerâncias abióticas) e Lacuna Eltoniana (déficits sobre as interações ecológicas) (Hortal et al., 2015).

As lacunas de conhecimento interagem de diferentes maneiras de acordo com a escala, cobertura espacial, taxonômica e temporal (Hortal et al., 2015) comprometendo a precisão e o realismo da biodiversidade. O déficit Wallaceano, por exemplo, resulta de vieses geográficos nas informações sobre a real distribuição das espécies e afeta diretamenteos déficits Hutchioniano e Eltoniano (Soberón et al., 2007; Cardoso et al., 2011). Em grupos sensíveis e dependentes das condições ambientais para o desenvolvimento, como as briófitas epífilas, a deficiência de conhecimento sobre a distribuição das espécies limita a compreensão sobre as estimativas de tolerância ambiental e força das interações para a determinação dos gradientes de biodiversidade (Poelen et al., 2014; Schemske et al., 2009; Hortal et al., 2015).

Apropriando-se do conhecimento que as briófitas epífilas estão diretamente relacionadas com filtros ambientais, como os níveis de umidade atmosférica, da pluviosidade e com características do substrato (Schofield, 1985), os déficits Wallaceano, Hutchioniano e Eltoniano poderão impactar diretamente na conservação dessas espécies, pois a área de distribuição é requisito usado frequentemente em planejamentos de conservação e quando combinados aos dados de tolerâncias abióticas e interação recebem maior prioridade. Diante disso, é necessário entender todos os aspectos ecológicos (interações bióticas e abióticas) para contribuir no entendimento eficaz do grupo e favorecer o processo de conservação. Com base nessas considerações, o trabalho em questão teve como objetivo geral ampliar o conhecimento sobre os padrões de diversidade e distribuição das briófitas epífilas da Mata Atlântica, verificando o atual estado de conservação, a influência das interações com o forófito e a relação das mudanças no clima na distribuição dos táxons.

2. ORGANIZAÇÃO DA TESE

A tese está organizada em três capítulos/manuscritos: O primeiro, está intitulado "**DIVERSITY PATTERNS AND KNOWLEDGE GAPS OF ATLANTIC FOREST EPIPHYLLOUS BRYOPHYTES: A HIGHLY NEGLECTED GROUP**", no qual fornecemos informações sobre os padrões de distribuição dos briófitos epífilos, identificação de regiões que representam lacunas de conhecimento, dados sobre forófitos e avaliação do atual estado de conservação dos briófitos epífilos na Mata Atlântica. Para isso, realizamos uma revisão sistematizada da literatura de produções científicas e acadêmicas sobre as briófitas epífilas da Mata Atlântica utilizando uma adaptação da recomendação ROSES e efetuamos uma busca dos registros de ocorrências dos espécimes de briófitas epífilas através dos bancos de dados virtuais Global Biodiversity Information Facility (GBIF) e *speciesLink*.

O segundo capítulo, está intitulado "**SILENT DUEL BETWEEN PHOROPHYTES AND CLIMATE: UNRAVELING THE ECOLOGICAL DETERMINANTS OF EPIPHYLLOUS BRYOPHYTES DISTRIBUTION IN THE ATLANTIC FOREST**", neste estudo, apresentamos uma abordagem comparativa para avaliar a influência relativa de fatores bióticos e abióticos na distribuição de briófitas epífilas na Mata Atlântica, usando modelos de nicho ecológico (ENMs). A presença de hospedeiros diversos aumenta as oportunidades de colonização, fornecendo microhabitats adequados para a sobrevivência das espécies, enquanto a especificidade de alguns hospedeiros sugere adaptações ecológicas. No entanto, interações bióticas específicas entre briófitas e hospedeiros podem ser desafiadoras em ecossistemas fragmentados, como a Mata Atlântica.

O terceiro capítulo, é intitulado "**EPIPHYLLOUS BRYOPHYTES OF THE ATLANTIC FOREST: CHALLENGES AND VULNERABILITY IN A CHANGING CLIMATE**", este estudo avalia a influência de forófitos específicos e da diversidade de forófitos na adequação ambiental e vulnerabilidade de briófitas epífilas na Mata Atlântica diante de cenários de mudanças climáticas. Utilizando Modelos de Nicho Ecológico (ENMs), o estudo projetou as distribuições futuras dessas espécies considerando diferentes cenários climáticos e forófitos.

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CAPÍTULO I

Diversity patterns and knowledge gaps of Atlantic Forest epiphyllous bryophytes: a highly neglected group

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Review article

Diversity patterns and knowledge gaps of Atlantic Forest epiphyllous bryophytes: a highly neglected group

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ABSTRACT

Background: Epiphyllous bryophytes are a group of plants with complex adaptations to colonize the leaves of vascular plants and are considered one of the most specialized and sensitive groups to environmental changes. Despite their specificity and ecological importance, these plants represent a largely neglected group in relation to scientific research and ecological data. This lack of information directly affects our understanding of biodiversity patterns and compromises the conservation of this group in threatened ecosystems. **Scope:** Based on the compilation of data from a systematic review and virtual herbarium databases, we provide the first biogeographic assessment of diversity patterns of epiphyllous bryophytes in the Atlantic Forest hotspot. We also identify their phorophytes and assess sampling bias, knowledge gaps, and the current conservation state of epiphyllous bryophytes. **Conclusions:** The state of knowledge about epiphyllous bryophytes in the Atlantic Forest is still incipient and taxonomic and geographically biased. Sampling effort and climate variation highly influenced species richness patterns. Notably, *Bromeliophila natans*, a threatened and endemic species, has not been recorded in the past 20 years, possibly indicating extinction due to anthropogenic activities such as habitat loss. We found that the occurrence information, distributed across the domain, was positively influenced by the presence of protected areas, forest cover and density of cities, whereas it was negatively influenced by distance to access roads and research centers. More fieldwork and taxonomic and molecular studies are urgently needed to uncover biodiversity patterns and conservation priorities of this sensitive group. Without an increased collection effort, we may lose important species and their contributions to people.

Keywords: Bryophyta; epiphyllism; species geographic distribution; species richness; sampling bias, biodiversity knowledge shortfalls.

INTRODUCTION

The Atlantic Forest, renowned for its high biodiversity and endemism, stands out as a crucial hotspot for conservation (Myers et al., 2000). It is composed of native forest and grassland formations and associated ecosystems (Ministry of the Environment, 2022), covering approximately 1.1 million km^2, and extends along much of the Brazilian coast (Ribeiro et al., 2009; Brazilian Institute of Geography and Statistics, 2019). However, this area is highly affected by anthropogenic activities, such as forest fragmentation, habitat loss, climate change, and urbanization (Ribeiro et al., 2009; Haddad et al., 2015; Zwiener et al., 2018; Lima et al., 2020; Parra-Sanchez and Banks-Leite, 2020). Despite the astonishing levels of diversity and endemism, such information is limited to the major biological groups that have historically been the focus of most studies, such as woody plants, birds, and amphibians (Garey et al., 2018; Hasui et al., 2017; Lima et al., 2015). Understanding the diversity and distribution of other and often neglected biological groups, such as epiphyllous bryophytes, is an important step in summarizing biodiversity patterns, conservation planning, and guiding sampling campaigns to fill knowledge gaps in the Atlantic Forest.

Biodiversity patterns are influenced by a series of factors acting at multiple scales, such as climate, historical contingencies, natural disturbances, and biotic interactions (Mežaka et al. 2020; Bahuguna et al., 2015; Kraft et al., 2015). Climate variation has been extensively reported as an essential determinant of diversity gradients (Mensah et al., 2023). In this sense, epiphyllous bryophytes are a group of plants adapted to shaded environments with moderate temperatures, high humidity and precipitation (Normann et al., 2010; Pócs et al., 2011; Jiang et al., 2018). At local scales, the occurrence and distribution of such species may also be driven by microclimate, altitudinal gradients, anthropogenic disturbances and biotic interactions with the trees that support them (i.e., phorophytes, sensu Ochsner, 1928; Jiang et al., 2018; Vanden Berghen, 1973; Frahm, 1990). Epiphyllous bryophytes have developed morphological and physiological adaptations that facilitate the colonization of vascular plant leaves and allow them to live on aerial substrates, such as reduced and modified leaves to minimize water loss, and production of small, lightweight spores (Mežaka et al. 2020; Kraichak, 2012; Gradstein, 1997). Some species of epiphyllous bryophytes present functional traits linked to phorophyte characteristics, such as height, girth and stem orientation (Mežaka et al. 2020), indicating a possible relationship of phorophytes in the assembly of epiphyllous bryophyte communities. Despite these adaptations, recent studies suggest that host-bryophyte interactions are mostly random, without clear specificity (Hu et al., 2021; Naranjo et al., 2019). As the abundance and distribution of these species can be closely related to environmental factors such as temperature, precipitation, luminosity and humidity (Gignac, 2009; Zotz and Bader, 2008; Frahm and Gradstein, 1991), climate change may threaten more sensitive species via microclimatic modification and lead to the reduction of bryophyte diversity (Alvarega and Pôrto, 2006). Understanding the influence of biotic and climatic factors is fundamental to test ecological hypotheses and support conservation decisions (Oliveira et al., 2017; Kraft et al., 2015; Brooks et al., 2006).

The epiphyllous bryoflora of Brazil is represented by 133 species, of which 110 are listed as occurring in the Atlantic Forest (Flora and Funga do Brasil, 2022). To date, this is the only species checklist for the Atlantic Forest, which is likely an underestimation, considering that there is no comprehensive biodiversity assessment of the group in the domain. In contrast to vascular plants, epiphyllous bryophytes are less frequently sampled in field inventories. This is probably because generating data for the group is a time-consuming process due to intensive sampling requirements, slow plant growth, and complex taxonomy (Zartman and Ilkiu-Borges, 2007; Zotz and Hiertz, 2001). In addition, the phorophytes that provide habitat and support epiphyllous bryophytes are rarely documented (Silva, 2013). These factors can lead to uncertainties in the geographical distribution of the group and its biological interactions, impinging on initiatives to understand and synthesize biodiversity patterns (Diniz-Filho et al., 2012; Hortal et al., 2015; Zartman and Ilkiu-Borges, 2007).

The difficulty in understanding the ecology and biodiversity patterns of less-studied groups is amplified because knowledge gaps interact (Hortal et al., 2015). For instance, due to a lack of publications, specimen records, and taxonomic and ecological studies, our understanding of epiphyllous bryophytes' diversity, their geographic coverage, and the determinants of occurrence and diversity may be very limited (Poelen et al., 2014). Furthermore, the available biodiversity data may be influenced by the proximity of roads, cities, and scientific institutions, a phenomenon known as sampling bias (Oliveira et al. 2016; Zwiener et al. 2021). These knowledge gaps and sampling biases affect our understanding of biodiversity and may diminish the relative importance of environmental factors and biological interactions in determining diversity gradients (Schemske et al., 2009). The first step toward a more comprehensive understanding of the group is to identify such knowledge gaps and biases to guide sampling initiatives (Moraes et al., 2022; Cerrejón et al., 2022), as the lack of knowledge compromise conservation initiatives and mitigation of climate change effects on biodiversity (Sporn et al., 2010; Hylander and Johnson, 2010; Gingnac, 2009).

In this study, we conducted a systematic review and compiled data to explore epiphyllous bryophytes' occurrence and distribution patterns in the Atlantic Forest, including which species are their phorophytes. We also identify sampling biases and regions within the Atlantic Forest that represent knowledge gaps of epiphyllous bryophyte species. More specifically, we sought to answer the following questions: (i) What are the species of epiphyllous bryophytes that occur in the Atlantic Forest and their respective phorophytes? (ii) What is the proportion of species that present exclusive or optional interactions with phorophytes, and are there species threatened by extinction? (iii) Is epiphyllous bryophyte richness influenced by sampling effort and climate and what is the relative contribution of climate variables? (iv) Which spatial factors affect the sampling effort (presence and abundance of records) of epiphyllous bryophytes across the Atlantic Forest?

Based on the ecology of epiphyllous bryophytes and recent evidence (Hu et al., 2021; Naranjo et al., 2019), we predict a higher proportion of species exhibiting facultative interactions with phorophytes. Furthermore, we expect that the occurrence and richness of epiphyllous bryophytes in the Atlantic Forest are predominantly influenced by climatic variables (Campelo and Pôrto, 2007; Lücking, 1997) and sampling effort (Sobral and Stehman, 2009; Zwiener et al., 2021). Finally, we anticipate that the uneven distribution of records is likely a consequence of sampling biases influenced by spatial factors and accessibility limitations (Zwiener et al., 2021; Gomes et al., 2021).

We combined different approaches and databases to address these questions and provide a synthesis highlighting the importance of studying underrepresented groups to understand biodiversity patterns and plan conservation better.

METHODS

Systematic review

We conducted a systematic review of the scientific literature on epiphyllous bryophytes in the Atlantic Forest. We searched the Scopus (https://www.scopus.com/home.uri) and Scielo (https://www.scielo.br/) databases for relevant publications from 1945 to December 2022. In each database, we used the search string method with the following keywords: ("*bryophytes*" OR "*bryophyte*" AND "*epiphyllous*" OR "*epiphyll*" AND "*Atlantic Forest*"). In addition, to complement the compiled published studies, we searched grey literature corresponding to theses and dissertations using the same combinations of keywords described above. We considered theses and dissertations published in English and Portuguese as valid articles.

Subsequently, we read the titles and abstracts obtained from the Scopus and Scielo databases. Duplicate studies, studies conducted in other Brazilian biomes, such as the Amazon, and studies that did not provide information on the location of the fieldwork or the occurrence of epiphyllous bryophytes from the Atlantic Forest were excluded. The literature search, screening, and selection process was based on an adaptation of the ROSES protocol for systematic reviews (details in Fig. S1, Haddaway et al., 2018).

While compiling the data from the systematic review, we checked whether the results of theses and dissertations were published as scientific articles in national and/or international journals. To avoid data duplication and inflated results, priority was given to including published scientific articles resulting from these studies. From each publication, we extracted the following information: the classification of the Atlantic Forest vegetation formations (dense montane forest, rainforest, montane grasslands, dense lowland forest, mixed forest, deciduous forest, and restinga) (Brazilian Institute of Geography and Statistics, 2012); and study type (floristic survey, conservation analysis, morphology, and anatomy or molecular biology). Furthermore, species were classified according to their epiphyllous niche as exclusive (if they occupied only the leaves of the plant) or facultative (if they occupied different substrates of the plant, including the leaves) (Gradstein, 1997).

Occurrence records

Based on the species list obtained from compiling the data, we searched the Global Biodiversity Information Facility (https://www.gbif.org/) and speciesLink (https://specieslink.net/) for occurrence records of epiphyllous bryophytes to complement the data generated in the systematic review. We considered only accepted names and retrieved all records with and without geographic coordinates. Records without coordinates but with information on location, year of collection, and collector were georeferenced using Google Earth Pro version 7.3. In addition, we carefully searched the obtained records for available information on the phorophyte. The organization of the specimens followed the currently accepted nomenclature based on the data available in the International Plant Names Index (2022), Tropicos version 3.3.2 (https://tropicos.org), and Flora e Funga do Brasil 2022 (https://floradobrasil.jbrj.gov.br/reflora/). For the definition of the threat categories for each species, we used current data from the Red List Authority for Plants in Brazil - (https:// http://www.cncflora.jbrj.gov.br/portal), together with information from the studies by Costa et al. (2005) and Costa and Santos (2009). Using the data gathered in the systematic review and from the occurrence records, we created a database on the epiphyllous bryophytes in the Atlantic Forest. All information was organized in a spreadsheet containing the species name, type of epiphyllous niche, conservation status and information about the phorophyte, which is available on Zenodo (https://zenodo.org/).

Data analysis

All data analyses were performed using R statistical software version 4.2.2 (R Core Team, 2022). Model assumptions and spatial autocorrelation were assessed using the 'DHARMa' package (Hartig, 2022). AICc comparisons were conducted with the 'AICcmodavg' package (Mazerolle, 2020), and the coefficient of determination was calculated using the 'rsq' package (Zhang, 2022). Variance partitioning was performed with the 'varPart' function of the 'modEvA' package (Barbosa et al., 2013).

To investigate biodiversity patterns, sampling bias and knowledge gaps for epiphyllous bryophytes within the Atlantic Forest, we overlaid the georeferenced data on a 0.5° resolution grid across the Brazilian Atlantic Forest. To assess gaps in the geographic coverage and intensity of sampling, we summed the number of records in each grid cell and compared the spatial distribution of sampling among regions. Species richness was determined by summing the number of species per grid cell. To assess patterns in species richness as a function of current climate conditions and sampling effort, we obtained bioclimatic variables in raster format from WorldClim v2.1 (https://worldclim.org/) (Fick and Hijmans, 2017) at 10' resolution. The bioclimatic variables were the used as predictors of bryophyte species richness in two different ways. First, we aimed to maximize the representation of climatic variability to assess its relative importance in comparison to sampling effort. For this purpose, we performed a principal component analysis (PCA) and the first six components of the PCA, representing more than 95% of the variability, were used as predictors. Second, we aimed at understanding the relative contribution of climatic variables to species richness gradients. For this goal, we excluded highly correlated variables ($|r| \geq 0.7$), and retained for analysis the following: temperature mean diurnal range (bio2), temperature seasonality (bio4), max temperature of warmest month (bio5), precipitation of wettest month (bio13) and precipitation of driest month (bio14).

To assess the relative contribution of climate and sampling effort to species richness, we fit generalized linear models (GLMs) with the number of species per grid cell (response), and climate variables (PCs of PCA) and number of records as predictor variables. We compared models with climate and sampling effort as predictors, separately, and with both variables combined. In addition, we fit a model with only the intercept as a null comparison. The relative contribution of climate and sampling effort was assessed by partitioning the variation explained by these explanatory factors.

To explore the relative contribution of bioclimatic variables to species richness, we also used GLMs with a negative binomial distribution, and all combination of the selected variables. We included the coordinates of each grid cell as fixed variables in the models to account for underling spatial structured unrelated to explanatory variables (Beale et al. 2010). The most parsimonious models were ranked based on Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) and on the proportion of variance explained (R^2).

Finally, to assess potential sampling bias on the presence and density of georeferenced information, we obtained five spatially explicit independent variables: distance from roads, distance from scientific centers (biodiversity graduate programs), forest cover, presence of cities, and protected area cover (Table S4). We fit a hurdle model with negative binomial distribution for count data (i.e., species abundance) and binomial distribution for presence/absence data (i.e., species incidence) to test the effects of the variables described above. All explanatory variables were standardized before the analyses. We used the 'pscl' package to fit the hurdle model (Zeileis et al., 2008).

RESULTS

Our systematic review resulted in 338 studies, of which 54 met our criteria and were analyzed (Table S2; Fig. S1). Regarding vegetation formations within the Atlantic Forest, rainforests (i.e., Atlantic Forest sensu stricto) had the highest number of studies, with 15 papers published in recent years compared to other vegetation formations in the biome (Fig. 1A). Although studies on epiphyllous bryophytes have increased in the last decade, the number of publications per year was highly variable and relatively low (average = 2.08, maximum = 5, minimum = 0) (Fig. 1B).

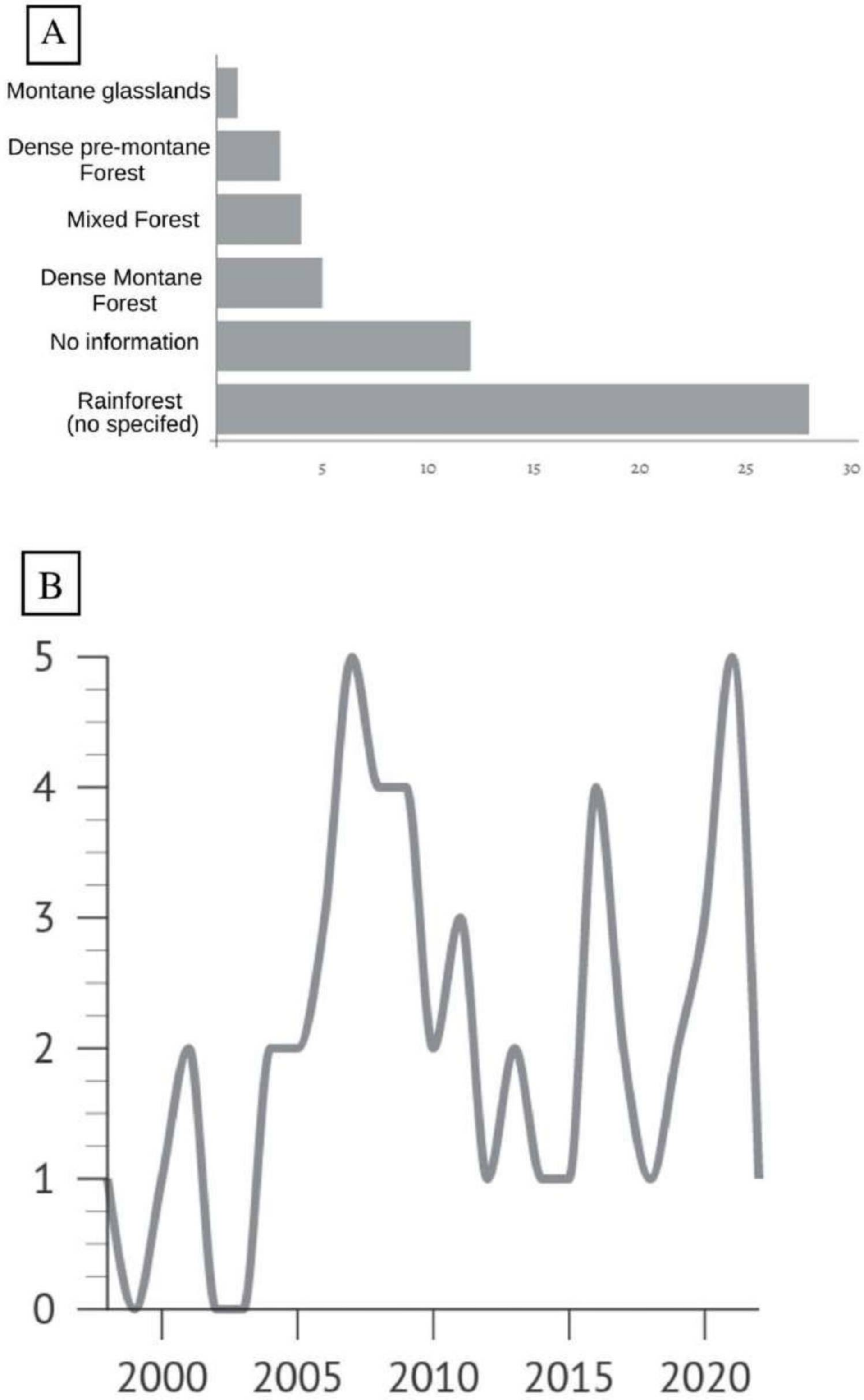

Figure 1: (A) Distribution of studies in ecoregions and (B) evolution in the number of publications on epiphyllous bryophytes in the Atlantic Forest. The classification of ecosystems follows Brazilian Institute of Geography and Statistics (2012): Dense Montane Forests correspond to forest formations from 400–1000m; Montane Grasslands are above 1000m; Lowland Dense Forests are distributed from 5–30m; Mixed Forests are interior forests characterized by the occurrence of the tree Araucaria angustifolia; Semideciduous Forests are interior forests characterized by a seasonal climate and species that partially lose their leaves during the dry season; and Restingas are pioneer formations that may have herbaceous, shrub and tree species adapted to nutrient limitation and harsh environments near the ocean.

A total of 1791 occurrence records were obtained from the virtual databases (GBIF and speciesLink), distributed in 106 Marchantiophyta species and seven Bryophyta species (Table S1). Most species were classified according to niche as facultative epiphyllous species (Fig. 2A). Only 85 phorophytes were classified to the family level, 84 to the genus level, and 59 to the species level. However, 54 epiphyllous bryophyte species had no information on interactive phorophytes (Table S1). Most of the phorophytes identified at the species level were angiosperms, followed by ferns and lycophytes with colonized fronds (Table S1). The compilation of CNCFlora threat categories revealed that most species have not been yet classified (107) and two are at risk of extinction (Fig. 2B). Published studies, theses, and dissertations included in the systematic review did not provide information on interactions between phorophytes and epiphyllous bryophytes (Table 1) (Fig. 2C).

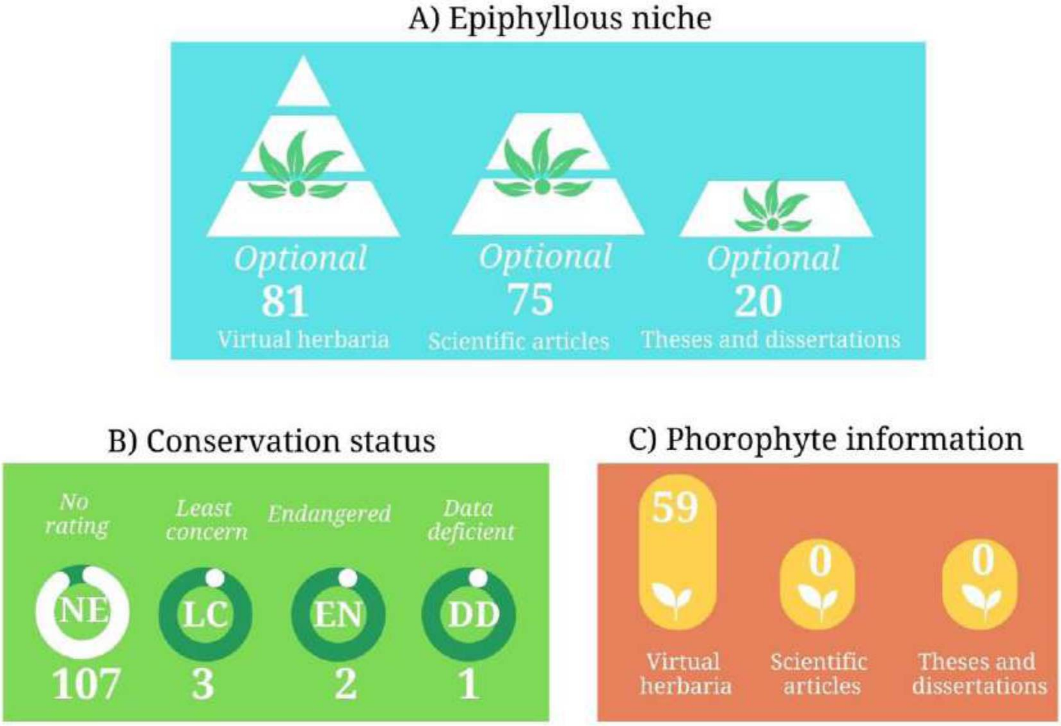

Figure 2. Compiled information on the epiphyllous niche (A), conservation status (B), and phorophytes (C) of bryophytes in the Atlantic Forest.

From the total grid cells (n=138), 28,5% (n=39) presented at least one record and only 5,9% (n=8) presented at least five records of epiphyllous bryophytes. The Brazilian regions with the highest number of surveys of epiphyllous bryophytes were the Northeast and Southeast, while geographical gaps of records coverage were mostly in the semi-deciduous seasonal forests of southern Brazil and in the mid of the Atlantic Forest domain (Fig. 3A). Such areas are located in the states of Paraná, Santa Catarina, Rio Grande do Sul (South), Mato Grosso do Sul (Midwest) and also northern Espirito Santo and Minas Gerais (Southeast).

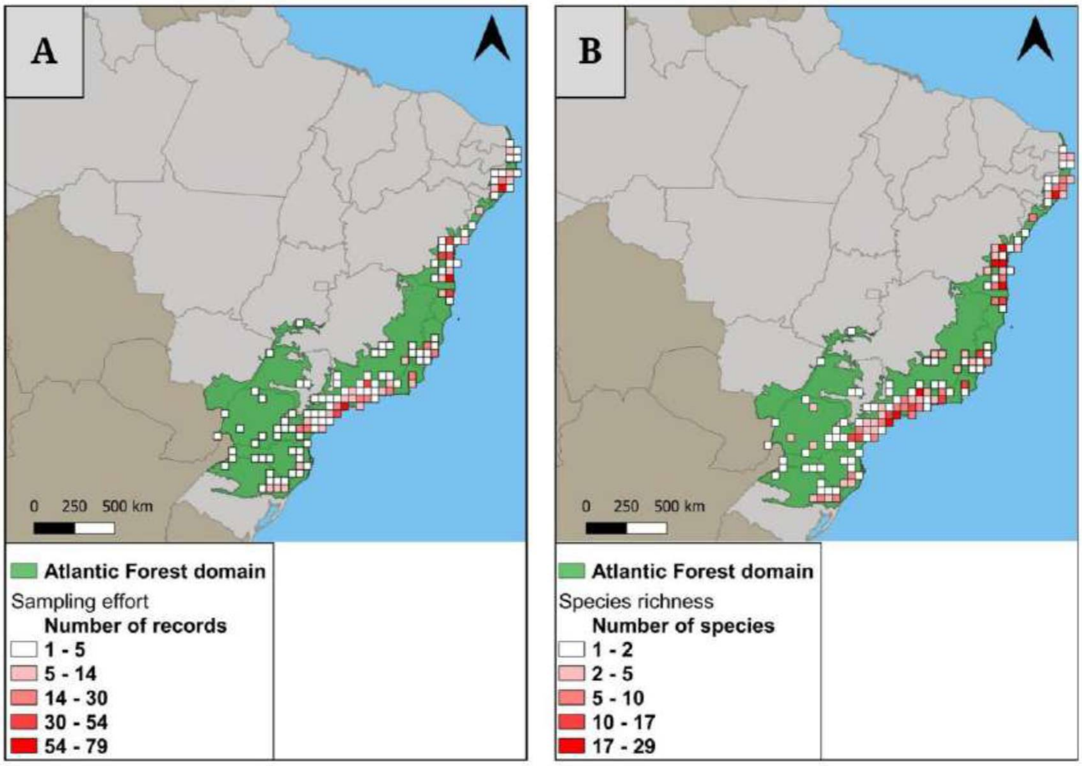

Figure 3: Sampling effort (A) and species richness (B) of epiphyllous bryophytes in the Atlantic Forest. Data was quantified using a grid of 0.5° resolution across the Atlantic Forest. Species richness was obtained based on the presence of species, and sampling effort was obtained based on the total number of records per grid cell.

The distribution pattern of epiphyllous bryophyte richness in the Atlantic Forest follows a similar pattern to sampling effort, where areas with a higher number of records also had higher species richness (Fig. 3B). We found a strong and positive correlation between species richness and number of records ($r = 0.95$). Model selection corroborated sampling effort and climate variation as important predictors of epiphyllous bryophytes richness since the best and most parsimonious model included the interaction between these variables (Table 2). Climate and sampling effort together explained 85% of the variation in species richness, whereas, separately, 64% of the variation was explained by sampling effort and 1% by climate (Fig. 4). The overlap of climate and sampling effort explained 2% of the variation (Fig. 4).

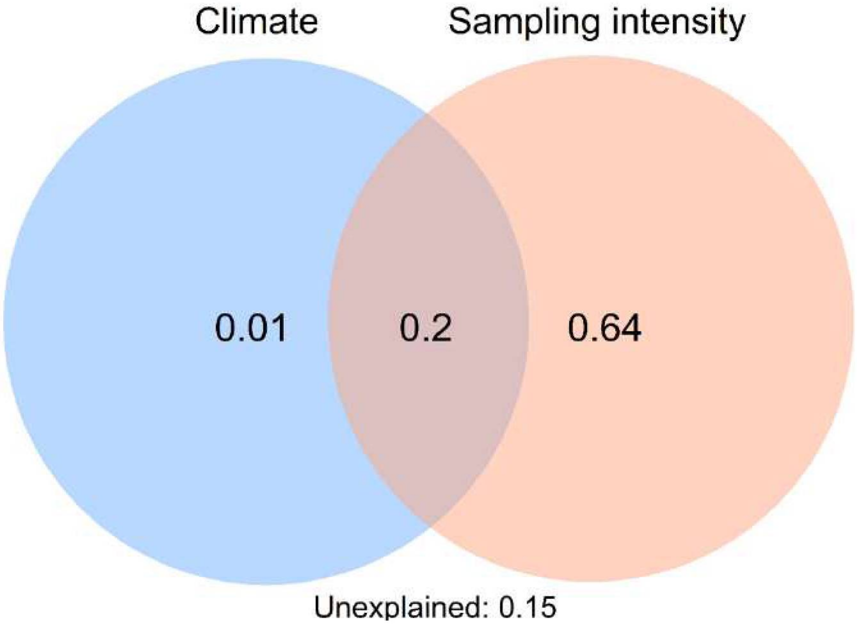

Figure 4. Variation partitioning of species richness as a function of climate and sampling effort. The climate variation is represented by the first six components of a principal component analysis (PCA) performed on climatic variables that represent more than 95% of climate variability across the Atlantic Forest. Sampling intensity is represented by the number of records per grid cell on a grid of 0.5° resolution across the Atlantic Forest.

In more detail, the bioclimatic variables presented a significant effect on species richness (Table S4; Fig. 5). The most parsimonious model included temperature mean diurnal range (bio2) and temperature seasonality (bio4).

The hurdle model revealed different effects of geographic variables leading to sampling bias of epiphyllous bryophytes in the Atlantic Forest (Table S3; Fig. 6). The presence of species occurrence information was negatively influenced by distance to the nearest road and institutions with graduate programs in botany or ecology, while urban density, protected area cover, and remaining forest cover had a positive effect. Conversely, these variables had no significant effect on the amount of species occurrence data.

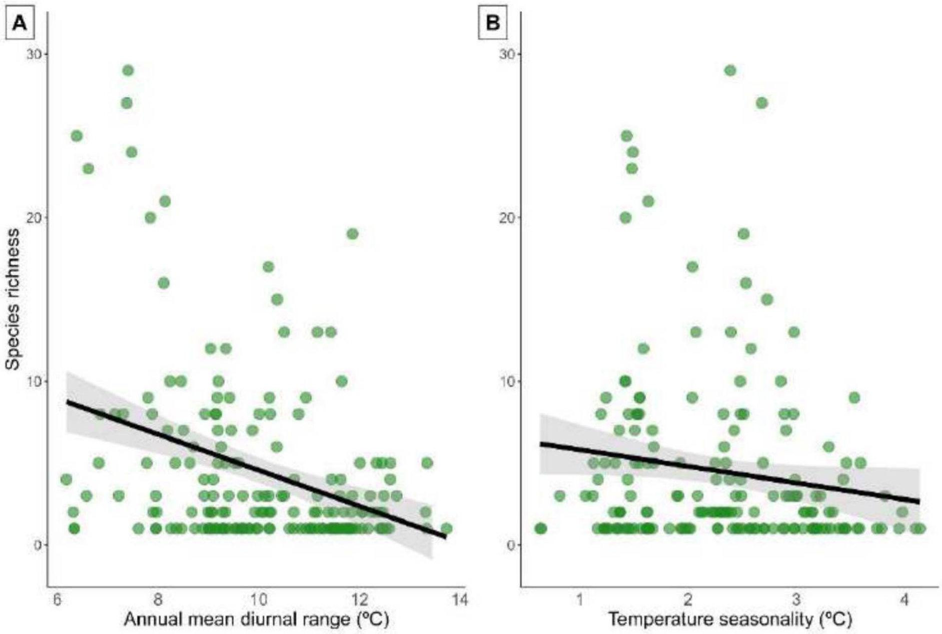

Figure 5. Influence of annual mean diurnal range (A) and temperature seasonality (B) on the number of epiphyllous bryophytes species in the Brazilian Atlantic Forest. Estimates were obtained based on model selection of the number of species per grid cell (0.5° resolution) fit with combinations of bioclimatic variables (predictors).

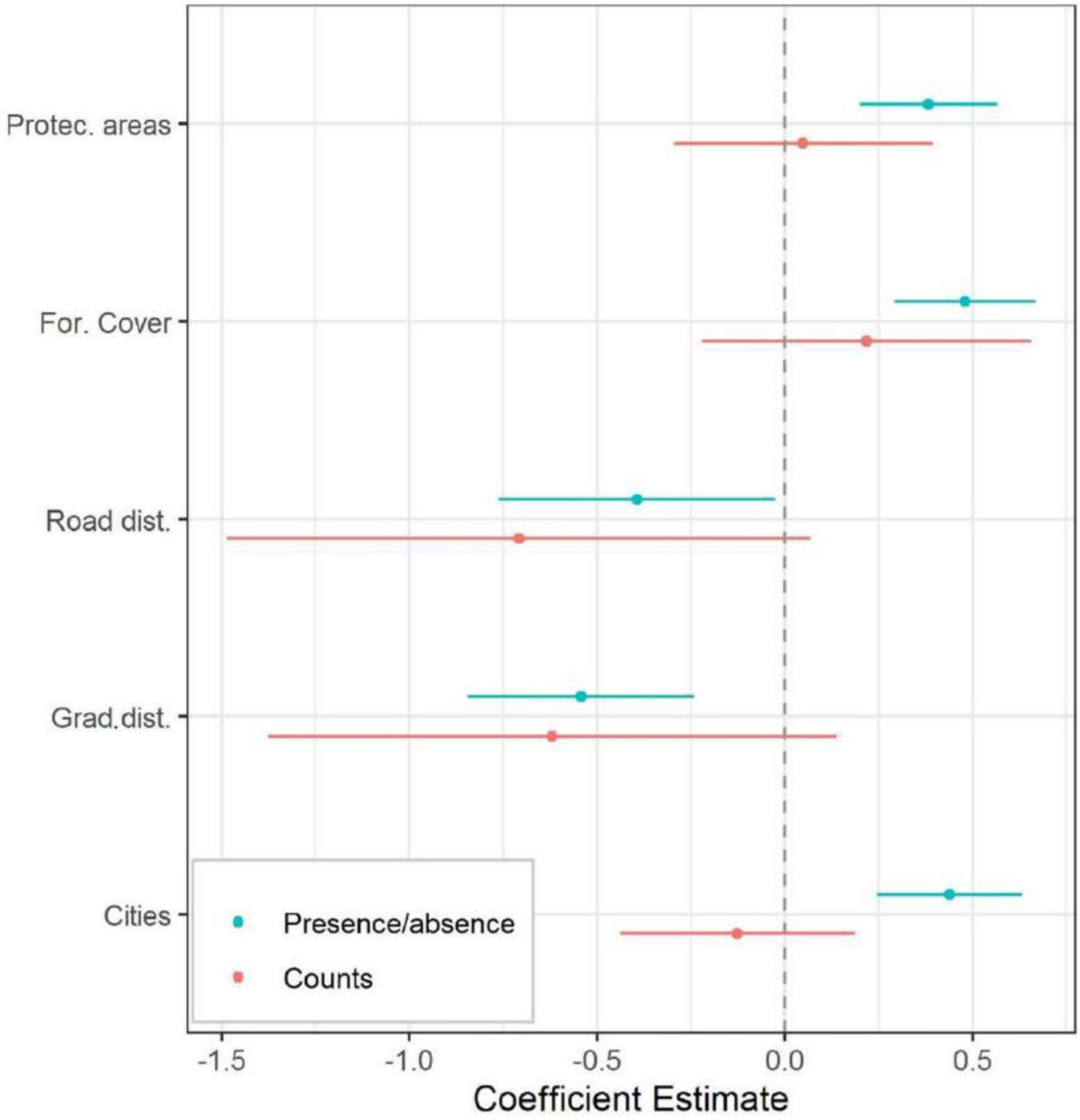

Figure 6: Influence of selected independent variables on the presence and density of epiphyllous bryophytes in the Brazilian Atlantic Forest. Legend: Protec. areas: area covered by protected areas; For. cover: remaining forest cover; Road dist.: distance to the closest federal or state road; Grad. dist.: distance to the closest institution with graduate programs in botany or ecology; Cities: density of cities.

DISCUSSION

Here, we provide the first biogeographic assessment of biodiversity patterns and knowledge gaps of epiphyllous bryophytes in the Atlantic Forest. The use of different databases was fundamental to increasing what is known about the ecology and distribution of these bryophytes in this region, in addition to highlighting the knowledge gaps that limit the biodiversity synthesis and conservation planning of this biological group. We found a critical pattern related to a lack of studies and sampling that imposes a strong bias on the available information about the diversity, biogeography and ecological determinants of epiphyllous bryophytes in the Atlantic Forest.

Epiphyllous bryophytes diversity and their phorophytes

We found a total of 113 epiphyllous bryophytes species and our results show that in recent years, scientific studies of the group within the Atlantic Forest have predominantly focused on inventories. These studies have described and cataloged bryophytes in specific areas (Alvarenga et al. 2009; Alvarenga and Pôrto, 2007; Oliveira and Oliveira, 2016; Silva and Porto, 2013). However, this number likely reflects a significant underrepresentation of the actual diversity of epiphyllous bryophytes in the Atlantic Forest. Tropical forests have characteristics that strongly support the development of these species. For instance, a study in a forested region of Panama documented 55 species of epiphyllous bryophytes on a single *Piper* species (Sierra et al., 2019), a remarkably high number compared to records from the Atlantic Forest. Therefore, while it is not possible to determine the exact number of epiphyllous bryophytes in the Atlantic Forest, we believe that the actual diversity far exceeds the 113 species reported in this study.

Most information, about 80% of the epiphyllous bryophytes in the Atlantic Forest, was available in virtual herbaria. Although the information on biodiversity in a virtual database facilitates the work of researchers (Fioravanti, 2020), there is a need to expand the scientific dissemination of information about epiphyllous bryophytes through bibliographic databases, since they are some of the most used search engines by the scientific and academic community (Nassi-Calò, 2016).

Sampling and research of epiphyllous bryophytes in the Atlantic Forest have not been motivated by the threat status of species, since 107 species in our compilation dealt with species that are "unclassified" by the CNC Flora red list (2022). The absence of classification does not necessarily imply that these species are not threatened, but rather reflects insufficient data to reliably assess their risk status. This data deficiency may stem from factors such as limited information on species occurrences, low representation in available databases and the relative understudied nature of bryophytes compared to vascular plants. For example, *Bromeliophila natans*, which is an endangered species endemic to the Atlantic Forest that occurs exclusively under the leaves of *Quesnelia arvensis* and *Aechmea nudicaulis* (Costa et al. Santos, 2009), has not been recorded in the last 20 years. This result may lead to the conclusion that *B. natans* is extinct due to anthropogenic activities, such as habitat loss (Schuster, 1994; Galindo and Câmera, 2003). However, considering the sampling gaps and bias reported here, conservation assessments of such species may rely on incomplete data and lead to erroneous conclusions.

Our results confirm that studies on the biological interactions of epiphyllous bryophytes (mainly with phorophytes) are still scarce and that this topic is little explored

(Silva et al., 2023). Despite the current evidence, including our results, that suggests that host-bryophyte interactions are mostly non-specific (Patiño and Gonzalez-Mancebo, 2011; Vergara-Torres et al., 2010), more studies evaluating the biological interactions of epiphyllous bryophytes with other plants are urgently needed to improve our understanding of the group. A general framework could be developed to promote scientific awareness among botanists and plant ecologists of the importance of collecting additional information on host-bryophyte interactions. Such practice is well spread among other biological systems, such as birds, bats, and fish parasites relationships (Poon et al., 2023; Hoesel et al., 2020; Cã, 2012), and it has contributed considerably to the understanding of interactions in these groups.

Although epiphyllous bryophytes are known for their substrate specificity (i.e., leaf), our results show that most species have wide niches occurring on different plant substrates (i.e., facultative epiphyllous or occasional epiphyllous bryophytes). The high occurrence of epiphyllous bryophytes on substrates other than leaves may be linked to their ability to adapt to environmental variations. Species with narrow niches are less likely to survive deforestation and other anthropogenic impacts compared to those with broader niches (Acebey et al., 2013).

The phorophyte data also showed that, in addition to a wide niche, the epiphyllous bryophytes in the Atlantic Forest do not preferentially occur on species with hairy leaves, contradicting the observations of Lücking and Lücking (1996). This result is confirmed by a recent study of epiphyllous bryophytes (Silva et al., 2023), which emphasizes that leaf hairiness does not directly influence the occurrence of epiphyllous species. Furthermore, the distribution on phorophytes with leaf apices with different characteristics, mainly among those typical of the Atlantic Forest, such as *Myrcia deflexa,* *Inga edulis* and *Asclepias curassavica* (Stehmann et al., 2009; Frodin, 2004), is a possible indication of the dominance of generalist species.

Knowledge gaps, sampling effort and effects of climate on species

Our results highlight the scarcity of primary biodiversity information for epiphyllous bryophytes in the Atlantic Forest. As a consequence, the little information available was highly correlated to sampling effort, constraining our understanding of ecological mechanisms. Nevertheless, we found a significant negative effect of temperature mean annual diurnal range and temperature seasonality on bryophyte richness (i.e., the higher the values of these bioclimatic variables, the lower the species richness). In more extreme seasonal environments, some bryophyte species may not be able to survive or reproduce during certain times of the year, which could constrain the diversity of the group (Gomes et al., 2021; Ruiz and Ceballos, 2004). Climate change in the 21st century presents significant challenges for the existence of epiphyllous bryophytes (Tuba et al., 2011), since the increase in global temperature, the decrease in precipitation patterns and extreme weather events can directly influence the alteration of reproductive cycles (Santos et al., 2023) and reduction of geographic distribution (Patiño et al., 2016). Most studies of epiphyllous bryophyte communities have also found this relationship between community structure and climatic variables (Campelo and Pôrto, 2007; Lücking, 1997). Furthermore, this provides valuable information into how climatic conditions affect community structure and diversity of epiphyllous bryophytes. Understanding these relationships is crucial for biodiversity conservation and the efficient management of these neglected and understudied biological groups.

Bryofloristic surveys in vegetation types and regions that have been less sampled may favor the complementarity and knowledge expansion about the diversity and distribution of the group. We have identified sampling gaps in regions such as dense rainforest in the south and southeast of Brazil (i.e., states of Espírito Santo, Paraná, Santa Catarina, and Rio Grande do Sul), semi-deciduous seasonal forest, which is highly impacted and reduced, and restinga ecosystems. Studies that explore the distribution of epiphyllous bryophytes, their abundance, and composition will contribute to filling knowledge gaps about the environmental requirements of the species, the relative contribution of biological interactions, and their potential distribution in poorly sampled areas in the Atlantic Forest. Such information is fundamental to support sampling initiatives and the development of public policies aimed at protecting this highly threatened biodiversity hotspot.

Sampling bias and biodiversity distribution

Based on the hurdle model, the information on epiphyllous bryophytes distribution in the Atlantic Forest may be directly related to the proximity of research centers and the accessibility of areas. This suggests a "museum effect" in the knowledge of epiphyllous bryophytes, where areas close to research centers are generally better studied than those further away (Sobral and Stehman, 2009; Zwiener et al., 2021). The largest number of studies in areas close to research centers and institutions has been reported in other studies investigating plant diversity (Kramer et al., 2023; Zwiener et al., 2021; Guerra et al., 2020), which suggests that ease of access may limit current knowledge of diversity patterns.

It is worth mentioning that Santa Catarina, with a complete and systematized forest inventory (Vibrans et al., 2010; Gasper et al., 2013), is one of the states with the least information on epiphyllous bryophytes, which may be directly related to the lack of specialists in this group in the state (Yano and Bordin, 2022). Increasing botany classes to train more people is an important step to reducing the scarcity of data in the long term and increasing records of taxa, which would contribute to strategies used to avoid the loss of biological heritage and species richness of these less studied groups (Guimarães and Schmidt, 2017; Habel et al., 2013). However, this is not easy and may require educational reform in curricula from preschool to graduate school, including botanical education as a key component in understanding the role and ecosystem importance of bryophytes and other lesser-studied plant groups to nature and society (Stroud et al., 2022).

CONCLUSION

The state of knowledge about epiphyllous bryophytes in the Atlantic Forest is still incipient, especially regarding epiphyllous-phorophyte interactions. Using virtual databases of biodiversity information improved our understanding of species distributions and interactions; however, we found that such data is geographically and taxonomically biased. Despite the high sensitivity and specificity of the group to environmental changes, climatic variables did not explain a significant part of the species richness in our study.

We recommend that more inventories and molecular and taxonomic studies be conducted in areas that are still poorly known (e.g., in southern Brazil) to increase the amount of information and the number of taxa studied. Future studies could explore spatial priorities for sampling in order to fill gaps in a complementary way (Divieso et al. 2020). Furthermore, we encourage that this increase in sampling be associated with different spatial scales and environmental gradients, helping to fill knowledge gaps about species distributions and environmental tolerance. Beyond filling these gaps, we emphasize the importance of conducting metapopulation studies and implementing long-term monitoring programs. These approaches are crucial for understanding the ecological dynamics of epiphyllous bryophytes, shedding light on how populations interact within fragmented landscapes and how species adapt to environmental changes over time.

Additionally, in the long term, training more people in the field of botany is essential to increase knowledge of epiphytic bryophytes where these professionals are scarce. Through these concerted efforts, we can improve our understanding of this unique group of plants and contribute to effective conservation strategies.

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TABLES

Table 1. Total number of retrieved information for geographic coordinates, epiphyllous niche, and description of the phorophyte for epiphyllous bryophytes in the Atlantic Forest (based on different sources).

Source	**(GBIF and *species*Link)**	**Published Papers**	**Dissertations and Theses**
Geographic coordinates	1.791	535	27
Epiphyllous niche	Exclusive (33) Facultative (81)	Exclusive (38) Facultative (75)	Exclusive (15) Facultative (20)
Phorophyte information	59	0	0

Table 2. Model selection based on an AIC_c comparison of generalized linear models (GLMs) describing the influence of the number of records and climate variables on the epiphyllous bryophyte richness.

Model	**df**	**AICc**	**ΔAICc**	**AICcWt**
Richness ~ records + climate	9	818.13	0	0.92
Richness ~ records	3	823.29	5.16	0.070
Richness ~ climate	8	1131.51	313.37	0
Richness (null)	2	1162.19	344.05	0

The response variable was the number of epiphyllous bryophyte species per grid (i.e., species richness) and the explanatory variables were the number of records, climate and the number of records + climate. df = degrees of freedom; AIC_c = Akaike's information criterion; ΔAIC_c = AIC_c difference from the best model; AIC_cWt = proportion of the total amount of predictive power provided by the complete set of models.

SUPPLEMENTARY FILES

Table S1. Bryophytes epiphyllous of Atlantic Forest, epiphyllous niche, and information about the phorophytes available on *species*Link and GBIF.

Species	Epiphyllous niche	Phorophyte
Marchantiophyta		
Lejeuneaceae		
Brachiolejeunea laxifolia (Taylor) Schiffn.	Optional	*Polylepis sericea* (stalk), *Espeletia schultzii*, *Podocarpus rospigliosii* (stalk), *Vochysia duckei* (stalk), *Espeletia barclayana* (stalk)
Bromeliophila natans (Steph.) R.M.Schust.	Exclusive	*Quesnelia arvensis* (leaf); *Aechmea nudistalk* (leaf)
Caudalejeunea lehmanniana (Gottsche) A.Evans	Optional	*Avicenia schaueriana* (stalk), Myristicaceae (leaf)
Ceratolejeunea ceratantha (Nees & Mont.) Steph.	Optional	No information
Ceratolejeunea coarina (Gottsche) Schiffn.	Optional	No information
Ceratolejeunea cornuta (Lindenb.) Schiffn.	Optional	*Theobroma grandiflorum* (stalk), *Cassia apoucouita* (stalk)

Ceratolejeunea filaria (Taylor ex Lehm.) Steph.	Optional	No information
Ceratolejeunea minuta G. Dauphin	Optional	No information
Ceratolejeunea rubiginosa Gottsche ex Steph.	Optional	*Laguncularia racemosa* (stalk)
Cheilolejeunea filiformis (Sw.) W. Ye, R.L. Zhu & Gradst.	Optional	No information
Cheilolejeunea tonduzana (Steph.) W. Ye, R.L. Zhu & Gradst.	Optional	No information
Cololejeunea camillii (Lehm.) A. Evans	Exclusive	*Geonoma* sp. (stalk)
Cololejeunea cardiocarpa (Mont.) A.Evans	Optional	*Tabebuia* sp. (stalk), Palmae (leaf), Myrtaceae (stalk), Lauraceae (leaf), Anonaceae (leaf), *Crecopia* sp. (stalk), *Cyclodium meniscioides* (leaf), *Bolbitis serratifolia* (frond), *Thelypteris* sp. (frond), *Maranta* sp. (leaf), *Rhizophora mangle* (stalk), *Ternstroemia brasiliensis* (stalk), *Pthecellobium* sp. (stalk), *Sorocea* sp. (leaf), *Schinus* sp. (stalk), *Blechnum* sp.(leaf), *Adiantum* sp. (leaf)
Cololejeunea cingens (Herzog) Bernecker & Pócs	Exclusive	No information
Cololejeunea diaphana A. Evans	Optional	*Pteris* sp. (leaf), *Didymochlaena trunculata* (leaf), *Bolbitis serratifolia* (frond), *Ctenitis* sp. (frond), *Adiantum* sp. (leaf), *Adiantopsis radiata* (frond)
Cololejeunea gracilis (Ast.) Pócs	Exclusive	No information

Cololejeunea hildebrandii (Austin) Steph.	Exclusive	No information
Cololejeunea microscopica (Taylor) Schiffn.	Optional	No information
Cololejeunea microscopica var. *exigua* (A. Evans) Pócs	Exclusive	No information
Cololejeunea microscopica var. *africana* (Pócs) Pócs & Bernecker	Optional	No information
Cololejeunea minutilobula Herzog	Exclusive	*Acianthera* sp. (leaf)
Cololejeunea obliqua (Nees & Mont.) Schiffn.	Exclusive	Rubiaceae (leaf), *Maranta* sp. (leaf), *Heliconia* sp. (leaf), Amarantaceae (leaf), Musaceae (leaf), Proleaceae (leaf), Sapotaceae (leaf), *Pteris* sp. (leaf), Araceae (leaf), Commelinaceae (leaf), *Psychotria* sp. (leaf), *Polypodium* sp. (leaf)
Cololejeunea papilliloba (Steph). Steph.	Optional	No information
Cololejeunea platyneura (Spruce) S.W.Arnell	Exclusive	No information
Cololejeunea sintenisii (Steph.) Pócs	Exclusive	No information
Cololejeunea subcardiocarpa Tixier	Exclusive	*Actinostemon concolor* (leaf), *Celtis iguanaea* (leaf), Aspidiaceae (leaf), Bromeliaceae (leaf), *Hennecardtia omphalandra* (leaf), *Palicourea marcgravii* (leaf)
Cololejeunea submarginata Tixier	Exclusive	Solanaceae (leaf), Palmae (leaf), *Citrus* sp. (leaf)

Cololejeunea subscariosa (Spruce) R.M.Schust.	Exclusive	No information
Cololejeunea surinamensis Tixier	Optional	Palmae (leaf), Menispermaceae (leaf), *Attlale attaleoides* (leaf), Melastomataceae (leaf), Arecaceae (leaf), Sapotaceae (leaf), *Protium* sp. (stalk)
Cololejeunea verwimpii Tixier	Exclusive	*Quesnelia arvensis* (leaf), *Citrus* sp. (leaf)
Cololejeunea vitaliana Tixier	Exclusive	No information
Colura cylindrica Herzog	Optional	No information
Colura greig-smithii Jovet-Ast	Optional	Araceae (leaf)
Colura tenuicornis (A.Evans) Steph.	Optional	*Citrus* sp. (leaf)
Colura tortifolia (Nees & Mont.) Steph.	Optional	No information
Colura ulei Jovet-Ast	Optional	Palmae (leaf), *Asclepias curassavica* (leaf), Rubiaceae (leaf), Cyperaceae (leaf), Musaceae (leaf)
Cyclolejeunea accedens (Gottsche) A.Evans	Exclusive	No information
Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans	Optional	Poaceae (stalk), *Bauhinia* sp. (stalk), Melastomataceae (stalk), *Musa* sp. (leaf), *Eperua bijuga* (stalk), *Attlale attaleoides* (stalk), Rubiaceae (leaf), *Asplenium trichomanes* (leaf), Amaranthaceae (stalk), Palmae (leaf)

Cyclolejeunea peruviana (Lehm. & Lindenb.) A.Evans	Optional	Orchidaceae (leaf), Sapotaceae (leaf), Palmae (leaf), Cyperaceae (leaf), Cecropiaceae (stalk), Araceae (leaf)
Dicranolejeunea axilaris (Nees & Mont.) Schiffn.	Optional	No information
Diplasiolejeunea cubatensis R.Prudêncio, Z.R.Mello & D.P.Costa	Exclusive	No information
Diplasiolejeunea latipuensis Tixier	Optional	No information
Diplasiolejeunea pellucida (Meisn.) Schiffn.	Exclusive	Rubiaceae (leaf), Lauraceae (leafs), *Dichorisandra* sp. (leaf), Palmae (leaf), *Polypodium* sp. (leaf)
Diplasiolejeunea rudolphiana Steph.	Optional	*Rizhophora mangle* (stalk), *Asclepias curassavica* (leaf), *Pisonia aculeata* (leaf), *Laguncularia racemosa* (stalk), *Pthecellobium* sp. (stalk), *Protium* sp. (stalk), *Citrus* sp. (stalk), *Hibiscus tiliaceus* (stalk), *Pterogyne nitens* (stalk), *Inga edulis* (leaf), *Euphorbia heterophylla* (leaf)
Drepanolejeunea aculeata Bischl.	Exclusive	No information
Drepanolejeunea bidens (Steph.) A.Evans	Optional	Solanaceae (leafs), Anonaceae (leaf), Proteaceae (leaf)
Drepanolejeunea biocellata A.Evans	Exclusive	No information
Drepanolejeunea campanulata (Spruce) Steph.	Optional	No information

Drepanolejeunea crucianella (Taylor) A.Evans	Exclusive	Poaceae(leaf), Melastomataceae (leaf)
Drepanolejeunea fragilis Bischl.	Optional	No information
Drepanolejeunea grollei E.Reiner & Schäfer-Verw.	Exclusive	No information
Drepanolejeunea inchoata (Meisn.) Schiffn.	Optional	No information
Drepanolejeunea lichenicola (Spruce) Steph.	Optional	No information
Drepanolejeunea mosenii (Steph.) Bischl.	Optional	Rubiaceae (leaf), Bromeliaceae (leaf), Begoniaceae (leaf), *Laguncularia racemosa* (stalk), Marantaceae (leaf)
Drepanolejeunea orthophylla (Nees & Mont.) Bischl.	Exclusive	Rubiaceae (leaf), Palmae (leaf), Araceae (leaf), Cyperaceae (leaf), Bromeliaceae (leaf)
Drepanolejeunea palmifolia (Nees) Steph.	Optional	Palmae (leaf)
Drepanolejeunea subdissitifolia Herzog	Exclusive	No information
Harpalejeunea subacuta A. Evans	Optional	*Araucaria angustifolia* (stalk), *Avicenia* sp. (stalk)
Lejeunea acanthogona Spruce	Optional	No information
Lejeunea acanthogona var. *cristulata* (Steph.) Gradst. & C.J. Bastos	Optional	No information

Lejeunea adpressa Nees	Optional	*Theobroma cacao* (stalk), Musaceae (leaf), *Polybotria* sp. (leaf)
Lejeunea asperrima Spruce	Optional	No information
Lejeunea bermudiana (A.Evans) R.M.Schust.	Optional	No information
Lejeunea cancellata Nees & Mont.	Optional	*Theobroma cacao* (stalk)
Lejeunea flaccida Lindenb. & Gottsche	Optional	No information
Lejeunea flava (Sw.) Nees	Optional	*Theobroma cacao* (stalk), *Dicksonia* sp. (stalk), *Thuja* sp. (stalk), Bromeliaceae (leaf), *Tipuana* sp. (stalk), *Guttiferae* sp. (stalk), Melastomataceae (stalk), *Campomanesia* sp. (stalk), *Syagrus* sp. (stalk), *Mangifera indica* (stalk), *Pandanus* sp. (stalk), *Cocos nusciferanuma* (stalk), *Blechnum brasiliense* (leaf), *Jambosa* sp. (stalk), *Eucalyptus* sp. (stalk), Rubiaceae (leaf), *Ligustrum* sp. (stalk), *Byrsonima crassifolia* (stalk), *Calathea zebrina* (leaf), *Tabebuia* sp. (stalk), Myrtaceae (stalk), *Licuala grandis* (stalk), *Delonix regia* (stalk), *Cyathea* sp. (stalk), *Camellia sinensis* (stalk), *Brysonima serioca* (stalk), *Phyllodendrum* sp. (stalk), *Ficus elastica* (stalk), *Philodendron* sp. (leaf), *Myrcia deflexa* (stalk)
Lejeunea grossitexta (Steph.) E.Reiner & Goda	Optional	No information
Lejeunea perpapillosa E.Reiner & Pôrto	Optional	No information

Lejeunea puiggariana Steph.	Optional	*Avicenia schaueriana* (stalk), *Rhizophora mangle* (stalk)
Lejeunea setiloba Spruce	Optional	*Sloanea* sp. (stalk), *Rhizophora mangle* (stalk)
Lejeunea subsessilis Spruce	Optional	No information
Lejeunea trinitensis Lindenb.	Optional	*Cecrópia* sp. (stalk)
Lepidolejeunea involuta (Gottsche) Grolle	Optional	No information
Leptolejeunea brasiliensis Bischl.	Exclusive	No information
Leptolejeunea diversilobulata Bischl.	Exclusive	*Heliconea* sp. (leaf), Araceae (leaf)
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	Optional	Araceae (leaf), *Pisonia aculeata* (leaf), *Heliconea* sp. (leaf), *Asclepias curassavica* (leaf), *Althaea officinalis* (leaf), Palmae (leaf), Apocynaceae (leaf), Meliaceae (leaf), Myrtaceae (stalk), *Theobroma cacao* (stalk), Lecythidaceae (leaf), *Asplenium* sp. (leaf), Bromeliaceae (leaf), Rubiaceae (leaf), Marantaceae (leaf), *Attalea* sp. (leaf), Zingeberaceae (leaf), *Pimpinella anisum* (leaf), Zingiberaceae (stalk), *Adiantum* sp. (leaf), Cecropiaceae (leaf), *Musa* sp. (stalk), *Protium* sp. (leaf), *Rubus buergeri* (leaf)
Leptolejeunea exocellata (Spruce) A.Evans	Optional	Melastomataceae (leaf), *Pseudobombax* sp. (leaf), Rubiaceae (leaf), Rutaceae (leaf), *Adiantum* sp. (frond), Hymenophyllaceae (leaf),

		Heliconia sp. (leaf), *Attalea* ssp. (leaf), *Polypodium s*p. (leaf), Maranthaceae (leaf)
Leptolejeunea maculata (Mitt.) Schiffn.	Exclusive	No information
Leptolejeunea moniliata Steph.	Exclusive	No information
Marchesinia bongardiana (Lehm. & Lindenb.) Trevis.	Optional	No information
Metalejeunea cucullata (Reinw. et al.) Grolle	Exclusive	*Rhizophora mangle* (stalk)
Microlejeunea cystifera Herzog	Optional	*Tabebuia* sp. (stalk)
Microlejeunea epiphylla Bischl.	Optional	*Araucaria angustifolia* (stalk), *Clusia* sp. (stalk), *Licania tomentosa* (stalk), *Eriotheca crenulaticalyx* (stalk), *Laguncularia racemosa* (stalk), Lythraceae (stalk), *Byrsonima chrysophylla* (stalk), *Ligustrum* sp. (stalk)
Microlejeunea subulistipa Steph.	Optional	*Laguncularia* sp. (stalk), Arecaceae (stalk), *Byrsonima chrysophylla* (stalk)
Odontolejeunea decemdentata (Spruce) Steph.	Optional	No information
Odontolejeunea lunulata (Weber) Schiffn.	Optional	Rubiaceae (leaf), *Heliconda* sp. (leaf), Proteraceae (leaf), Lauraceae (leaf), *Adiantum tomentosum* (leaf), *Rizophora mangle* (stalk), *Campomanesia* sp. (stalk)
Odontolejeunea rhomalea (Spruce) Steph.	Optional	*Rhizophora mangle* (stalk), *Laguncularia racemosa* (stalk)

Prionolejeunea aemula (Gottsche) A.Evans	Optional	No information
Prionolejeunea denticulata (Weber) Schiffn.	Optional	*Guapira opposita* (stalk), *Licania octandra* (stalk), *Eriotheca crenulaticalyx* (stalk)
Prionolejeunea scaberula (Spruce) Steph.	Optional	No information
Stictolejeunea squamata (Willd. ex Weber) Schiffn.	Optional	No information
Symbiezidium barbiflorum (Lindenb. & Gottsche) A. Evans	Optional	*Theobroma cacao* (stalk), *Licania octandra* (stalk), *Sterculia* sp. (stalk)
Verdoornianthus griffinii Gradst.	Optional	No information
Vitalianthus aphanellus (Spruce) Bechteler, G.E. Lee, Schäf.-Verw. & Heinrichs	Optional	No information
Metzgeriaceae Raddi		
Metzgeria aurantiaca Steph.	Optional	*Rhizophora mangle* (stalk)
Metzgeria cratoneura Schiffn.	Optional	No information
Metzgeria furcata (L.) Dumort.	Optional	*Camelia sinensis* (stalk), *Campomanesia* sp. (stalk), *Cinnamomum* sp. (stalk), *Ficus* sp. (stalk), *Schinus* sp. (stalk), *Ligustrum* sp. (stalk)
Metzgeria scyphigera A.Evans	Optional	No information
Metzgeria subaneura Schiffn.	Optional	*Theobroma cacao* (stalk)

Radulaceae K. Müll.		
Radula angulata Steph.	Optional	No information
Radula flaccida Lindenb. & Gottsche	Optional	*Elaphoglossum schomburgkii* (leaf), *Phylodendron* sp. (leaf), *Metaxya rostrata* (leaf), *Cyclodium meniscioides* (leaf), *Bauhinia* sp. (leaf), *Salpichlaena volubilis* (leaf), *Microgramma loretense* (leaf), *Arabidea* sp. (leaf), *Phylodendron elaphoglossoides* (leaf), *Avicenia schaueriana* (stalk), *Inga* sp. (leaf), *Psychothria* sp. (leaf), *Pecluma* sp. (leaf), *Rapatea paludosa* (leaf)
Radula mammosa Spruce	Exclusive	No information
Radula mexicana Lindenb. & Gottsche	Optional	*Theobroma cacao* (stalk)
Radula stenocalyx Mont.	Optional	No information
Trichocoleaceae K. Müll.		
Trichocolea brevifissa Steph.	Optional	No information
Bryophyta		
Leucomiaceae Broth.		
Philophyllum tenuifolium (Mitt.) Broth.	Optional	*Nidularium* sp. (leaf)

Pilotrichaceae Kindb.		
Crossomitrium epiphyllum (Mitt.) Müll. Hal.	Optional	No information
Crossomitrium patrisiae (Brid.) Müll. Hal.	Optional	*Theobroma cacao* (leaf), *Pseudobombax* sp. (leaf), *Citrus* sp. (stalk)
Crossomitrium saprophilum Broth.	Exclusive	No information
Lepidopilum subsubulatum Geh. & Hampe	Optional	No information
Sematophyllaceae Broth.		
Meiothecium boryanum (Müll.Hal.) Mitt.	Optional	*Laguncularia racemosa* (stalk)
Pterogonidium pulchellum (Hook.) Müll.Hal.	Optional	*Ficus* sp. (stalk), *Micomia* sp. (stalk), *Camellia sinensis* (stalk)

Table S2. Scientific productions with epiphyllous bryophytes of the Atlantic Forest selected through the ROSES method.

Title	**Publication type**	**Kind of study**	**Authors**	**Ecorregions**	**Number of species of epiphyloous bryophyte**
Bryophytes from a forest remnant in the campus of the Universidade Federal de São Carlos, municipality of Sorocaba, State of São Paulo, Brazil	Scientific article	Floristic survey	Koga et al. 2021	Semideciduous Forest	6
Bryophytes of the Parque Nacional da Serra da Bocaina, São Paulo State, Brazil	Scientific article	Floristic survey	Lima and Peralta, 2021	Dense Ombrophilous Forest	37
Survey of bryophytes on the Pessegueirinho trail, Curitibanos, Santa Catarina State, Brazil	Scientific article	Floristic survey	Remor et al. 2021	Mixed Ombrophilous Forest	2
The first 100 species of bryophytes, with seven new records for southern Brazil identified in the Parque Estadual de Itapeva, Torres, Rio Grande do Sul State	Scientific article	Floristic survey	Dewes et al. 2021	-	12
Bryophytes of the Parque Estadual da Serra do Brigadeiro, an Atlantic Forest Remnant in Southeastern Brazil	Scientific article	Floristic survey	Cifuentes-García et al. 2020	Semideciduous Forest	8

Title	**Publication type**	**Kind of study**	**Authors**	**Ecorregions**	**Number of species of epiphyloous bryophyte**
Bryophytes from Campos do Jordão State Park, São Paulo State, Brazil	Scientific article	Floristic survey	Amélio et al. 2019	Mixed Ombrophilous Forest	21
Bryophytes in Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, São Paulo State, Brazil	Scientific article	Floristic survey	Carmo et al. 2016	Montana Dense Ombrophilous Forest and Upper Montana Dense Ombrophilous Forest	27
Epiphyllous Bryophytes of Atlantic Forest Fragments of Reserva Ecológica Michelin, Bahia State, Brazil	Scientific article	Floristic survey	Oliveira and Bastos, 2014	Rainforest	24
The bryophytes of Trindade Island, South Atlantic, Brazil	Scientific article	Floristic survey	Faria et al. 2012	-	1
Bryophytes from a remnant of Atlantic Forest in the municipality of Ubajara, Ceará State, Brazil	Scientific article	Floristic survey	Siqueira et al. 2011	Rainforest	7

Title	**Publication type**	**Kind of study**	**Authors**	**Ecorregions**	**Number of species of epiphyloous bryophyte**
Bryophytic and phytogeographical aspects of two types of forest of the Serra do Mar State Park, Ubatuba/SP, Brazil	Scientific article	Floristic survey	Santos et al. 2011	Dense Ombrophilous Forest	22
Pleurocarpic Mosses of the Ibiapaba Plateau, Ceará, Brazil	Scientific article	Floristic survey	Oliveira and Bastos, 2010	Rainforest	
Liverwort conservation in the Atlantic Rain Forest of Southeastern Brazil: a regional survey in Rio de Janeiro State	Scientific article	Conservation analysis	Costa and Santos, 2009	-	4
Hornworts (Anthocerotophyta) and thallose liverworts (Marchantiophyta) from Ibiapaba Plateau, Ceará, Brazil	Scientific article	Floristic survey	Oliveira and Bastos, 2009	Rainforest	2
Bryophytes of the urban center of Caxias do Sul, Rio Grande do Sul State, Brazil	Scientific article	Floristic survey	Bordin and Yano, 2009	Mixed Ombrophilous Forest	5
The importance of Private Natural Heritage Reserves for conservation of Atlantic rain forest bryoflora: a study at El Nagual, Magé, Rio de Janeiro State, Brazil	Scientific article	Floristic survey	Santos and Costa, 2008	Humid Tropical Forests	11

Title	Publication type	Kind of study	Authors	Ecorregions	Number of species of epiphyloous bryophyte
New bryophytes occurrences in Brazilian states	Scientific article	Floristic survey	Peralta et al. 2008	-	1
Bryophytes from Ilhabela, São Paulo State, Brazil	Scientific article	Floristic survey	Yano and Peralta, 2008	Lowland Dense Ombrophilous Forest	5
Bark bryophytes of the riparian Forest along the Uruguai River, before flooding of the area by the dam of the electric power plan of Itá, between the states of Santa Catarina and Rio Grande do Sul in Brazil	Scientific article	Floristic survey	Peralta and Filho, 2008	Mixed Ombrophilous Forest	3
New occurrences of bryophytes to Pernambuco, Brazil	Scientific article	Floristic survey	Alvarenga et al. 2007	Lowland Dense Ombrophilous Forest	3
Epiphyllous and epiphyllous Brioflora from RPPN Frei Caneca, Jaqueira, PE, Brazil	Scientific article	Floristic survey	Campelo and Pôrto, 2007	Dense Ombrophilous Forest	34
Additions to Bryoflora of the State of Ceara, Brazil	Scientific article	Floristic survey	Oliveira and Alves, 2007	Humid Tropical Forests	9

Title	**Publication type**	**Kind of study**	**Authors**	**Ecorregions**	**Number of species of epiphyloous bryophyte**
Bryophytes from Ilha do Bom Abrigo, São Paulo State, Brazil	Scientific article	Floristic survey	Yano and Peralta, 2007	Dense Ombrophilous Forest	3
The genera *Lepidopilidium, Lepidopilum, Pilotrichum* and *Thamniopsis* (Pilotrichaceae, Bryophyta) in Rio de Janeiro State, Brazil	Scientific article	Floristic survey	Vaz and Costa, 2006	-	1
Hepatics (Marchantiophyta) from a fragment of Atlantic Forest in Serra da Jibóia, in the Municipality of Santa Teresinha, Bahia State, Brazil	Scientific article	Floristic survey	Valente and Pôrto, 2006	Montana Dense Ombrophilous Forest	17
Bryophytes from flooded forest, Zacarias municipality, northwest of São Paulo State, Brazil	Scientific article	Floristic survey	Peralta and Yano, 2005	Swamp Woods	4
Diversity and importance of the bryophyte taxa in the conservation of the ecosystems of the Rio de Janeiro state	Scientific article	List of species	Costa et al. 2005	Rainforest and altitude fields	51
New records of bryophytes for the Pernambuco State, Brazil	Scientific article	Floristic survey	Germâno and Pôrto, 2004	-	2

Title	Publication type	Kind of study	Authors	Ecorregions	Number of species of epiphyloous bryophyte
Bryophytes from sea-shores of the São Paulo State, Brazil	Scientific article	Floristic survey	Visnadi, 2004	Restinga	10
Bryophytes from the Alcatrazes, Bom Abrigo, Casca, and Castilho islands of São Paulo State, Brazil	Scientific article	Floristic survey	Visnadi and Vital, 2001	-	3
Bryophytes from the arboretum of the Botanical Garden of Rio de Janeiro	Scientific article	Floristic survey	Molinaro and Costa, 2001	Rainforest	6
Bryophytes from the National Park of Sete Quedas, Guaíra, Paraná, Brazil	Scientific article	Floristic survey	Yano and Colletés, 2000	-	3
Epixylic Bryophytes of an remnant area of the Atlantic Forest (Timbaúba, PE, Brazil): 2. Lejeuneaceae	Scientific article	Floristic survey	Germano and Pôrto, 1998	Submontane Ombrophilous Forest	3
Altitudinal gradient drives regional and local diversity and composition patterns of epiphyllous bryophytes in ecological refuges	Scientific article	Floristic survey	Araújo et al. 2022	Altitude swamps	29
Bryophytes of Rio Turvo State Park (SP), Brazil: integrating floristics, geographical distribution, reproduction and ecological traits	Scientific article	Floristic survey	Koga and Peralta, 2021	Dense Ombrophilous Forest	31

Title	**Publication type**	**Kind of study**	**Authors**	**Ecorregions**	**Number of species of epiphyloous bryophyte**
to support the conservation of an Atlantic Forest fragment					
The importance of Serra do Mar State Park for liverworts conservation in the Atlantic Rainforest	Scientific article	Floristic survey	Prudêncio et al., 2020	Dense Ombrophilous Forest	1
Floristic composition and vertical zonation of epiphyllous bryophytes in Dense Montane Ombrophilous Forest in southern Brazil	Scientific article	Floristic survey	Santos et al., 2018	Dense Montane Ombrophilous Forest	11
Bryophytes of the cloud forest of Pico do Marumbi State Park, Paraná, Brazil	Scientific article	Floristic survey	Santos et al., 2017	Dense High Mountain Ombrophilous Forest	23
Biodiversity survey, ecology and new distribution records of Marchantiophyta in a remnant of Brazilian Atlantic Forest	Scientific article	Floristic survey	Souza et al., 2017	Dense montane ombrophilous forest	4
How does reproductive strategy influence demography? A case study in the tropical, unisexual epiphyllous moss *Crossomitrium patrisiae*	Scientific article	Floristic survey	Alvarenga et al., 2016	Dense Ombrophilous Forest	1

Title	Publication type	Kind of study	Authors	Ecorregions	Number of species of epiphyloous bryophyte
Vertical distribution of epiphyllous bryophytes in Atlantic forest fragments in Northeastern Brazil	Scientific article	Floristic survey	Oliveira and Oliveira, 2016	Lowland Tropical Rainforest	16
Diversity of bryophytes in priority areas for conservation in the Atlantic forest of northeast Brazil	Scientific article	Floristic survey	Silva and Pôrto, 2015	Dense Ombrophilous Forest	2
Bryophyte communities along horizontal and vertical gradients in a human-modified Atlantic Forest remnant	Scientific article	Floristic survey	Silva and Pôrto, 2013	Dense Ombrophilous Forest	15
Richness preservation in a fragmented landscape: a study of epiphyllous bryophytes in an Atlantic forest remnant in Northeast Brazil	Scientific article	Floristic survey	Oliveira et al., 2011	Dense Ombrophilous Forest	11
Spatial structure of bryophyte communities along an edge-interior gradient in an Atlantic Forest remnant in Northeast Brazil	Scientific article	Floristic survey	Silva and Pôrto, 2010	Dense Ombrophilous Forest	20
Relations Between Regional–Local Habitat Loss and Metapopulation Properties of Epiphyllous Bryophytes in the Brazilian Atlantic Forest	Scientific article	Floristic survey	Alvarenga et al., 2009	Dense Ombrophilous Forest	11

Title	Publication type	Kind of study	Authors	Ecorregions	Number of species of epiphyloous bryophyte
Patch size and isolation effects on epiphyllous and epiphyllous bryophytes in the fragmented Brazilian Atlantic forest	Scientific article	Floristic survey	Alvarenga and Pôrto, 2007	Dense Ombrophilous Forest	5
Bryophyte communities in an Atlantic forest remnant, state of Pernambuco, Brazil	Scientific article	Floristic survey	Germano and Pôrto, 2006	Dense Ombrophilous Forest	8
Composição química das ceras cuticulares em espécies de Bryophyta (musgos) e Marchantiophyta (hepáticas)	Dissertation	Morphology	Matos, 2020	-	4
As bases estruturais da relação de epifilismo entre briófitas e plantas vasculares	Tese	Morphology and anatomy	Silva, 2016	-	14
Taxonomia e Ecologia de Briófitas urbanas na cidade de Santos, São Paulo, Brasil	Dissertation	Floristic survey	Mello, 2013	-	4
DNA – Barcode de Metzgeria Raddi (Marchantiophyta) do Brasil	Tese	Molecular biology	Dantas, 2019	-	5

Table S3. Description, calculation method and source where the explanatory variables were obtained to investigate potential sampling bias for the occurrence and density of records of epiphyllous bryophytes in the Atlantic Forest.

Variable	**Description - Calculation**	**Source**
Protec. areas	Area covered by protected areas - The shapefiles were rasterized by calculating the *cover* in each pixel	Ministério do Meio Ambiente (http://mapas.mma.gov.br/i3geo/datadownload.htm) World Database on Protected Areas (WDPA) 1.0 (https://www.unep-wcmc.org/resources-and-data/wdpa)
For. Cover	Remaining forest cover - The shapefile with forest remnants was rasterized by calculating the cover in each pixel	Fundação SOS Mata Atlântica (2017) (https://ww.sosma.org.br)
Road dist.	Distance from the nearest federal or state highway - The shapefile for roads was transformed into a binary raster,	Instituto Brasileiro de Geografia e Estatística (https://portaldemapas.ibge.gov.br)

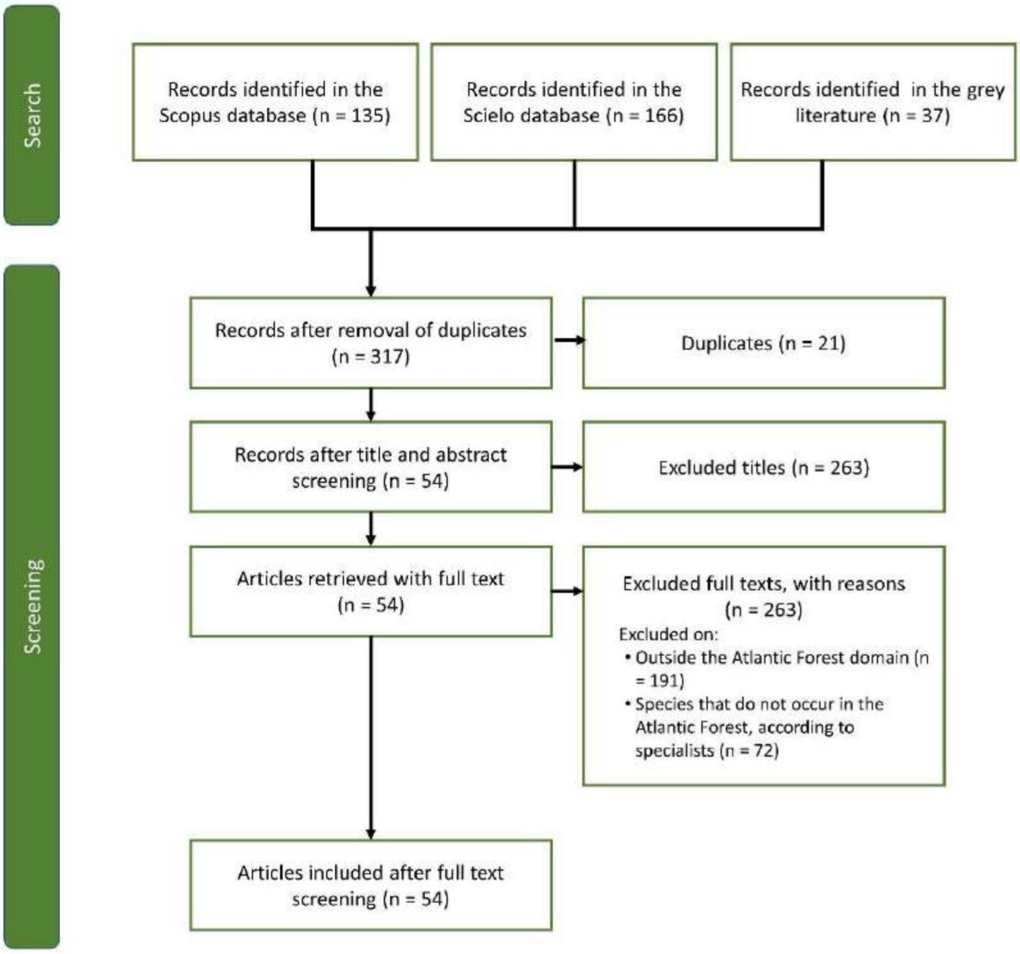
	and the geographic distance to the nearest pixel with a road was calculated	
Grad dist.	Distance from the nearest institution with graduate programs in Botany or Ecology - The list of graduate programs was assigned coordinates for the municipalities and rasterized into binary data. The minimum geographic distance to any pixel with the presence of an institution was calculated	Plataforma Sucupira (2019) (https://sucupira.capes.gov.br/sucupira/)
Cities	Density of cities - The shapefile with the centroids for capitals and municipalities was rasterized by counting the number of centroids per pixel	Instituto Brasileiro de Geografia e Estatística (https://portaldemapas.ibge.gov.br)

Table S4. Best selected generalized linear models (GLMs) based on AIC comparison describing the influence of the climate variables on the epiphyllous bryophyte richness. Only the most parsimonious models are exhibited (ΔAIC ≤2).

Model	**df**	**AIC**	**ΔAIC**	**Weight**
Richness ~ bio2 + bio4 + latitude + longitude	6	871.66	0	0.14
Richness ~ bio2 + bio4 + bio5 + latitude + longitude	7	873.05	1.38	0.07
Richness ~ bio2 + bio4 + bio14 + latitude + longitude	7	873.42	1.75	0.06

The response variable was the number of epiphyllous bryophyte species per grid (i.e., species richness) and the explanatory variables were the bioclimatic variables from Worldclim. Abbreviations: df = degrees of freedom; AIC = Akaike's information criterion; ΔAIC = AIC difference from the best model; Weight = proportion of the total amount of predictive power provided by the complete set of models. Only the most parsimonious models are exhibited (ΔAIC ≤2).

Fig. S1. Step scheme of the systematic review based on the ROSES methods.



CAPÍTULO 2

SILENT DUEL BETWEEN PHOROPHYTES AND CLIMATE: UNRAVELING THE ECOLOGICAL DETERMINANTS OF EPIPHYLLOUS BRYOPHYTES DISTRIBUTION IN THE ATLANTIC FOREST

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Original article

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ABSTRACT

This study presents a comparative approach to assess the relative influence of biotic and abiotic factors on the distribution of epiphyllous bryophytes in the Atlantic Forest, using ecological niche models (ENMs). The results show that the combination of specific climatic factors and host diversity are essential for the environmental suitability of the species, highlighting the complexity of their ecological niche. The presence of diverse hosts increases colonization opportunities, providing suitable microhabitats for species survival, while the specificity of some hosts suggests ecological adaptations. However, specific biotic interactions between bryophytes and hosts can be challenging in fragmented ecosystems, such as the Atlantic Forest, where habitat loss and fragmentation affect the persistence of these species. In addition, water availability, especially during dry periods, and climatic conditions such as temperature and precipitation are critical for the survival and distribution of epiphyllous bryophytes. While species show adaptations to tolerate seasonal variations, moisture scarcity represents a significant risk, particularly with climate change. The conservation of epiphyllous bryophytes in the Atlantic Forest requires strategies that integrate climatic factors and host diversity, as well as long-term research and monitoring to understand how climate change will affect these species and enable effective corrective actions.

Key-words: Epiphyllous bryophytes, ecological niche models, host diversity, climate change.

INTRODUCTION

Understanding the factors that shape species distributions in tropical forests, ecosystems rich in biodiversity and essential for global climate balance, is a challenge in ecology (Wang et al. 2024). These ecosystems exhibit highly variable microclimates, where changes in humidity and complex ecological interactions play a central role in defining the environmental conditions adapted to each species (Åkesson et al. 2021; Lőrincz et al. 2024). However, ecological niche models (ENMs) and species distribution models (SDMs), widely used to predict distributions, often consider only abiotic variables, ignoring biotic interactions such as competition and herbivory (Soberón and Peterson 2005). This simplification may fail to capture the processes shaping community formation, such as that of bryophytes, where establishment reflects the interaction between environmental variables, ecological relationships, and species dispersal ability (Zambonim et al. 2024; Soberón and Peterson 2005). Integrating biotic variables into these models could significantly improve predictive capacity and contribute to more effective conservation planning (Thuiller et al. 2019; Palacio and Girini 2018).

Biotic interactions are fundamental to ecology and have generated great interest in studies of their effects on species distribution and community formation (Blois et al. 2013; Urban et al. 2012; Guisan and Rahbek 2011). Despite this, the role of these interactions in defining species distributions and the spatial scales at which they are relevant remains largely unknown (Soberón 2007; Peterson and Soberón 2005). In many cases, biotic interactions occur between individuals, leading to a perception that their effects are predominantly local and random at larger geographical scales, as proposed by the Eltonian Noise Hypothesis ((Soberón e Nakamura 2009; Peterson et al.

2011). However, evidence indicates that essential biotic interactions, such as those mediated by pollinators, food resources, or hosts, exert significant influences on species distributions at large geographical scales (Winz et al. 2013; Gaston 2003). In this context, ecological niche correlation models, which typically rely solely on abiotic variables (Anderson 2012; Guisan and Thuiller 2005), have limitations. Recent approaches in modeling have integrated biotic interactions into correlation models, with promising results to enhance predictive accuracy and better capture ecological complexity (Blois et al. 2013; Meier et al. 2010).

Epiphyllous bryophytes, being highly dependent on specific microhabitats and biotic interactions with their hosts, are excellent models for studying the impact of ecological interactions on species distribution (Hu et al. 2021; Mežaka et al. 2020; Jiang et al. 2018). In the BAM diagram (Fig. 7A) (Soberón and Peterson 2005), this concept is addressed by integrating three essential factors: abiotic (A), biotic (B), and movement and dispersal (M). While abiotic factors (A), such as temperature, humidity, and light, define the fundamental niche limits (Fig. 7B), biotic factors (B), such as interactions with hosts, can function as ecological filters, determining the presence of bryophytes by influencing colonization based on tree characteristics (Fig. 7C) (Mežaka et al. 2020; Naranjo et al. 2019, Hu et al., 2021).

Thus, the intersection between A and B indicates that epiphyllous bryophyte distribution depends on the proper alignment between environmental factors and the presence of hosts that provide favorable interactions for these organisms (Zatman and Ilkiu-Borges 2007, Zatman 2003). Therefore, the combination of these three factors ($A \cap B \cap M$) (Fig. 7A) reflects the realized niche of epiphyllous bryophyte species (Fig. 7D), as the interaction between microclimate, hosts, and dispersal facilitates the establishment and growth of these species in tropical forests (Sousa-Pereira and Costa 2022; Campelo and Pôrto 2007).

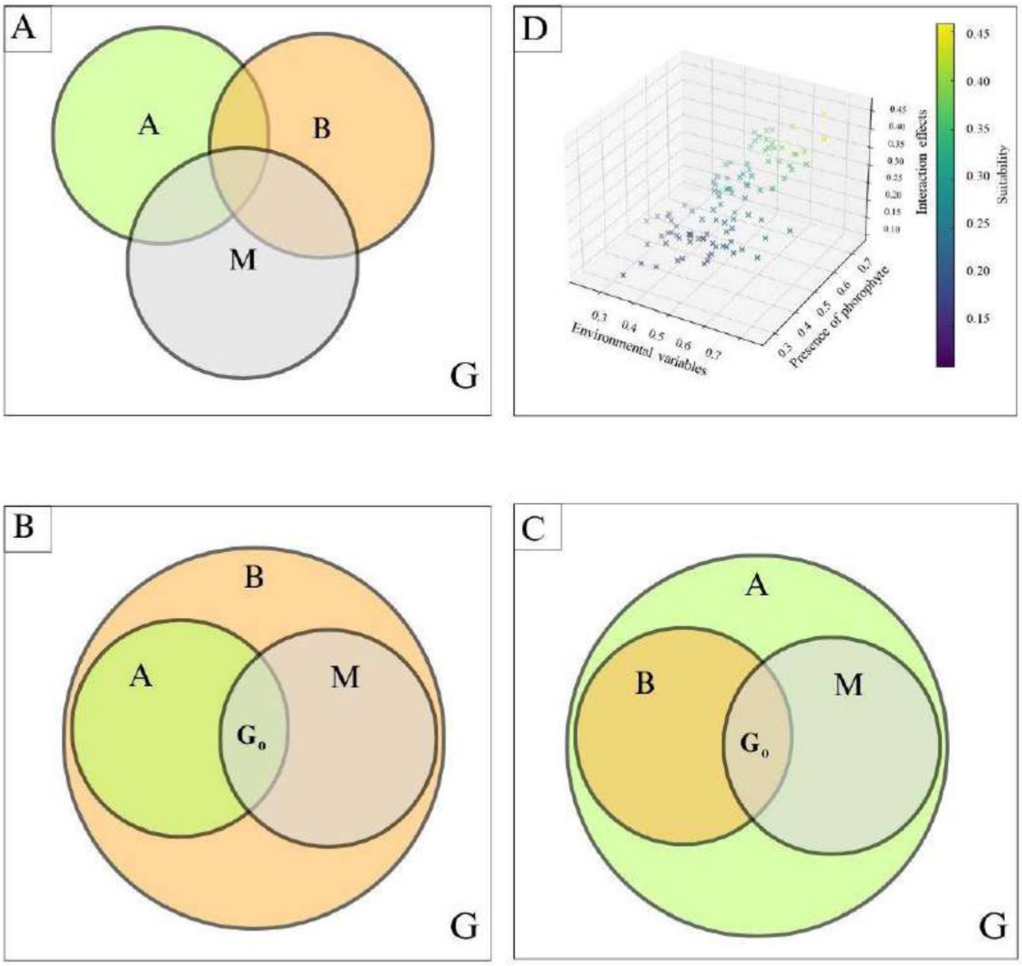

Figure 7. A: BAM diagram representing the integration of factors affecting the geographical distribution of species. G: Geographic area of interest; A: Set of environmental characteristics that allow species survival (fundamental niche); B: Biotic variables that may or may not limit species occurrence; M: Species movement/dispersal area. Adapted from Soberón and Peterson 2005. In this configuration, the BAM diagram represents the hypothesis where the geographic region of occurrence of epiphyllous bryophytes (Go) is expressed by the intersection of these three factors. (B) Configuration of the BAM diagram representing the hypothesis where biotic interactions are diffuse and non-limiting or manifested at a local scale, not affecting the distribution of epiphytic bryophyte species. (C) Configuration of the BAM diagram representing the hypothesis where biotic interactions with hosts restrict the distribution of epiphyllous bryophytes, and abiotic conditions are not determinant due to this restriction. (D) Representation of the multidimensional hypervolume of the realized niche of epiphytic bryophytes. On the X-axis: environmental variable represents one environmental variable; on the Y-axis: presence of phorophytes refers to the presence of hosts; on the Z-axis: interaction effect reflects the interaction effect between the variables. Lighter shades (such as yellow) indicate higher suitability, while darker shades (such as purple) indicate lower suitability.

However, the complexity of the environmental and biotic factors that shape the niche of these species is still not fully understood, which hinders the application of conservation policies and the understanding of the factors that impact the abundance and distribution of these species (Löffler and Pape 2019, Silva et al., 2025). In this context of environmental suitability for epiphyllous bryophytes, different hypotheses can be raised to understand which factors determine their distribution (Fig. 8C), and ecological niche modeling (ENMs) provides tools that aid in understanding this dynamic (Soberón and Peterson 2005; Guisan et al. 2017; Elith and Leathwick 2009). A climatic approach considers that species suitability is primarily driven by bioclimatic variables, however, a specialist model commonly suggests that suitability is defined by specific interactions between bryophytes and hosts, indicating a high degree of specificity (Fig. 8C). On the other hand, the generalist model is driven by both climatic variables and host richness to determine the distribution of these species. ENMs allow for the identification of potentially favorable environmental conditions for species occurrence, defining the characteristics of the ecological niche and helping to understand both biotic and abiotic factors (Soberón and Peterson 2005).

Thus, understanding the biodiversity patterns of epiphyllous bryophytes requires the integration of approaches based on climatic variables and biotic interactions (Silva et al., 2025) (Fig. 8D), as these models can be useful in improving the accuracy and understanding the ecological mechanisms that favor species distribution. The aim of this study is to explore the complex relationships between climate and biotic interactions that influence the environmental suitability of epiphyllous bryophytes in the Atlantic Forest. Specifically, we aim to assess how the presence and richness of hosts influence the suitability of epiphyllous bryophytes. With this, we seek to answer the following questions: i) How do climatic variables, such as temperature and precipitation, influence the environmental suitability of epiphyllous bryophytes in the Atlantic Forest? ii) What is the role of host richness and specific hosts in the environmental suitability of epiphyllous bryophytes? iii) How do the combination of climatic and biotic (host) variables affect the macroecological patterns of species richness for epiphyllous bryophytes?

It is expected that the results of this study will contribute to a better understanding of the factors influencing the dimensions of the ecological niche and the geographic distribution patterns of organisms with a strong component of biological interaction, such as epiphyllous bryophytes, which are largely neglected in biogeographical studies.

MATERIAL AND METHODS

The methodological structure of this study consisted of three main stages: i) data collection and processing. In this stage, occurrence data of epiphyllous bryophytes and hosts were obtained from scientific articles, as well as publicly available virtual databases such as speciesLink and GBIF, which are extensively available in the study by Sousa et al. (2025); ii) ENMs, using occurrence records and predictor variables; and finally, iii) model evaluation and statistical analysis. This stage involved validating the generated models to verify their accuracy and performance, using statistical analyses such as AUC, Akaike delta, and omission rate. In addition, statistical analyses were performed to identify ecological patterns, such as the relative influence of environmental variables on species distribution.

Occurrence Data

The occurrence data to model epiphyllous bryophyte species and hosts were based on the Global Biodiversity Information Facility (https://www.gbif.org/citation-guidelines#occDataDownload/) and speciesLink (https://specieslink.net/) databases (Fig. 8A). For the selection of epiphyllous bryophyte species, the following inclusion criteria were applied: a) occurrence recorded in the Atlantic Forest; b) availability of information on the host where the species occurs in the literature or virtual databases; c) presence of at least eight occurrence records. The selection of hosts was conducted based on the species of epiphyllous bryophytes, such that the modeled hosts acted as a host for the epiphyllous species (Fig. 8A). All analyses were performed in R version 4.2.2 (R Core Team, 2022). We considered records from all of South America for epiphyllous bryophytes and hosts to ensure a comprehensive description of the species' realized niche, as this type of procedure is shown to outperform models of individual populations (Kuemmerle et al. 2018).

To filter erroneous coordinates (Zizka, 2019), the records were processed using the 'CoordinateCleaner' package (Fig. 8B). To reduce the effects of sampling bias and spatial autocorrelation, we performed a rarefaction of the occurrence points after cleaning, maintaining records that were at least 10 km apart (Boria et al. 2014).

The delimitation of areas for model calibration (component "M", Fig. 7), which defines areas accessible to species in ecological time, was performed for each epiphyllous species and host, considering their potential for dispersal and taking into account environmental barriers and biogeographical limits (Barve et al. 2011). To do this, a minimum convex polygon (MPC) was constructed from the occurrence records using the 'convex_area' function from the 'ellipsenm' package, with a 100 km buffer to account for possible accessible areas beyond the recorded occurrence points (Fig. 8B).

Environmental and Biotic Predictors

The set of predictors for modeling the hosts consisted of variables that represented climatic conditions, while for epiphyllous bryophytes, the predictors were variables that separately characterized the specific host plant, climatic conditions, host richness, climatic conditions associated with host richness, and host richness associated with the specific host plant (Fig. 8D).

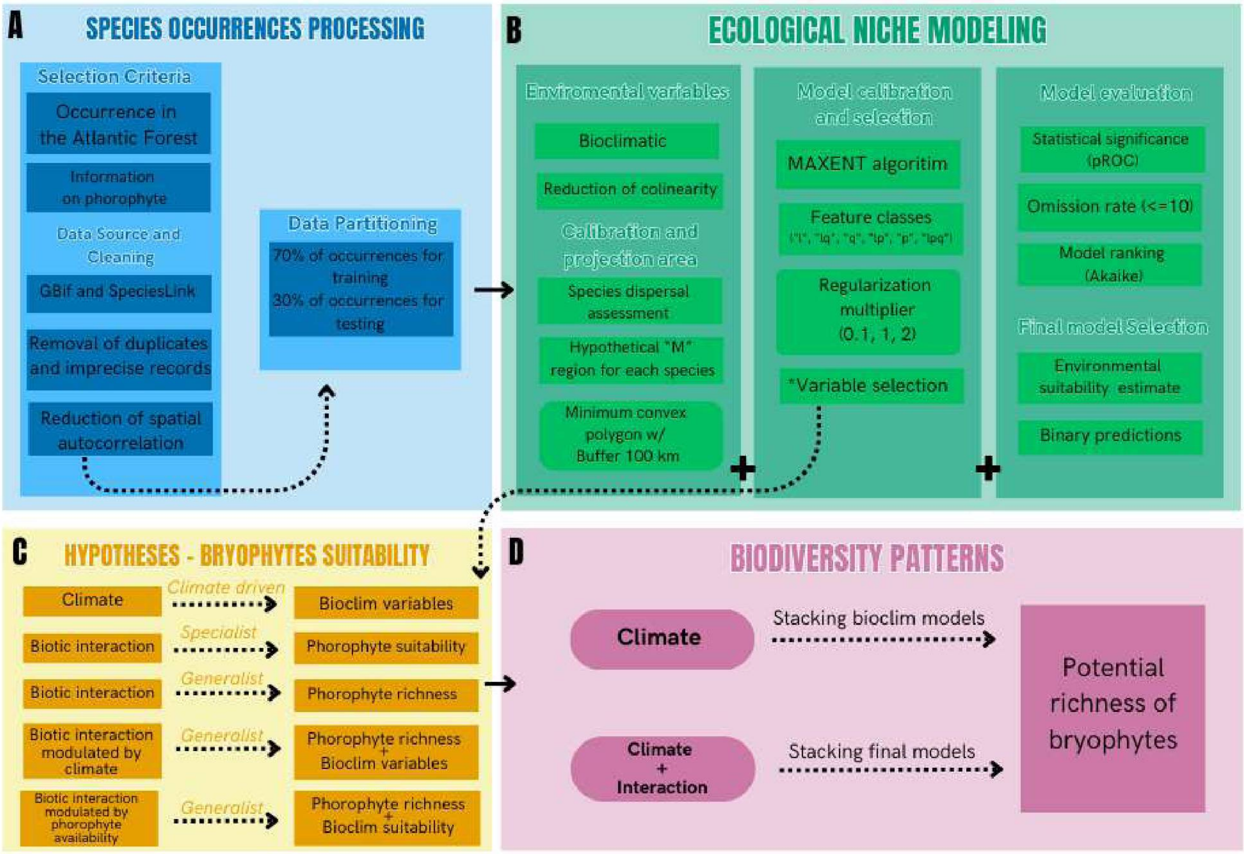

Figure 8. Methodological flowchart of the study on species distribution models (ENMs) for epiphyllous bryophytes in the Atlantic Forest. The process includes: (A) obtaining occurrence data from sources such as GBIF and SpeciesLink, with specific selection criteria; (B) data preprocessing, using coordinate filters and constructing minimum convex polygons (MCP); (C) species distribution modeling using MAXENT, including validation criteria such as omission rates and Akaike; and (D) defining strategies with different combinations of environmental and biotic predictors for species modeling.

The climatic data consisted of 19 bioclimatic variables obtained from WorldClim, derived from monthly temperature and precipitation values with a resolution of 2.5 minutes (~ 4.5 km) (Fick and Hijmans, 2017). To avoid issues related to collinearity between environmental variables, we applied the Spearman correlation coefficient to remove highly correlated variables (r > .7) (Dormann et al., 2013). Finally, the bioclimatic variables retained for the modeling process of hosts and epiphyllous bryophytes were:

bio2 (mean daily range), bio4 (temperature seasonality), bio5 (maximum temperature of the hottest month), bio9 (mean temperature of the driest quarter), bio13 (precipitation of the wettest month), bio14 (precipitation of the driest month), and bio15 (precipitation seasonality).

Ecological Niche Modeling (ENM)

The ENMs were developed using the kuenm2 package (Cobos et al. 2024). To calibrate the distribution models, a calibration grid was generated to define the different combinations of predictors and their configurations. The regularization multiplier settings were 0.1, 1, and 2, in order to test models with different levels of complexity. The resource classes evaluated were specific, including 'l' (linear), 'q' (quadratic), 'p' (product), as well as their combinations ('l', 'lq', 'q', 'p', 'lpq'). From this, the models were calibrated using 70% of the occurrence data for training and 30% for testing. The selection of the best models was based on three criteria: i) statistical significance of the PROC value, ii) omission rate (<=10%), and iii) model complexity, evaluated by the Δ of the Akaike Information Criterion (<=2) (Fig. 8C). For the final selected models, response curves and the relative importance of predictors were generated, allowing for the interpretation of each environmental variable's influence on species distribution. In this stage, to evaluate differences in the percentages between the predictors, the Kruskal-Wallis test was used, a non-parametric analysis included to compare independent groups (Kruskal and Wallis, 1952).

To determine the predictor of host richness, the models generated for each host species were binarized using a threshold of 10% of the minimum suitability values at the presence points. Finally, the species richness in each cell was estimated by summing the stack of binarized models.

RESULTS

Ecological niche models (ENMs) were developed for 31 host species, which acted as predictor variables in the modeling of the distribution of 10 epiphyllous bryophyte species. These models allowed us to assess how the presence and diversity of hosts influence the environmental suitability for bryophytes in the Atlantic Forest.

The ENMs for epiphyllous bryophytes showed good predictive performance for all modeled species. Most of the models had omission rates ranging from 0.08 to 0.1, demonstrating that the models were effective in predicting the species' occurrence areas. Our results suggest that the predictors decreased in their median contributions, with the lowest contribution from the set of variables related to 'climate' and the highest contribution from the set of variables related to 'host richness + climate'. However, the variability within the groups contributes to the lack of statistical significance ($p = 0.406$), indicating that it cannot be asserted that the percentage contribution varies significantly between the evaluated predictors (Fig. 9).

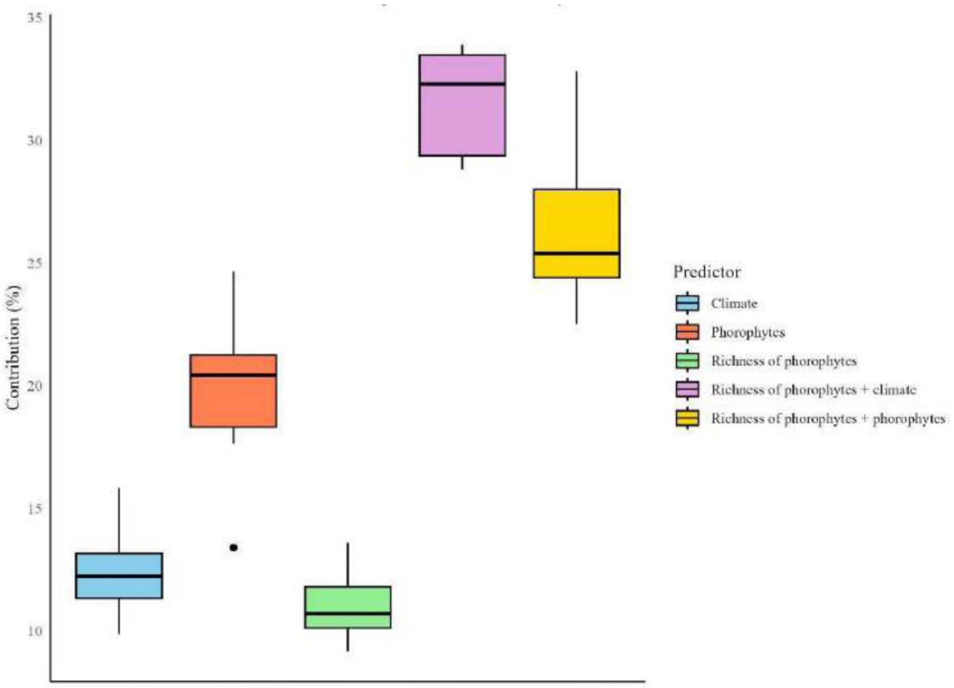

Figure 9. Contribution of different predictors in defining suitability areas for epiphytic bryophytes in the Atlantic Forest. The contribution of each predictor is expressed as a percentage and represented in colored boxplots. The predictor categories include: climate (blue), hosts (orange), host richness (green), host richness + climate (purple), and host richness + hosts (yellow).

The results suggest that host richness is a predictor with a high influence on the environmental suitability of some epiphyllous bryophytes. That is, areas with greater host diversity tend to show higher suitability, as observed for *Cololejeunea subcardiocarpa* and *Drepanolejeunea mosenii* (Fig. 10A-C and 10D-F).

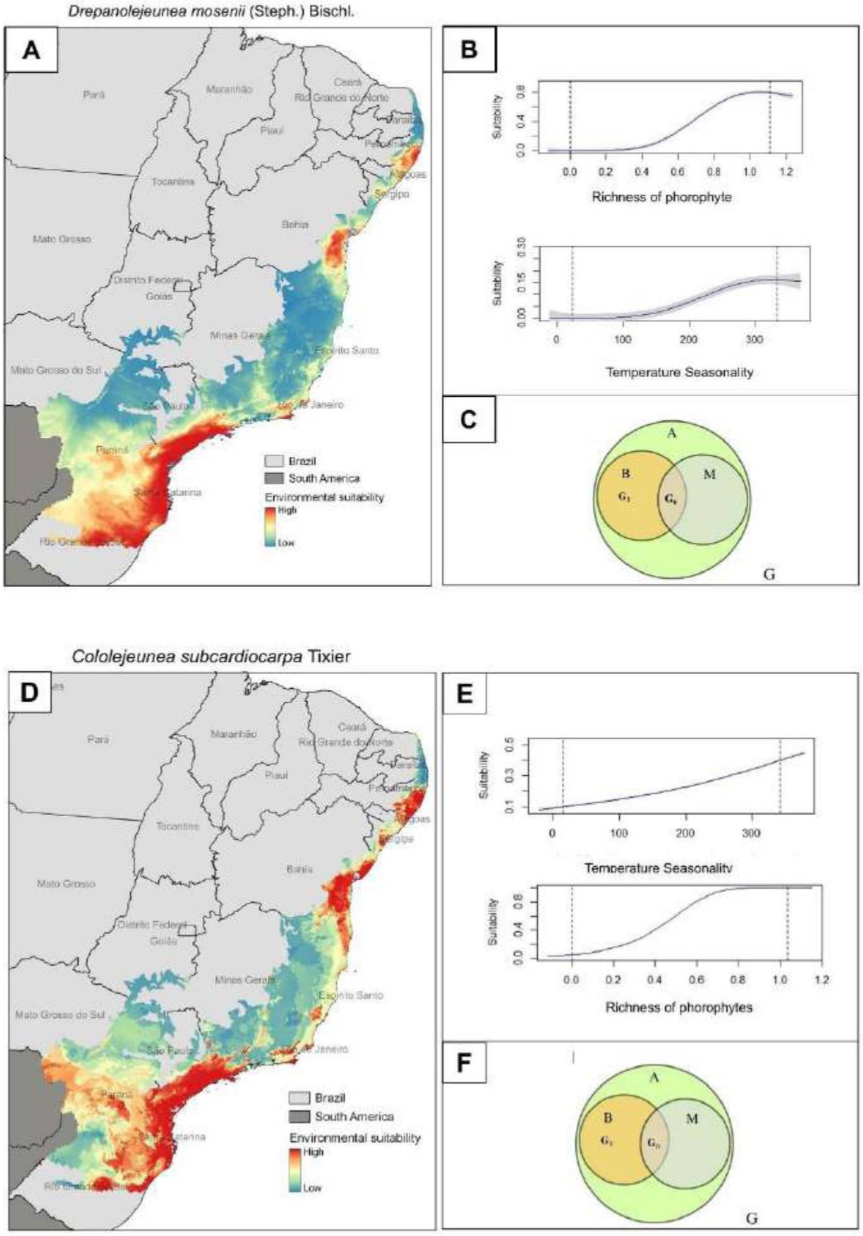

Figure 10. Distribution and environmental suitability analysis for two epiphyllous bryophyte species in the Brazilian Atlantic Forest. Maps (A and D): Represent the environmental suitability for *Drepanolejeunea mosenii* (A) and *Cololejeunea subcardiocarpa* (D). Red areas indicate high suitability, while blue areas indicate low suitability. Response graphs (B and E): Show the influence of specific environmental variables on the suitability of each species. BAM diagrams (C and F): Represent the ecological niche of the species, illustrating the overlap of environmental factors (A) and available biotic resources (B). These diagrams help visualize how environmental conditions and resources interact to determine the niche occupied by each species.

Additionally, some species exhibit dependence on specific hosts, such as *Cyclolejeunea convexistipa* (Fig. 11A-C), which is associated with *Celtis iguanaea*, and

Diplasiolejeunea rudolphiana (Fig. 11D-F-I), which is related to the presence of *Hibiscus tiliaceus* e *Asclepias curassavica.*

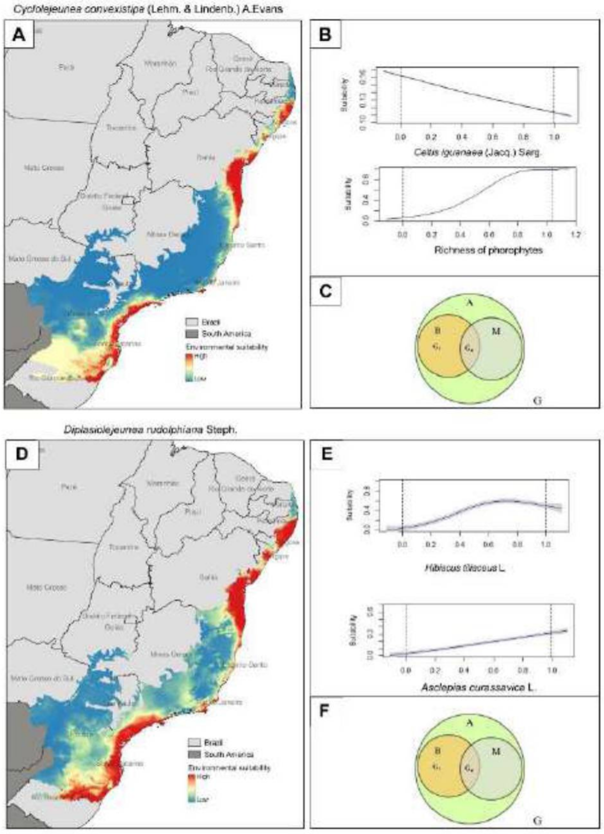

Figure 11. Distribution and environmental suitability analysis for two epiphyllous bryophyte species in the Brazilian Atlantic Forest. Maps (A and D): Represent the environmental suitability for *Cyclolejeunea convexistipa* (A) and *Diplasiolejeunea rudolphiana* (D). Red areas indicate high suitability, while blue areas indicate low suitability. Response graphs (B and E): Show the influence of specific environmental variables on the suitability of each species. BAM diagrams (C and F): Represent the ecological niche of the species, illustrating the overlap of environmental factors (A) and available biotic resources (B). These diagrams help visualize how environmental conditions and resources interact to determine the niche occupied by each species.

The results indicate that specific climatic variables, such as the maximum temperature of the hottest month and temperature seasonality, have a significant influence on determining the environmental suitability for several epiphyllous bryophyte species, including *Brachiolejeunea laxifolia* (Fig. 13P-R), *Ceratolejeunea rubiginosa* (Fig. 12J-L), *Cololejeunea cardiocarpa* (Fig. 12G-I), and *Lejeunea adpressa* (Fig. 12D-F). These variables suggest the species' ability to tolerate different temperature conditions and seasonal variations, which are critical aspects for survival in diverse microclimates.

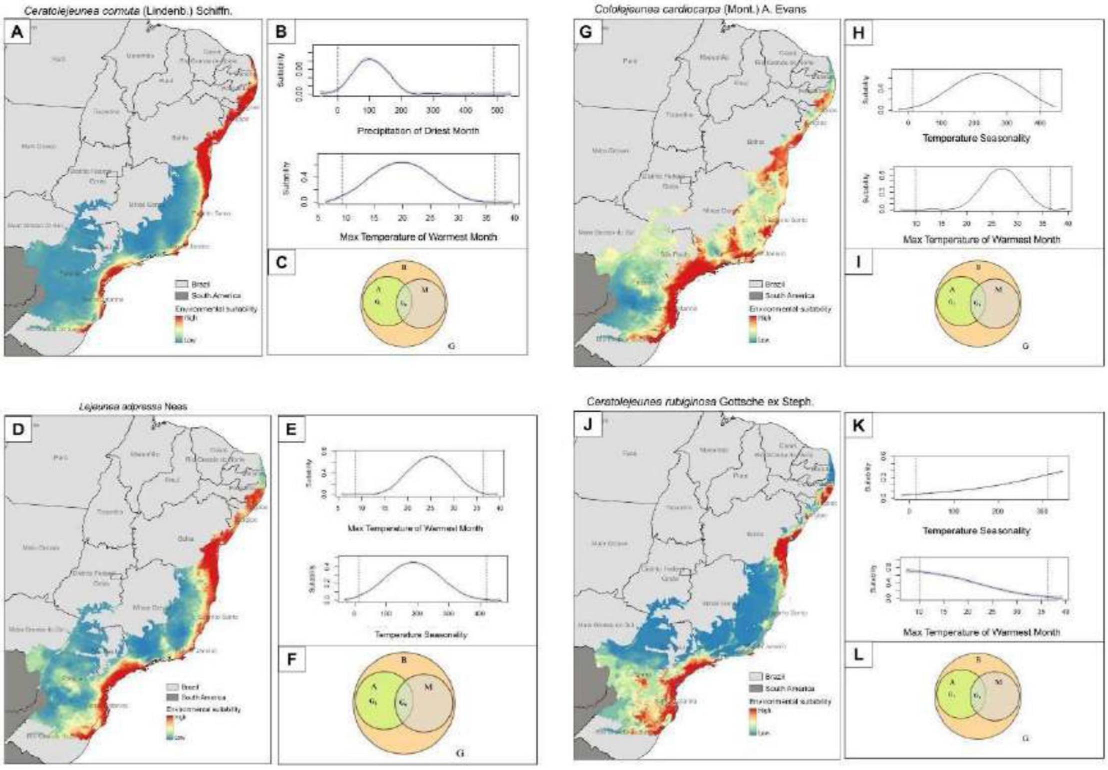

Figure 12. Distribution and environmental suitability analysis for four epiphytic bryophyte species in the Brazilian Atlantic Forest. Maps (A, D, G, J): Represent the environmental suitability for *Ceratolejeunea cornuta* (A), *Lejeunea adpressa* (D), *Cololejeunea cardiocarpa* (G), *Ceratolejeunea rubiginosa* (J). Red areas indicate high suitability, while blue areas indicate low suitability. Response graphs (B, E, H, K): Show the influence of specific environmental variables on the suitability of each species. BAM diagrams (C, F, I, L): Represent the ecological niche of the species, illustrating the overlap of environmental factors (A) and available biotic resources (B). These diagrams help visualize how environmental conditions and resources interact to determine the niche occupied by each species.

Although the precipitation of the driest month showed a peak in the response curve for *Ceratolejeunea cornuta* (Fig. 12A-C), the value on the Y-axis (p = 0.06) indicates that this variable has a low relative contribution in the model adjustment. Overall, the graph suggests that the species may be associated with drier regions, implying that water availability during dry periods is a critical factor. For *Leptolejeunea elliptica* (Fig. 13M-O), the precipitation of the wettest month also proved to be essential, suggesting that highly humid conditions are crucial to maintaining populations of this species in the Atlantic Forest.

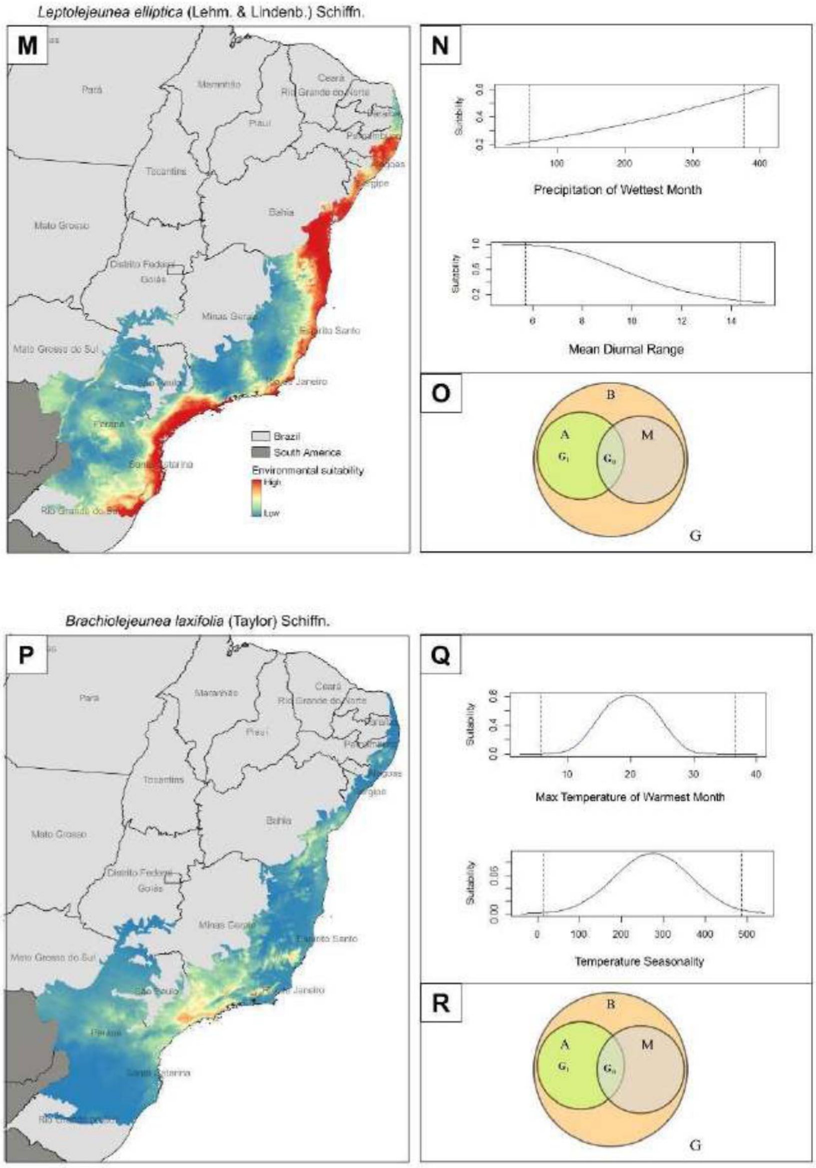

Figure 13. Distribution and environmental suitability analysis for four epiphytic bryophyte species in the Brazilian Atlantic Forest. Maps (M, P): Represent the environmental suitability for *Leptolejeunea elliptica* (M) and *Brachiolejeunea laxifolia* (P). Red areas indicate high suitability, while blue areas indicate low suitability. Response graphs (N, Q): Show the influence of specific environmental variables on the suitability of each species. BAM diagrams (O, R): Represent the ecological niche of the species, illustrating the overlap of environmental factors (A) and available biotic resources (B). These diagrams help visualize how environmental conditions and resources interact to determine the niche occupied by each species.

The models show that the inclusion of predictors related to hosts alters the patterns of potential distribution, focusing on areas of high suitability in specific regions along the Atlantic Forest when compared to the model based solely on climate (Fig. 14).

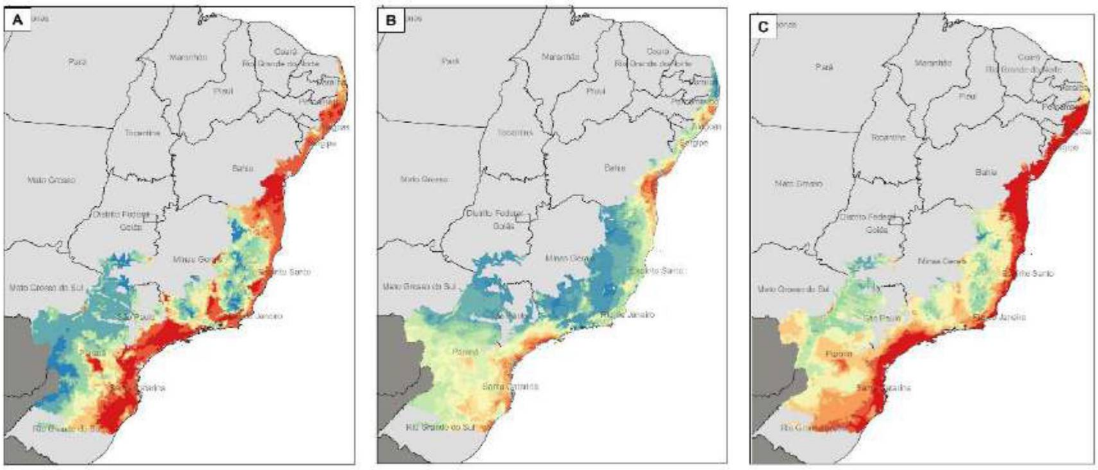

Figure 14. Environmental suitability maps based on different predictors. A: Areas of environmental suitability considering only bioclimatic variables. B: Suitability areas based on host richness, highlighting regions with greater host plant diversity. C: Map resulting from the overlap of final models, incorporating multiple predictors, showing areas of highest environmental suitability for epiphytic bryophytes based on an integrated analysis. Red areas indicate high suitability, while blue areas indicate low suitability.

DISCUSSION

In this study, we present a comparative approach that assesses the relative importance of different biotic and abiotic factors in determining the potential distribution of epiphyllous bryophyte species in the Atlantic Forest. The use of ecological niche models (ENMs) was essential in expanding our understanding of the ecological determinants influencing the suitability areas of these species. We found a consistent pattern where, for most of the epiphyllous bryophytes analyzed, their distribution depends on the combination of specific climatic factors and an adequate diversity of hosts to establish high-suitability areas. This interdependence between climatic conditions and host richness demonstrates the complexity of the ecological niche of epiphyllous bryophytes, highlighting the importance of considering multiple factors in distribution estimates and conservation planning for these species.

The ecological niche models for epiphyllous bryophytes showed robust predictive performance. The inclusion of host-related data improves the representation of these species' ecological niche. Previous studies emphasize the importance of biotic interactions, such as the presence of specific hosts, in the development and maintenance of epiphyllous species (Zotz and Hietz 2001). A key point in the analyses was the low omission rates, which indicate that the models managed to balance sensitivity and specificity without significantly underestimating suitable areas for the species (Monge-Najera 1989).

The dependency of epiphyllous bryophytes on host richness is understandable, considering that these species lack vascular structures for the effective transport of water and nutrients, making them reliant on the microhabitat provided by their hosts (Hu et al.

2021; Naranjo et al. 2019). Hosts from various species offer variations in bark texture and chemical composition of leaves (Silva et al. 2023; Mežaka et al. 2020), increasing the likelihood that the ecological needs of epiphyllous bryophytes will be met.

It is important to note that the absence of specificity to a particular host in most of the species analyzed may suggest accidental epiphytism or simply opportunistic use of a suitable microhabitat (Hoeber and Zotz 2022; Brock and Burns 2021). This behavior, favored by the structural heterogeneity of hosts, increases colonization opportunities (Mežaka et al. 2020) and offers protection against extreme environmental variations. Structurally complex habitats can harbor more niches, providing new opportunities for resource exploitation and contributing to species coexistence (Tews et al. 2004; MacArthur and Wilson 2001).

In contrast, the specificity of some hosts in determining suitability areas for certain epiphyllous bryophytes may suggest coevolution or ecological adaptation that allows these bryophytes to explore highly specialized niches (Naranjo et al. 2019). Although characterizing ecological specialization is challenging, as it involves multiple definitions and evaluations at different scales (Poisot et al. 2011; Blüthgen et al. 2007), we consider that the physical characteristics of the host, such as leaf chemistry (Silva et al. 2023), may favor a specific spectrum of epiphytes (Zotz and Hietz, 2001). In general, these specific hosts may have a set of convergent characteristics that positively influence the performance and maintenance of epiphyllous species over time (Wagner et al. 2015).

However, these specific biotic interactions between bryophytes and hosts may present challenges in fragmented ecosystems, such as the Atlantic Forest (Lima et al. 2020; Zwiener et al. 2018; Ribeiro et al. 2009). Habitat loss and fragmentation, whether due to anthropogenic activities or climate change, negatively affect the persistence of host species (Laurance et al. 2004), as edge effects alter the forest microclimate and vegetation structure (Didham and Lawton 1999; Laurance et al. 2004). Given the linear dependence between some epiphyllous bryophyte species and hosts, this loss can directly impact the survival and distribution of epiphyllous bryophytes. Thus, the role of hosts as predictors of environmental suitability underscores the importance of conserving tree species in the Atlantic Forest to preserve epiphyllous bryophytes (Lima et al. 2024; Sambuichi et al. 2008).

Nevertheless, host diversity alone was not sufficient to guarantee the establishment and maintenance of epiphyllous bryophytes. In addition to the availability of hosts, specific climatic conditions, such as temperature and precipitation, proved essential for the development of these species, as observed in other studies on this group (Campelo and Pôrto 2007; Lücking 1997). These variables help explain how extreme environmental conditions and seasonal variations influence species richness and distribution patterns (Ruiz and Ceballos 2004).

Tolerance to these variations may suggest the presence of morphophysiological adaptations (Mežaka et al. 2020; Laenen et al. 2015) that allow epiphyllous bryophytes to maintain stable metabolic processes even under adverse conditions, giving them greater flexibility in habitat occupation (Gignanc 2009; Gradstein 1997). In the context of climate change, this ability to tolerate seasonal variations may provide a relative advantage for these species, allowing populations to persist in altered environments, provided climatic conditions remain within tolerable ranges (Santos et al. 2023; Zotz and Bader 2008).

Despite these adaptations, the availability of consistent moisture proved to be a critical factor for the survival of some species, indicating that water scarcity poses a high risk to epiphyllous bryophyte biodiversity (Xia et al. 2018, Li 2004). In this sense, reduced precipitation due to climate change could limit suitable areas for species like *Leptolejeunea elliptica*. Therefore, climate change represents an additional challenge for the persistence of this species (Tuba et al. 2011; Alvarenga and Pôrto 2007).

Conserving epiphyllous bryophytes in the Atlantic Forest requires an approach that considers both climatic factors and the availability of specific microhabitats (hosts) (Naranjo et al. 2019). Conservation policies that focus solely on protecting climatically favorable areas, without considering host diversity, may be insufficient for preserving these species (Diniz-Filho et al. 2012; Zartman and Ilkiu-Borges 2007). It is essential to adopt a set of strategies that integrate both climatic factors and host diversity to ensure the effective conservation of epiphyllous bryophytes. Moreover, promoting long-term research is crucial to better understanding the relationships between epiphyllous bryophytes, hosts, and climate, which will assist in developing management strategies. Monitoring microclimatic conditions in areas where epiphyllous bryophytes occur is also vital, as it will help predict how climate changes might affect species survival and enable the implementation of corrective actions.

AUTHOR CONTRIBUTIONS

All authors contributed to all aspects of this work.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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CAPÍTULO 3

EPIPHYLLOUS BRYOPHYTES OF THE ATLANTIC FOREST: CHALLENGES AND VULNERABILITY IN A CHANGING CLIMATE

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*Artigo a ser submetido a Conservation Biology

Original article

EPIPHYLLOUS BRYOPHYTES OF THE ATLANTIC FOREST: CHALLENGES AND VULNERABILITY IN A CHANGING CLIMATE

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ABSTRACT

This study assesses the influence of specific phorophytes availability and phorophytes diversity on the environmental suitability and vulnerability of epiphyllous bryophytes in the Atlantic Forest in the face of climate change scenarios. Using Ecological Niche Models (ENMs), the study projected the future distributions of these species considering different climate scenarios and phorophytes. The results indicate that the availability of specific phorophytes is crucial for specialized species, such as *Cyclolejeunea convexistipa* and *Cololejeunea subcardiocarpa*, making them more vulnerable to the loss of suitable habitats due to climate change. On the other hand, species like *Cololejeunea cardiocarpa* and *Drepanolejeunea mosenii* showed greater environmental suitability in scenarios with higher phorophytes diversity, suggesting that diversity enhances the resilience of these species. Despite the observed variations, the differences in vulnerability indices between climate scenarios were not statistically significant. The results suggest that the complex interaction between specific phorophytes, phorophytes diversity, and climate factors influences bryophyte vulnerability, highlighting the need to consider multiple biotic and abiotic factors in conservation assessments of these species. The preservation of both specialized and diverse phorophytes is essential to mitigate the impacts of climate change and ensure the resilience of forest ecosystems. The research underscores the importance of adaptive management strategies for the conservation of epiphyllous bryophytes in the Atlantic Forest.

Key-words: Climate change vulnerability; Epiphyllous Bryophytes; Ecological Niche Models (ENMs); Ecological resilience.

INTRODUCTION

Global biodiversity has been severely impacted by climate change, and many species, despite having great potential to maintain ecosystem balance, face growing threats due to these alterations (Fortunel et al., 2014; Berllard et al., 2012). The ability of species to survive these changes will largely depend on their resistance and capacity to adapt to new habitats (Baumbach et al., 2021; Dury et al., 2018; Tzedakis et al., 2013).

In tropical forests, increased CO_2 levels are associated with various impacts, such as changes in biomass production (Vieilledent et al., 2016), higher tree mortality (Kubota et al., 2018; Esquivel-Muelbert et al., 2017), as well as changes in species distribution and abundance (Manes et al., 2021). The maintenance of ecosystems and their ability to respond to these changes is directly dependent on biodiversity (Thuiller et al., 2005). However, variations in precipitation rates, rainfall seasonality, and temperature increases are compromising the functioning of these environments (Bloor et al., 2010), affecting their stability and adaptability. Biodiversity loss, driven by these changes, may lead to a decrease in ecosystem resistance to extreme events, such as prolonged droughts and heatwaves, making them more vulnerable (Zanatta et al., 2020; Barlow et al., 2018). One group of organisms particularly sensitive to these changes are epiphyllous bryophytes, whose interactions within tropical ecosystems are still poorly understood and may play a crucial role in ecosystem functioning (Silvaet al., 2025).

In addition to affecting biodiversity and vegetation patterns, these changes can affect the dynamics of ecological interactions, which are fundamental for maintaining ecosystem balance (Hamann et al., 2021). Changes in these interaction patterns, such as pollination, seed dispersal, and symbioses, can compromise ecosystem resilience and affect essential ecological functions, such as nutrient cycling and water regulation (Bista et al., 2018; Becklin et al., 2016). The loss of key species and the weakening of these ecological relationships make ecosystems more susceptible to degradation (Brodie et al., 2012; Docherty et al., 1997), hindering their ability to recover from natural and anthropogenic disturbances. This can trigger a vicious cycle where biodiversity loss and climate change reinforce each other, accelerating the collapse of various essential environmental functions (Löffler and Pape, 2019; Grace, 1987).

The Ecological Resilience Theory (Holling, 1973) provides a conceptual framework to understand how ecosystems can, in theory, resist and adapt to changes, as long as they do not surpass a critical threshold of alterations. For example, climate change has been an increasing stressor, and the vulnerability of species sensitive to these changes can reflect nonlinear behavior in ecosystems. Thus, there are three distinct ways an environment can respond to stress and how these responses can manifest (Scheffer et al., 2000; Fig. 15). Curve "a" follows a linear pattern, where the continuous increase in stress, such as rising temperatures, can provoke a proportional and predictable response in the ecosystem. Meanwhile, curve "b" presents a more complex scenario, where the ecosystem can remain stable in the face of stress, such as changes in climate conditions, until it reaches a threshold point. When the ecosystem reaches this point, drastic and hard-to-predict consequences may occur, as when vulnerable species fail to adapt to rapid climate changes. Curve "c" is even more complex, highlighting that once this threshold is surpassed, the ecosystem may enter a new cycle where, even with reduced stress, the system does not return to its original state, a phenomenon known as hysteresis (Holling, 1973).

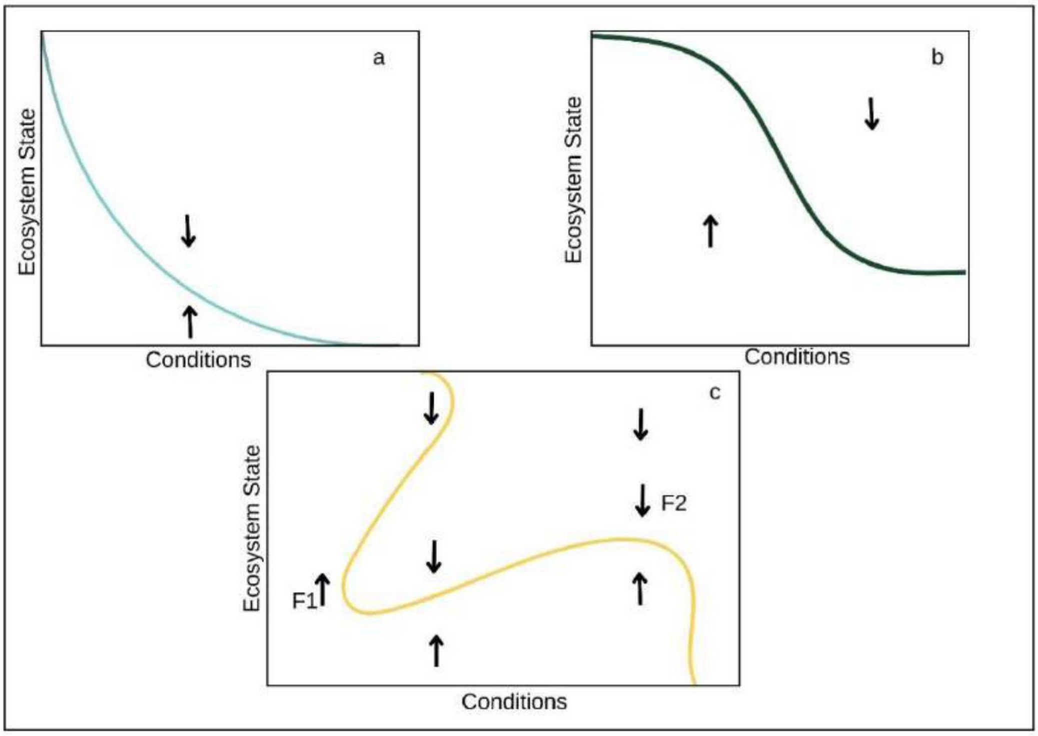

Figure 15. Forms of changes in an ecosystem undergoing a gradual increase in stress, adapted from Scheffer et al. (2000). Curve (a) represents a linear pattern with predictable environmental responses. Curve (b) is more complex, showing the ecosystem's ability to remain stable in the face of stress until it reaches a threshold point. Curve (c) is the most complex, occurring after surpassing the threshold point (F2), where the ecosystem may enter a new cycle and not return to its original state.

Within this context, epiphyllous bryophytes represent a group highly sensitive to environmental changes due to their physiology and dependence on specific microhabitats (Mežaka et al., 2020; Jiang et al., 2018; Pócs et al., 2011). These species use plant surfaces, such as leaves, as substrates for their growth and development (Vanden Berghen, 1973). However, variations in temperature and humidity can alter the structure and composition of these plant surfaces, modifying the availability and quality of habitats for epiphyllous bryophytes (Gignac, 2009; Zotz and Bader, 2008). This process can trigger a cycle of irreversible changes, in which more sensitive epiphyllous bryophyte species are replaced by other species more tolerant of the new climatic conditions, compromising the resilience and balance of forest ecosystems (Zanatta et al., 2020; Alvarega and Pôrto, 2006).

The survival of epiphyllous bryophytes is directly linked to the stability of climatic variables and the integrity of the habitats provided by phorophytes (Hu et al., 2021; Mežaka et al., 2020). Thus, the loss of suitable microhabitats due to climate change can lead to a sharp decline in their populations, resulting in a nonlinear change in ecosystems (Holling, 1973; Scheffer et al., 2000). Ecological Niche Models (ENMs) are tools that can be applied to help understand the impacts of future climate change on the distribution of epiphyllous bryophytes (Guisan et al., 2017; Soberón and Peterson, 2005). By associating environmental conditions with species occurrence, ENMs may allow the identification of biotic and abiotic factors important for species and help predict how the geographic distribution may be altered with climate change (Elith and Leathwick, 2009; Soberón and Peterson, 2005).

To evaluate the climatic impacts on epiphyllous bryophyte species, this study uses specific phorophytes and phorophyte richness as variables in the ecological niche models (ENMs) to predict the future distribution of species. The inclusion of these factors allows for a more accurate approach in assessing the vulnerability of epiphyllous bryophytes, as the availability and diversity of phorophytes play an important role in their distribution and persistence (Zotz and Hietz 2001). Therefore, we aim to answer the following questions: i) How do interactions with phorophytes influence future projections of the distribution of epiphyllous bryophytes under different climate scenarios? ii) does dependence on specific phorophytes make epiphyllous bryophytes more susceptible to climate change? iii) does the interaction between climatic variables and phorophytes influence vulnerability patterns of epiphyllous bryophytes?

It is expected that the results will contribute to a better understanding of the importance of specific phorophytes and phorophyte richness in the distribution and vulnerability of epiphyllous bryophytes in the Atlantic Forest in the face of future climate change, reinforcing the need for conservation strategies that consider not only bryophyte species but also the integrity of phorophytes.

MATERIAL AND METHODS

Ecological Niche Models (ENMs) (Soberón and Peterson, 2005; Guisan et al., 2017; Elith and Leathwick, 2009) were used, employing the kuenm2 package (Cobos et al., 2024). The study methodology was divided into three main stages: i) obtaining and processing climate data. In this stage, future climate variables from WorldClim for SSP 245 and SSP 585 emission scenarios were obtained, using global climate models (GCMs) MIROC6, HadGEM3-GC31-LL, and MPI-ESM1-2-HR. The choice of GCMs was based on the improved quality and resolution of the models providing a better representation of climate system responses, which is of great interest for vulnerability impact assessment studies (Stouffer et al., 2017). Current climate variations were also obtained and organized, including information on phorophyte richness; ii) ecological niche modeling (ENMs), where the distribution models of epiphyllous bryophyte species were adjusted using current climate variations and then projected for the future (2081-2100); iii) model evaluation and suitability change analysis, in which consensus among the GCMs was obtained regarding the gain, loss, and stability of suitable areas for the species.

Obtaining and Processing Climate Data

Species Distribution Models (ENMs) were developed for six species of epiphyllous bryophytes. These models allowed the evaluation of how the presence of specific phorophytes and phorophyte diversity influence environmental suitability for bryophytes in the Atlantic Forest under a climate change scenario. The species was chosen based on the following inclusion criteria: i) stable taxonomy; ii) having at least eight occurrence points; iii) relationship with the phorophyte known in the literature (Silva et al., 2025). Future climate variations were downloaded using the geodata package

(Hijmans et al., 2024) with the 'cmip6_world' function, encompassing three global circulation models (GCMs): MIROC6, HadGEM3-GC31-LL, and MPI-ESM1-2-HR for the future period 2081-2100, with SSP 245 and SSP 585 emission scenarios and a resolution of 2.5 minutes (~ 4.5 km) (Fick and Hijmans, 2017; IPCC, 2014). Using multiple models within a set is generally more effective for evaluating variability among earth system models (Homsi et al., 2020).

Climate variation and calibration area were delimited for each species by applying the M hypothesis, which defines the areas accessible to species in ecological time, considering environmental barriers and biogeographical limits (Barve et al., 2011). In addition to future climate variables, current climate variations were integrated with phorophyte richness and specific phorophyte data. Model validation for the species' region of interest is essential as it allows evaluating how well these models represent the current climate (Raju and Kumar, 2020).

Ecological Niche Modeling (ENMs)

ENMs were developed using the *kuenm2* package (Cobos et al., 2024). To generate projections of future epiphyllous bryophyte distributions, a distribution model was adjusted using current climate variations, serving as a calibration base. Then, projected future variables were incorporated, allowing the projections for the years 2081-2100 to be made based on different emission scenarios and GCMs. This process enables comparison of the predictions with observed values, providing an indication of the differences between predicted and real values (Hanke et al., 2001).

In addition to climate temperatures, information about phorophyte richness and specific phorophytes for each projection period was included. These additional variables were used to refine projections, considering that the interaction between epiphyllous bryophytes and phorophytes can influence habitat suitability for the species (Mežaka et al., 2020). To ensure that all variables have the same spatial resolution, a re-sampling process of the variable layers was performed, adjusting them to the same size and format as the climate variations.

Model Evaluation

The evaluation of the generated models involved habitat suitability analysis and quantification of species vulnerability to future climate changes, using different habitat indicators such as suitable area. The binarization of models was done by applying a threshold of 10% of suitability on presence points, where areas with values higher than this threshold were considered suitable for bryophyte species occurrence. The binarized model was then limited to the calibration area by applying the M hypothesis, specifically within the Atlantic Forest. This procedure ensures that the habitat suitability analysis is restricted to areas where the species is potentially present, excluding regions outside the Atlantic Forest.

For each binarized model, the total suitable area for the species was calculated. The area was determined by summing the binary values (1 for presence, 0 for absence) multiplied by the spatial resolution of the raster, resulting in the total area in square units. Additionally, a fragmentation analysis was performed to identify the number of habitat fragments (patches) using the ‘patches’ function from the terra package. Small fragments may indicate isolated areas or areas difficult for species dispersal (Ribeiro, 2009).

Future suitability richness was calculated considering that, for an area suitable for the species, at least one GCM should indicate that the area was in a favorable state, i.e., stable or gaining. For this, the suitability rasters for the future climate scenarios (SSP245 and SSP585) were binarized, assigning the value 1 to the areas that corresponded to suitable sites (presence) and the value 0 to the other areas. Areas with missing data (NA) were ignored. Finally, a suitability richness was obtained by summing the suitable areas for all bryophyte species in each climate scenario, providing an estimate of the total habitat suitability for the species in the future.

A vulnerability index was calculated for each binarized raster, considering the suitable area and the number of fragments (Liu et al., 2013). This index helps identify habitat quality, where higher values indicate lower vulnerability (greater suitable area and less fragmentation), and lower values indicate higher vulnerability (less suitable area and more fragmentation). The index was calculated using the following formula:

$$Vulnerability\ Index = \frac{(Suitable\ Area)}{(Number\ of\ Fragments)}$$

Finally, to verify whether there are significant differences in the vulnerability index across the different scenarios, a Kruskal-Wallis test was performed, a non-parametric analysis used to compare vulnerability indices between independent groups (Kruskal and Wallis, 1952).

RESULTS

Our analyses suggest that although there are some visible variations between the scenarios, they are not sufficient to justify a significant difference in vulnerability indices among them (p = 0.39) (Fig. 16).

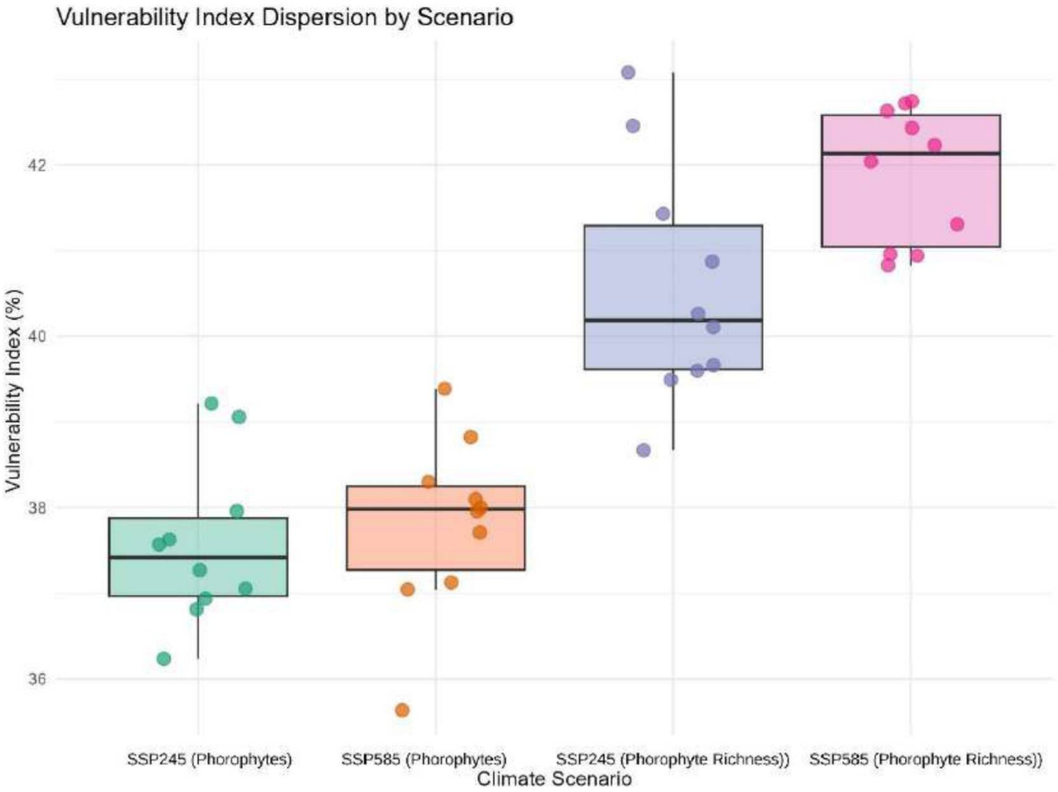

Figure 16. Vulnerability Index Distribution by Climate Scenario: Boxplots representing the distribution of the vulnerability index (%) for different climate scenarios (SSP245, SSP245 with specific phorophytes, SSP585, and SSP585 with phorophyte richness).

The availability of phorophytes was identified as an important variable for many species. For *Cyclolejeunea convexistipa* (Fig. 17), the SSP 245 scenario, considering specific phorophytes, presented a larger suitable area (27.57 km^2) compared to the scenarios that considered phorophyte richness in the same scenario (Table 4). This suggests that phorophyte richness plays a secondary role in the distribution and vulnerability of the species, resulting in no significant variations in the vulnerability indices between the scenarios tested. The loss of suitability (Fig. 17B e 17C) indicates that the species may experience significant changes in its geographic distribution in the future, being more vulnerable in more extreme climate scenarios.

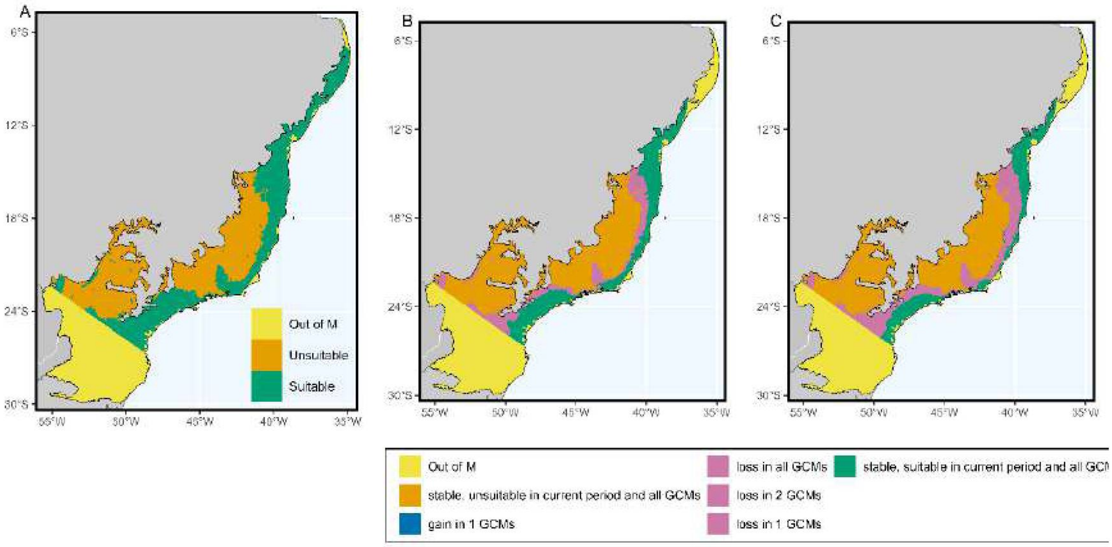

Figure 17. Habitat suitability for *Cyclolejeunea convexistipa* under different climate scenarios. (A) Current suitability considering climate temperatures. (B) Future suitability (SSP245) considering climate variables from three GCMs and the interaction with phorophytes. (C) Future suitability (SSP585) considering climate variables from three GCMs and the interaction with phorophytes.

The same pattern was observed for *Cololejeunea subcardiocarpa* (Fig. 18B and 18C), where data analysis revealed that the availability of specific phorophytes is the most important variable for environmental suitability and vulnerability of the species in response to climate change. In both climate scenarios (SSP 245 and SSP 585), the species showed a larger suitable area when specific phorophytes were considered (Table 4), suggesting that *Cololejeunea subcardiocarpa* is more vulnerable to more severe climatic conditions when the availability of specific phorophytes decreases.

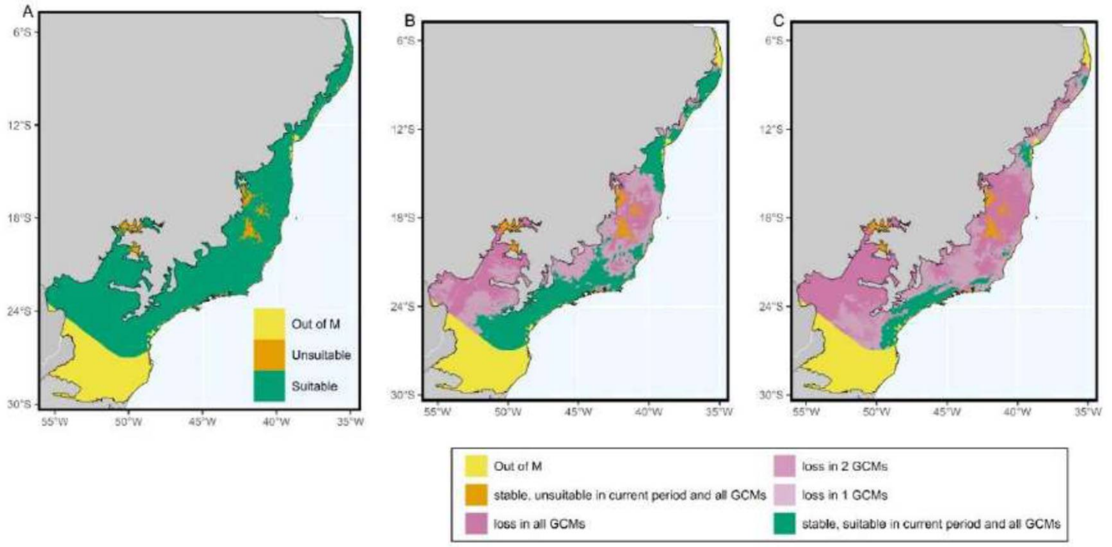

Figure 18. Habitat suitability for *Cololejeunea subcardiocarpa* under different climate scenarios. (A) Current suitability considering climate temperatures. (B) Future suitability (SSP245) considering climate variables from three GCMs and the interaction with phorophytes. (C) Future suitability (SSP585) considering climate variables from three GCMs and the interaction with phorophytes.

For the species *Diplasiolejeunea rudolphiana* , a suitable area was also observed in scenarios that considered specific phorophytes (Table 4). In the SSP 245 scenario, the suitable area was 69.34 km², while the SSP 585 scenario reduced (Fig. 19B e 19C) this area to 58.47 km², indicating an increase in vulnerability as climatic conditions become more severe.

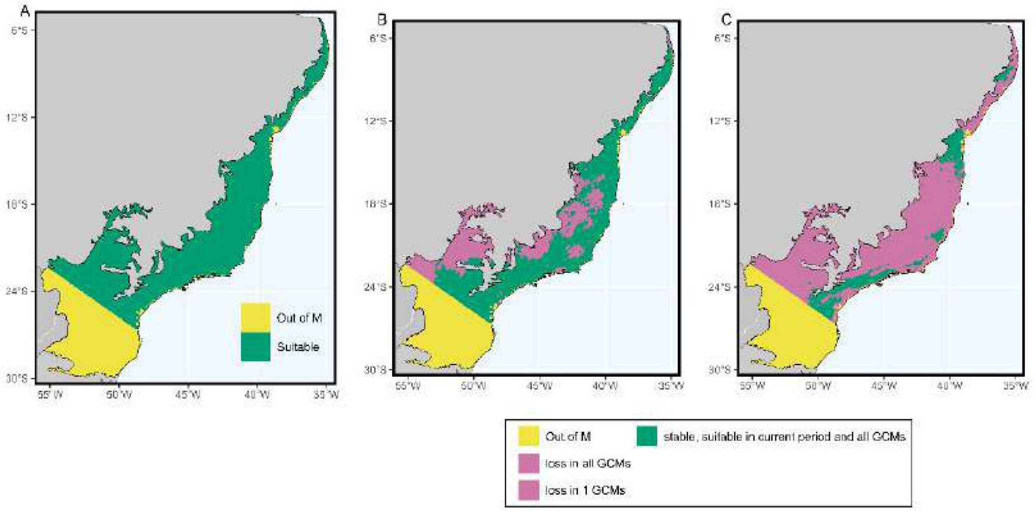

Figure 19. Habitat suitability for *Diplasiolejeunea rudolphiana* under different climate scenarios. (A) Current suitability considering climate temperatures. (B) Future suitability (SSP245) considering climate variables from three GCMs and the interaction with phorophytes. (C) Future suitability (SSP585) considering climate variables from three GCMs and the interaction with phorophytes.

On the other hand, for *Cololejeunea cardiocarpa* (Fig. 20), *Drepanolejeunea mosenii* (Fig. 21), and *Lejeunea adpressa* (Fig. 22), a larger suitable area was observed in scenarios that considered phorophyte richness, compared to models adjusted with only specific phorophytes (Table 4). This suggests that greater phorophyte diversity favors a wider distribution for these species. For *Cololejeunea cardiocarpa*, in the SSP 245 scenario, the suitable area was about 88.17 km², while the same scenario with specific phorophytes presented a suitable area of 77.13 km². The same pattern was observed for *Drepanolejeunea mosenii* and *Lejeunea adpressa*, which showed larger suitable areas in SSP 245 when phorophyte richness was considered, with approximately 19.13 km² and 51.21 km², respectively.

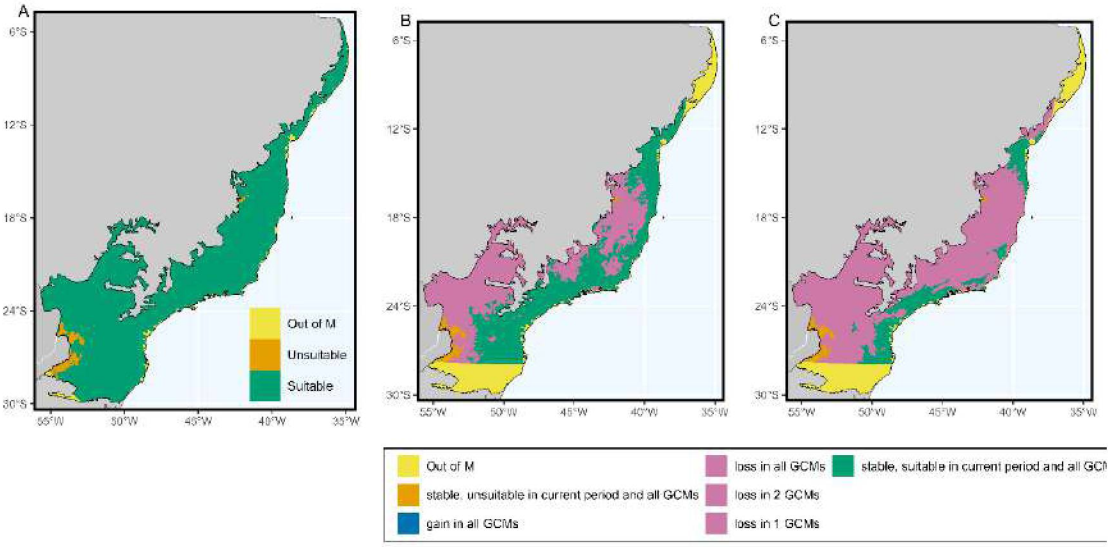

Figure 20. Habitat suitability for *Cololejeunea cardiocarpa* under different climate scenarios. (A) Current suitability considering climate temperatures. (B) Future suitability (SSP245) considering climate variables from three GCMs and the interaction with phorophytes. (C) Future suitability (SSP585) considering climate variables from three GCMs and the interaction with phorophytes.

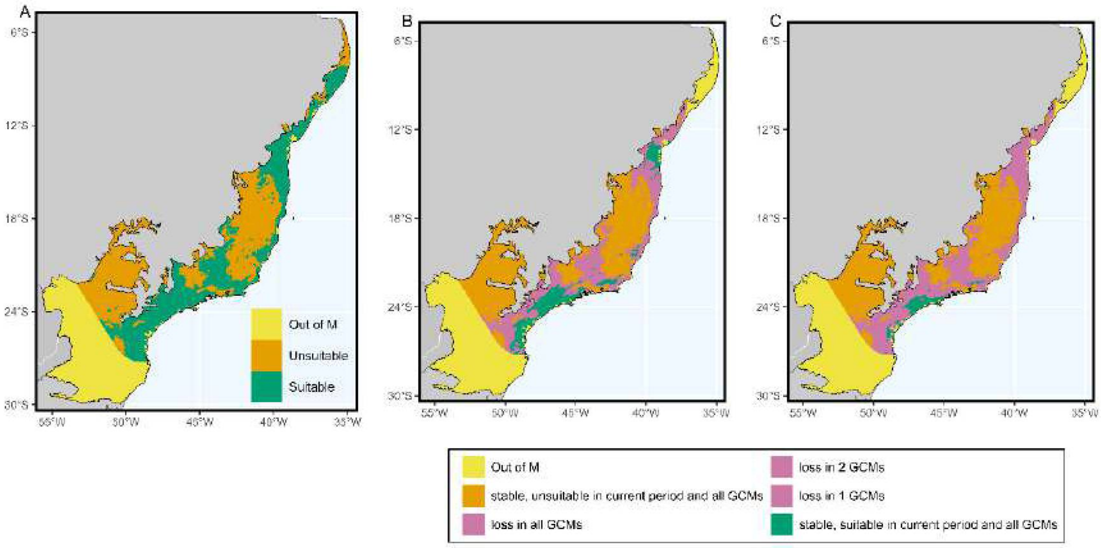

Figure 21. Habitat suitability for *Drepanolejeunea mosenii* under different climate scenarios. (A) Current suitability considering climate temperatures. (B) Future suitability (SSP245) considering climate variables from three GCMs and the interaction with phorophytes. (C) Future suitability (SSP585) considering climate variables from three GCMs and the interaction with phorophytes.

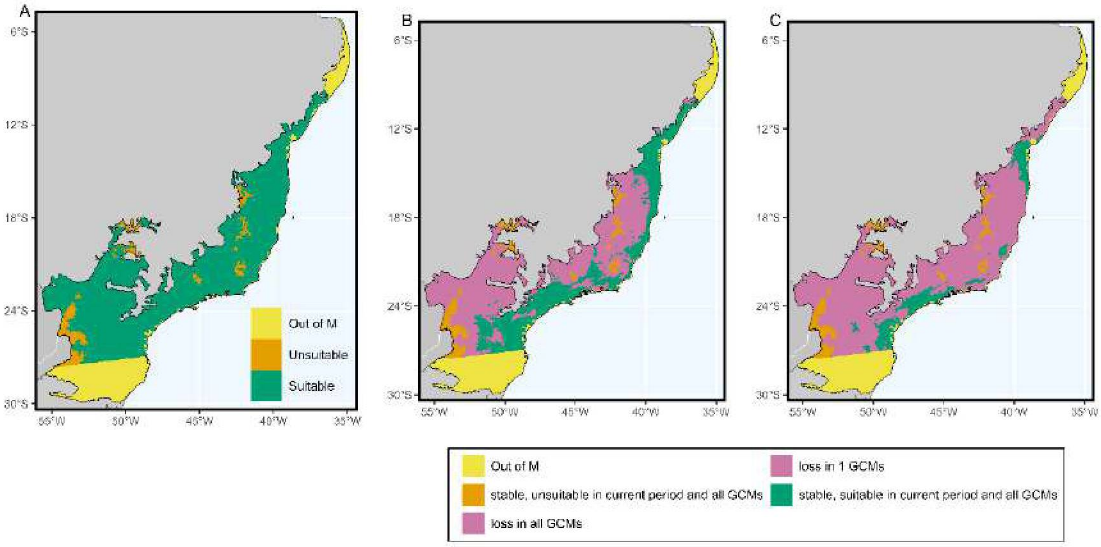

Figure 22. Habitat suitability for *Lejeunea adpressa* under different climate scenarios. (A) Current suitability considering climate temperatures. (B) Future suitability (SSP245) considering climate variables from three GCMs and the interaction with phorophytes. (C) Future suitability (SSP585) considering climate variables from three GCMs and the interaction with phorophytes.

The suitability wealth project reveals that as the climate changes, some areas that are currently unsuitable for epiphyllous bryophytes may become less suitable or even non-existent (Fig. 23), especially under more severe climate change scenarios, hindering the ability of bryophytes to maintain themselves in the environment.

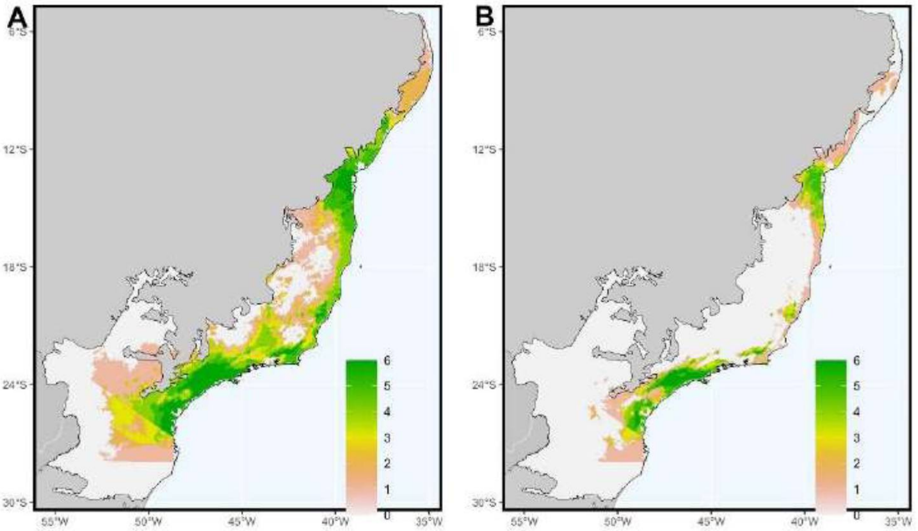

Figure 23. Suitability richness of bryophyte species under different future climate scenarios. (A) Suitability richness in the future (SSP 245). (B) Suitability richness in the future (SSP 585). The color scale indicates suitability richness, with higher values (green) representing areas with greater suitability for the species and lower values (orange and pink) representing areas with lower suitability.

DISCUSSION

In this study, we present a comparative approach that evaluates the influence of the availability of specific phorophytes and phorophyte richness on the environmental suitability and vulnerability of epiphyllous bryophytes in the Atlantic Forest, considering future climate change scenarios. The use of Ecological Niche Models (ENMs) was crucial for enhancing the understanding of how different biotic and abiotic variables affect the distribution and survival of epiphyllous bryophytes under future climate scenarios.

Our results suggest that the availability of specific phorophytes plays a crucial role in environmental suitability and species vulnerability, especially for more specialized species, such as *Cyclolejeunea convexistipa* and *Cololejeunea subcardiocarpa*. Ecological specialization in defining suitability areas may reflect deep ecological adaptation, allowing bryophytes to explore highly specialized habitats (Naranjo et al., 2019). This specificity in ecological interactions is important for the development and maintenance of epiphyllous and epiphytic species (Silva et al., 2025; Zotz and Hietz, 2001).

However, highly specialized species may become more vulnerable in a future climate scenario, as the availability of specific habitats may be significantly reduced due to climate change. This occurs because the structural homogenization of phorophytes limits colonization opportunities and protection against external factors, with less complex habitats (Hoerber and Zotz, 2022; Mežaka et al., 2020; Tews et al., 2004).

On the other hand, for species like *Cololejeunea cardiocarpa, Drepanolejeunea mosenii,* and *Lejeunea adpressa*, phorophyte richness has a positive impact on environmental suitability, indicating that greater phorophyte diversity allows for a wider distribution and greater resilience to climate change. Phorophyte diversity provides epiphyllous bryophyte species with a higher probability of having their ecological needs met (Gignac, 2009; Gradstein, 1997). Therefore, phorophyte diversity may act as an adaptability mechanism that allows epiphyllous bryophytes to spread across a wider range of microhabitats and survive more extensive climatic variations (Ruiz and Ceballos, 2004).

In terms of vulnerability, despite visible differences between the specific areas and indices, our results suggest that the interaction between specific phorophytes and phorophyte richness did not lead to a substantial difference in the vulnerability of epiphyllous bryophytes, which may be explained by the functional proximity of these two variables (Mouchet et al., 2010). This finding relates to existing literature discussing the complex interaction between biotic and abiotic variables and how these interactions can be difficult to model in complex ecological systems (Thuiller et al., 2005; Barlow et al., 2018). Thus, the ability of epiphyllous bryophytes to adapt to different climatic conditions may, therefore, be influenced by factors beyond the mere presence of phorophytes (Naranjo et al., 2019; Jiang et al., 2018), or the dispersal capacity of phorophyte species, factors that can be harder to quantify and model.

In accordance with the Ecological Resilience Theory (Holling, 1973), the results suggest that for many species of epiphyllous bryophytes, the ecological system may not have reached a critical vulnerability point yet, and climate change may be causing a nonlinear response, following either curve b or c (Scheffer et al., 2000). However, for species more specialized in specific phorophytes, such as *Cyclolejeunea convexistipa* and *Cololejeunea subcardiocarpa*, severe changes in climatic conditions may cause a tipping point, leading to greater vulnerability.

Thus, our results emphasize the importance of considering multiple biotic factors, such as the interaction between phorophyte diversity and climatic conditions, in assessing species vulnerability (Silva et al., 2025; Löffler and Pape, 2019). This type of modeling can significantly contribute to the conservation of epiphyllous bryophytes by helping to identify the most specific areas and conditions for species persistence, allowing for targeted conservation and management strategies (Diniz-Filho et al., 2012).

For effective conservation of the biodiversity of epiphyllous bryophytes in the Atlantic Forest in the face of climate change, it is necessary to protect and restore phorophytes throughout the Atlantic Forest, preserving both specialized species and those requiring greater phorophyte diversity. Future studies could expand this understanding by incorporating additional variables, such as bryophyte dispersal dynamics and interaction with other ecosystem species. Furthermore, the use of more refined predictive models can also provide crucial information for adaptive management strategies, involving not only the protection of epiphyllous species but also the maintenance of forest ecosystem resilience in response to future climate change.

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TABELAS

Table 4. Data on environmental suitability and vulnerability of epiphyllous bryophytes.

Species	Variables/SSP	Suitable área (Km^2)	Patches	Vulnerability index
Cololejeunea cardiocarpa	Phorophytes-SSP245	77.13715	4	19.28429
	Phorophytes-SSP585	57.40278	4	14.35069
	Phorophyte Richness-SSP245	88.17014	4	22.04253
	Phorophyte Richness-SSP585	67.99132	4	16.99783
Cololejeunea subcardiocarpa	Phorophytes-SSP245	59.34201	4	14.8355
	Phorophytes-SSP585	41.11111	4	10.27778
	Phorophyte Richness-SSP245	59.34201	4	14.8355
	Phorophyte Richness-SSP585	41.11111	4	10.27778
Cyclolejeunea convexistipa	Phorophytes-SSP245	27.56597	4	6.891493
	Phorophytes-SSP585	23.75868	4	5.93967
	Phorophyte Richness-SSP245	27.51042	4	6.877604
	Phorophyte Richness-SSP585	24.67188	4	6.167969
Diplasiolejeunea rudolphiana	Phorophytes-SSP245	69.34201	4	17.3355
	Phorophytes-SSP585	58.47049	4	14.61762
	Phorophyte Richness-SSP245	66.04514	4	16.51128
	Phorophyte Richness-SSP585	53.2691	4	13.31727
Drepanolejeunea mosenii	Phorophytes-SSP245	17.59549	4	4.398872
	Phorophytes-SSP585	11.7934	4	2.948351
	Phorophyte Richness-SSP245	19.13021	4	4.782552
	Phorophyte Richness-SSP585	12.34375	4	3.085938
Lejeunea adpressa	Phorophytes-SSP245	50.65278	4	12.66319
	Phorophytes-SSP585	37.7934	4	9.448351
	Phorophyte Richness-SSP245	51.21875	4	12.80469
	Phorophyte Richness-SSP585	38.18229	4	9.545573

6. CONSIDERAÇÕES FINAIS

O estudo realizado trouxe importantes *insights* sobre os fatores bióticos e abióticos que modulam os padrões de diversidade e a distribuição das briófitas epífilas em florestas tropicais úmidas, apesar do incipiente aporte teórico sobre como se dão as relações de interação entre este grupo de plantas e seus forófitos. Entretanto, o entendimento sobre o papel relativo dos fatores biológicos e ambientais para explicar os padrões de distribuição e a persistência das briófitas epifilas ao longo da Mata Atlântica ainda apresenta vieses decorrentes de aspectos metodológicos de coleta (Frahm, 2003), da incompletude das informações disponíveis nas base de dados virtuais (Fioravanti, 2020) e da baixa disponibilidade de especialistas desenvolvendo estudos que levem em consideração os aspectos biológicos das espécies e suas interações com os forófitos.

Os resultados obtidos neste estudo mostram a importância de fatores ambientais como a umidade atmosférica e as características do forófitos para determinação do padrão de distribuição das briófitas epífilas. A redução de precipitações, associada às mudanças climáticas, pode limitar a área de distribuição dessas espécies, especialmente aquelas com requisitos ecológicos muito específicos (Patiño et al., 2016; Tuba et al., 2011). Além disso, a dependência de algumas espécies de briófita epífilas por microhabitats específicos, como as folhas de certos forófitos (Silva et al., 2025), aumenta a vulnerabilidade da espécie às alterações nos padrões climáticos e na disponibilidade de hospedeiros.

A fragmentação habitat e as mudanças no uso do solo, podem reduzir a disponibilidade de forófitos adequados, representando riscos diretos para as espécies de briófitas, pois poderá limitar severamente a colonização e a sobrevivência dessas espécies. Além disso, a fragmentação pode isolar as populações, dificultando a troca genética e aumentando a vulnerabilidade das espécies a extinção local, uma vez que, a dispersão de esporos, fica restrita a áreas menores e mais isoladas (Santos et al., 2023).

Em decorrência disso, que o uso de tecnologias mais avançadas, como a modelagem preditiva, pode ajuda a entender melhor os fatores ambientais que influenciam na distribuição dessas plantas e a identificar as áreas prioritárias para a sua conservação. Por essa razão, as perspectivas futuras para esta pesquisa envolvem a continuidade no desenvolvimento de modelos preditivos para outras espécies de briófitas epífilas, com o objetivo de expandir a compreensão sobre a distribuição geográfica e padrões ecológicos dessas plantas. A construção de modelos preditivos mais refinados, combinando dados abióticos e bióticos, será fundamental para uma visão mais específica das necessidades ecológicas das espécies e de como elas podem responder as mudanças climáticas e aos impactos causados pelas ações humanas.

Portanto, a criação de um banco de dados abrangente, que reúna informações sobre a distribuição das briófitas epífilas e suas interações com o ambiente, poderá ser uma ferramenta valiosa para futuras pesquisas. A integração dessas informações ajudará a preencher as lacunas de conhecimento existentes e fornecerá dados importantes para a conservação e gestão de briófitas epífilas, contribuindo significativamente para a preservação da biodiversidade da região. Além disso, a escassez de informações sobre a distribuição geográfica das espécies de briófitas epifilas e suas interações ecológicas pode ser reflexo da predominância de estudos taxonômicos dentro do grupo, bem pode estar associada ao baixo número de estudos que considerem escalas amostrais mais amplas e incluam áreas ainda pouco exploradas, como aquelas localizadas na região sul do Brasil (Silva et al., 2025). Ademais, o investimento na capacitação de botânicos e ecologistas é um fator crucial para o avanço nas pesquisas e inventários detalhados sobre o grupo e, consequentemente, para o fortalecimento da compreensão sobre a ecologia e a dinâmica das populações de briófitas epífilas, colaborando para a implementação de políticas públicas mais práticas para conservação dessas espécies.

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