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ECOSYSTEMS

Distribution pattern in the rupiculous genus *Orthophytum* (Bromelioideae/ Bromeliaceae) reveals high microendemicity in different types of rocky outcrops

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Abstract: This study aimed to recognize the biogeographic patterns, richness, and diversity levels of the Brazilian endemic genus Orthophytum and identify their biotic components through a parsimony analysis of endemicity (PAE), to better understand the evolutionary history of this group and develop strategies for the conservation of its species. We prepared a database for the 54 currently known species of Orthophytum, including their geographical locations as obtained from digital databases of the principal herbaria of Brazil, Europe, and the USA. A parsimony analysis of endemicity (PAE) was used to delimit the areas of endemism based on two grids' sizes (1º x 1º and 2º × 2º). The majority rule consensus tree resulting from the PAE indicated three areas of endemism with high bootstrap, diversity, and richness indices: the northern portion of the Espinhaço Range, the southern portion of the Espinhaço Range, and the central portion of the Atlantic Forest. The recognition of those distribution patterns reveals a high number of microendemic species, which is discussed here.

Key words: Bromelioideae, Areas of Endemism, Rocky outcrops, Microendemism, PAE, Poales.

INTRODUCTION

The patterns and processes of biotic distribution, also known as biogeographic patterns (Morrone 2009), play important roles in understanding the evolution of biodiversity, and represent essential elements for the reconstruction of the Earth's geological history. Those patterns are related to the organization and distribution of groups of organisms in geographic space, which can be approached in many different ways as well as at different scales. Important historical and biogeographic factors are believed to influence those patterns, such as dispersal, vicariance, and extinction (Morrone 2009). Additionally, diverse ecological processes may also play relevant roles in shaping the geographic distributions of plants observed today (Wiens & Donoghue 2004) – with environmental factors affecting their spatial distributions and consequently their richness and species compositions. It is therefore necessary to analyze multiple variables in biogeographic studies, such as water availability, elevation, temperature, and edaphic features (Pausas & Austin 2001, Austin 2013), as those climatic or physical features can function as barriers that prevent certain organisms from colonizing certain habitats (Wiens & Donoghue 2004, Wiens 2011).

One of the tools used in historical biogeography to investigate the natural distribution patterns of organisms is Parsimony Analysis of Endemicity (PAE) (e.g., Silva & Oren

1996, Posadas & Miranda-Esquivel 1999, Garcia-Barros et al. 2002, Manrique et al. 2003, Rovito et al. 2004, Sigrist & Carvalho 2008). PAE basically consists of classifying areas of endemism and constructing cladograms based on the parsimonious cladistic analysis of presence-absence matrices of species. An area of endemism is defined when the distributions of different endemic species converge to the same region (Morrone 1994, Szumik et al. 2002). The identification of such areas provide important information for the field of biogeography and for studies of biodiversity conservation, and can contribute to effective conservation planning. Congruent occurrence patterns can easily be recognized where endemic species (those found only in an exclusive region) are frequent, and can be delimited to propose areas of endemism and then analyze their inter-relationships (Szumik et al. 2002, Morrone 1994).

The Neotropical biogeographical region (which stretches from Mexico to southern South America) comprises tremendous taxonomic and habitat diversity as well as a complex geological history (Morrone 2009). Most studies of distributional patterns and areas of endemism in this region have been based on relatively well studied animal groups (see Cracraft 1985, Silva 1995, Amorim & Pires 1996, Ron 2000, Costa et al. 2000, Silva & Oren 1996) or on tree species (see de Lima et al. 2020, Françoso et al. 2016, ter Steege et al. 2013, 2015). Despite the crucial importance of non-tree plants for understanding biodiversity and ecosystem functioning, there are still large gaps in our knowledge of their distributions in the Neotropics. One of the most species-rich and ecologically important non-tree monocotyledonous families in the Neotropics – Bromeliaceae Juss. (Smith & Downs 1974). The family comprises 83 genera and approximately 3.744 species (Butcher & Gouda 2023, Last Access May 2023), and includes epiphytic, saxicolous, and terrestrial life forms that occupy a wide variety of habitats from sea level up to 4000 meters above sea level (masl) (Benzing 2000, Butcher & Gouda, Last Access May 2023).

One of the first divergent lineages of the Bromelioideae (the second largest clade of the family) to experience considerable diversification in (what is today) Brazil was the genus *Orthophytum* Beer, which is saxicolous (rarely terrestrial) and endemic to the eastern region of that country. *Orthophytum* comprises 54 species (Louzada 2020) that inhabit different types of rocky outcrops: granitic inselbergs in the Atlantic Forest and Caatinga domain and rocky quartzite outcrops in Campos Rupestres (rocky altitudinal fields) along the Espinhaço Range (Louzada & Wanderley 2010). Martinelli et al. (2008) indicated a possible center diversity of the genus in the Atlantic Forest, where its species usually inhabit inselbergs and rock outcrops and are often restricted to small geographic areas (with many microendemic taxa). Those environments, which are spatially and ecologically isolated, exhibit barriers to dispersal and migration, and evidence high levels of species diversity and endemism (Echternacht et al. 2011).

Studies of bromeliad species adapted to neotropical rock outcrops have already improved the understanding of speciation and the processes of endemicity in naturally isolated environments (Barbará et al. 2009, Palma-Silva et al. 2011). However, despite the immense importance of non-arboreal plants to understanding biodiversity, ecosystem functioning, and macroevolutionary and macroecological processes, there are still large gaps in the knowledge of how they are distributed in the Neotropics (Engemann et al. 2015).

In order to better understand the processes that led to the considerable diversification of *Orthophytum*, it will be necessary to use biogeographic reconstruction analysis and formulate hypotheses concerning the ancestral area of the genus, when it emerged, how its dispersal occurred, and how some species became fixed in restricted regions. Biogeography is used to document and understand the spatial patterns of biodiversity, species interactions and their organization, as well as spatial processes (Brown & Lomolino 1998, Troppmair 2002). Therefore, in addition to supporting an understanding of the evolution of different plant groups, biogeography can help reduce biodiversity losses by indicating potential areas for species preservation (Goldani 2012).

We tested here the hypothesis that the Espinhaço Mountain Range and the Atlantic Forest in Brazil are areas of endemism of *Orthophytum,* and that microendemism is the predominant pattern in the genus. To test that hypothesis, we sought to identify distribution patterns, richness, diversity, and use parsimony analysis of endemicity (PAE) to identify areas of endemism and their biotic components.

The identification of areas of endemism and testing them as evolutionary geographical units are the first steps towards the development of a cladistic biogeography. At the same time, biogeography can improve our knowledge of the evolutionary history of this group and help future researchers develop conservation strategies for its species.

MATERIALS AND METHODS

Taxa and Data collection

The geographic coordinates of *Orthophytum* specimens were obtained from the Global Biodiversity Information Facility (https://www.gbif.org/), CRIA-speciesLink (http://www.splink.org.br/) and Reflora Virtual Herbarium (http://floradobrasil.jbrj.gov.br/) digital databases, which include specimen records from the principal herbaria of Brazil, Europe, and the USA. Only specimens identified by specialists in the genus were used. The species included in the analysis followed the taxonomic revision of Louzada & Wanderley (2010) and the Species List of Brazilian Flora (Louzada 2020); the latter includes a new species described after the last revision. Records without original geographic coordinates were assigned to the location or municipality recorded on the specimen label. The geographic coordinates of the sample location or municipality were obtained from the GeoNames website (http://geonames.com) or by using the geoLoc tool (available from the Environmental Information Reference Center website [SpeciesLink - http://splink.cria.org.br/geoloc]). Records that could not be georeferenced to at least the municipality level, vouchers with dubious identifications or without collector number, as well as duplicates, were excluded from the dataset. After data cleaning, the dataset comprised 695 records of 54 species. The nomenclature of the species follows The International Plant Names Index (https://www.ipni.org/), Tropicos (https://www.tropicos.org/home), and New Bromeliad Taxon List digital databases (Butcher & Gouda continuously updated, last accessed in Dec 2022).

Grid size

The choice of grid cells size is decisive and important for biogeographic analysis. Several authors discussed how distinct grid sizes can affect the identification of the areas of endemism (see Morrone & Escalante 2002, Morrone 1994, Szumik et al. 2002, Casagranda et al. 2009, Navarro et al. 2009). Usually, the use of small grid cells results in discontinuous distributions, in a more detailed resolution (where only small areas of endemism are identified) and can produce poorly resolved area cladograms. Meanwhile, large grid cells generally detected larger areas of endemism, which increases the congruence of species (many species appearing as endemic) and could camouflage disjunctions (Morrone & Escalante 2002). Therefore, employing different grid sizes is the most suitable way to establish the results to recognize endemic areas and to be able to identify different patterns if some taxonomic groups display congruence at different scales (Aagesen et al. 2009, Casagranda et al. 2009, Navarro et al. 2009).

For all the analyses presented here (richness, diversity and PAE), we choose two sizes of grid cells, 1° x 1° (ca. 100 km x 100 km) and 2° x 2° (ca. 200 km x 200 km). The grid cells were produced using DIVA-GIS software (Hijmans 2001).

Richness and diversity analysis and distribution patterns

Richness and Diversity (Shannon Index; Magurran 1988) analyses were performed using DIVA-GIS software. The visualization of the species distribution, the maps construction and the visualization of the main conservation reserves was performed using QGIS software (QGIS Development Team 2021).

Distribution patterns were assessed based on the plotted dots on the maps, following Menini-Neto & Forzza (2013), and were coded as follows: (1) widespread distribution (WD), when encountered in more than five grid squares; (2) intermediate distribution (ID), when found in two to four grid squares; (3) restricted distribution (RD), when found in only one grid square, but with more than five known sites of occurrence; and (4) microendemic distribution (MED), when restricted and exclusive to a vegetation physiognomy and found in only one grid square and only one to four known sites of occurrence.

Endemicity analyses

Morrone (1994) proposed PAE as a tool to identify endemic areas as primary biogeographic homology, using grid cells as operational units (without inferring relationships or hierarchies between areas) based on their common species, defining an endemism area as a group of grid cells of at least two taxa endemic to the region.

We draw the grid-cells on a map of Brazil, including grids only where at least one locality of one species was recorded. Visualizations of the species were also performed using the QGIS software (QGIS Development Team 2021). Based on the occurrence of the species, a presence/absence matrix (Tables III and IV) was constructed using the software Mesquite, version 3.16. (Maddison & Maddison 2021), where the presence of a given taxon in each sampled area was coded as “1”, and the absence of that taxon was coded as “0”. A hypothetical area coded as “0” was added to the matrix as an outgroup to root the tree.

The PAE was conducted using PAUP* 4.0 software (Swofford 2003) to infer the centers of endemism and to reconstruct the most parsimonious tree, using a heuristic algorithm with 1000 replications from random additions and TBR (tree-bisection-reconnection) branch-swapping, saving two trees per replication; the same commands were used for bootstrap analysis.

Here, for more robust results, we define an endemism area when the clades in the consensus area cladograms received bootstrap support ≥ 50% and shared three or more species. The data matrix is available upon request to the corresponding author.

RESULTS

Patterns of geographic distribution, richness and diversity

We obtained a database with 692 records distributed among 54 species of *Orthophytum* using the parameters and methods described above. The distribution maps for all *Orthophytum* species are presented in Figures 4 – 10. Its species are endemic to eastern Brazil with the following limits: north, the municipality of Alcântaras, Ceara State (40°30’W, 03°34’S), where *O. cearense* Leme & F.Monteiro occurs; south, the municipality of Domingos Martins, Espírito Santo State (40°36’W, 20°21’S), where *O. foliosum* L.B.Sm. occurs; east, the municipality of Jaqueira, Pernambuco State (35°30’W, 08°25’S), where *O. disjunctum* L.B.Sm. occurs; and west, the municipality of Água Quente, Bahia State (44°18’W, 13°10’S), where *O. harleyi* Leme & M.Machado has been recorded. The species with the greatest numbers of records were *O. disjunctum*, *O. maracasense* L.B.Sm., and *O. foliosum* with 175, 86 and 70 records respectively. Four categories were established to represent the distribution patterns of these taxa: widespread, intermediate, restricted, and microendemic. Seven species evidenced widespread distribution patterns, 19 species have intermediated distributions, four species have restricted distributions, and 24 species evidenced a microendemic distribution pattern. The distribution patterns, number of grids, and the phytogeographical domain in which they occurred are presented in Table I for each species.

The richness analysis found 70 grids in 1° x 1° size and 26 grids in 2° x 2° size (Fig. 1). The regions with the greatest richness are represented by the grid squares A52 and A67 in the smaller grid size (comprising together 18 species, with 7 exclusives to those areas), which coincides with the areas in the larger grid size with the A20 and A26 areas with the greatest richness (comprising together 28 species, with 14 exclusives). These areas encompassing the central portion of the Espinhaço Range (in the north of Minas Gerais, grid A52 in smaller grid size and A20 in the larger one), and the inselbergs of Espírito Santo and its boundary with Minas Gerais (grid A67 in smaller grid size and A26 in the larger one). Even the grids with low to medium richness still included exclusive species, such as grids A17 (with one exclusive species), A31 (1 sp.), A38 (2 spp.), A43 (2 spp.), A54 (2 spp.), A58 (1 sp.), A63 (1 sp.), A66 (4 spp.) and A69 (2 spp.) in the smaller grid size and A10 (2 spp.), A13 (1 sp.), A17 (2 spp.), A18 (2 spp.), A21 (2 spp.), A23 (1 sp.) and A24 (3 spp.) in the larger grid size. Our results therefore indicated two main centers of *Orthophytum* species richness: the central portion of Espinhaço Range (CPER) and the central portion of the Atlantic Forest (CPAF).

The diversity analysis (Fig. 2) as the richness analysis also produced 70 grids in 1° x 1° size and 26 grids in 2° x 2° size. The regions with the greatest diversity are represented by grid squares A52, A58, A59 and A67 (with Shannon index H’ between 1.58 - 2.0) in the smaller grid size, encompassing the north and northeast of Minas Gerais and the inselbergs of Espirito Santo. The larger grid size has the A17, A18, A20, A21 and A26 areas with high diversity (H’ between 1.77 - 2.19), encompassing the central portion of Espinhaço Range (in the north and northeast of Minas Gerais and south of Bahia) and the inselbergs of Espirito Santo and its boundaries with Minas Gerais. In summary, the main difference between the two analyses is found in areas A17 and A18 (in larger grid size) – the central portion of Espinhaço Range in Bahia – which presents a relatively reduced

Table I. **Distribution patterns of *Orthophytum* species with the associated vegetation and number of grids (in 2-degree grid size) that each species are present. CA: Caatinga; CE: Cerrado; AF: Atlantic Forest; MED: Microendemic Distribution; ID: Intermediated Distribution; RD: Restricted Distribution; WD: Widely Distribution.**

Species	Number of grids	Phytogeographical Domains	Distribution Pattern
Orthophytum alagoanum Leme & A.P.Fontana	1	CA	MED
Orthophytum alvimii W. Weber	2	CA, AF	ID
Orthophytum arcanum Leme	1	AF	MED
Orthophytum argentum Louzada & Wand.	1	CA	MED
Orthophytum atalaiense J.A.Siqueira & Leme	1	AF	MED
Orthophytum boudetianum Leme & L.Kollmann	1	AF	RD
Orthophytum braunii Leme	3	CA	ID
Orthophytum buranhense Leme & A.P.Fontana	1	AF	MED
Orthophytum cearense Leme & F.Monteiro	3	CA, AF	ID
Orthophytum conquistense Leme & M.Machado	2	AF	ID
Orthophytum cristaliense Leme	1	CE	MED
Orthophytum diamantinense Leme	2	CE	ID
Orthophytum disjunctum L.B.Sm.	9	CA, AF	WD
Orthophytum duartei L.B.Sm.	2	AF	ID
Orthophytum eddie-estevesii Leme	1	CA	MED
Orthophytum elegans Leme	2	AF	ID
Orthophytum erigens Leme	1	CA	MED
Orthophytum estevesii (Rauh) Leme	1	AF	MED
Orthophytum falconii Leme	4	CA, AF	ID
Orthophytum foliosum L.B.Sm.	5	CE, AF	WD
Orthophytum fosterianum L.B.Sm.	1	AF	MED
Orthophytum glabrum (Mez) Mez	2	CE, AF	ID
Orthophytum graomogolense Leme & C.C.Paula	2	CE, AF	ID
Orthophytum grossiorum Leme & C.C.Paula	1	AF	MED
Orthophytum guaratingense Leme & L.Kollmann	1	AF	MED
Orthophytum gurkenii Hutchison	2	AF	ID
Orthophytum harleyi Leme & Machado	3	CA	ID
Orthophytum horridum Leme	5	CA, AF	WD
Orthophytum jabrense G.S.Baracho & J.A.Siqueira	2	CA, AF	ID
Orthophytum jacaraciense Leme	1	CA	MED
Orthophytum lanuginosum Leme & C.C.Paula	1	AF	MED
Orthophytum lemei E.Pereira & I.A.Penna	8	CA, AF	WD
Orthophytum leprosum (Mez) Mez	5	CA, CE, AF	WD
Orthophytum macroflorum Leme & M.Machado	1	CA	MED
Orthophytum magalhaesii L.B.Sm.	3	AF	ID
Orthophytum maracasense L.B.Sm.	7	CA, AF	WD
Orthophytum mello-barretoi L.B.Sm.	3	CE, AF	ID
Orthophytum minimum Leme & O.B.C.Ribeiro	1	CE	MED
Orthophytum piranianum Leme & C.C.Paula	2	CE	ID
Orthophytum pseudostoloniferum Leme & L.Kollmann	1	AF	MED
Orthophytum pseudovagans Leme & L.Kollmann	1	AF	RD
Orthophytum riocontense Leme	3	CA, AF	ID
Orthophytum roseolilacinum Leme	1	AF	MED
Orthophytum santaritense Leme, S.Heller & Zizka	1	AF	MED
Orthophytum santosianum Leme	2	CA, CE	ID
Orthophytum saxicola Ule	7	CA, AF	WD
Orthophytum schulzianum Leme & M.Machado	1	CE, AF	RD
Orthophytum sp. nov.	1	CA	MED
Orthophytum striatifolium Leme & L.Kollmann	1	AF	MED
Orthophytum sucrei H.Luther	1	AF	MED
Orthophytum toscanoi Leme	3	CA, CE	ID
Orthophytum triunfense J.A.Siqueira & Leme	1	CA	RD
Orthophytum vasconcelosianum Leme	1	AF	MED
Orthophytum zanonii Leme	1	AF	MED

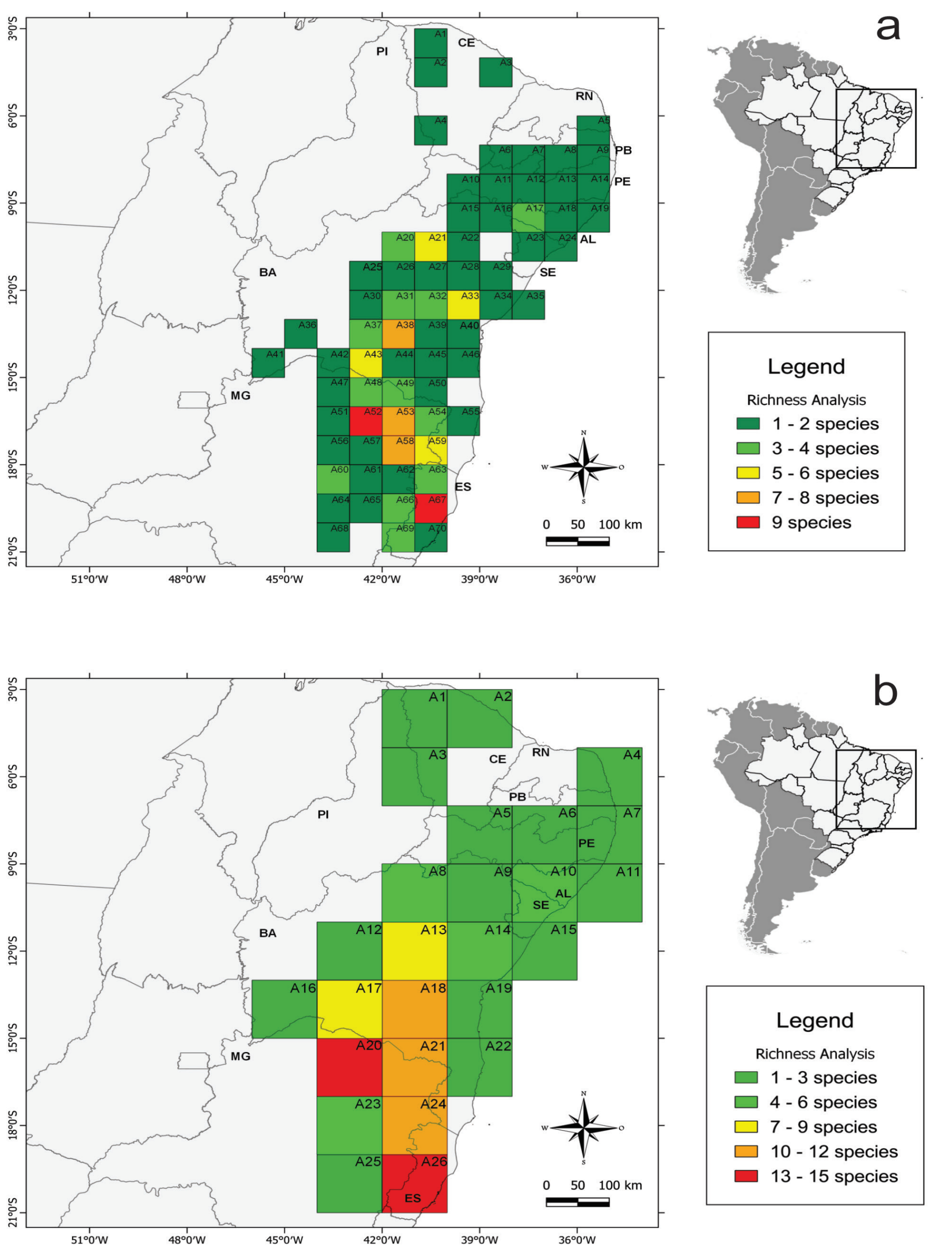

Figure 1. Richness map showing the analyses in 1-degree (a) and 2-degree (b) cells. PI: Piauí; CE: Ceará; PB: Paraíba; PE: Pernambuco; AL: Alagoas; SE: Sergipe; ES: Espírito Santo; BA: Bahia; MG: Minas Gerais.

richness (nine and ten species respectively) but high diversity (H' = 1.77 – 2.19). Therefore, our results indicate two main centers of diversity of *Orthophytum*: the Central Portion of Espinhaço Range (CPER) and the Central Portion of Atlantic Forest (CPAF).

Parsimony analysis of endemicity

As the same as the above analyzes, the total number of occupied areas (grid-cells) varied according to PAE quadrat size, 70 grid-cells in 1° x 1° and 26 in 2° x 2°, which both represent the entire distribution of the genus in Brazil.

For the 1-degree quadrat matrix, PAE produced 5000 equally parsimonious trees, with CI (consistency index) = 0.79 and RI (retention index) = 0.62, based on 28 parsimony-informative characters. The strict consensus tree (Fig. 3) revealed a basal polytomy for most areas, but

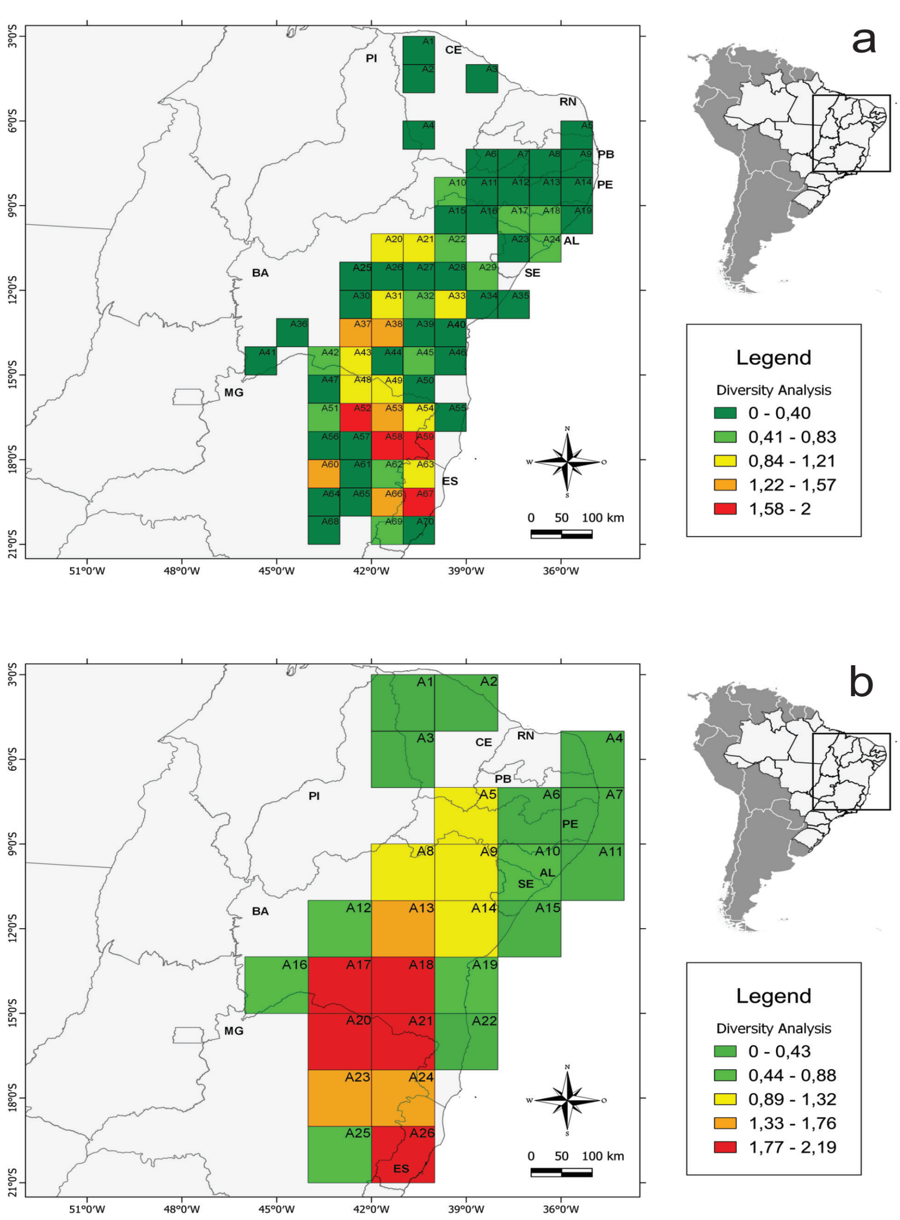

Figure 2. Diversity map showing the analyses in 1-degree (a) and 2-degree (b) cells. PI: Piauí; CE: Ceará; PB: Paraíba; PE: Pernambuco; AL: Alagoas; SE: Sergipe; ES: Espírito Santo; BA: Bahia; MG: Minas Gerais.

15 remaining quadrats were grouped into six minor clades – AFMG (Atlantic Forest of Minas Gerais), AFES (Atlantic Forest of Espírito Santo), NBA (North of Bahia), CD (Chapada Diamantina), GM (Grão Mogol) and CT (Caetité) and in three major ones – CPAF (Central Portion of Atlantic Forest), NER (North of Espinhaço Range) and CPER (Central Portion of Espinhaço Range). Thus, three major clades with bootstrap support ≥ 50% and three or more species shared can effectively be observed in this analysis and considered areas of endemism.

For the 2-degree quadrat matrix, PAE produced 1416 equally parsimonious trees, with CI = 0.71 and RI = 0.63, based on 24 parsimony-informative characters. The strict consensus tree (Fig. 3) also revealed a basal polytomy for 16 quadrats, but ten remaining quadrats were grouped into three major clades – CPAF, NER and SER (South of Espinhaço Range), considered areas of endemism.

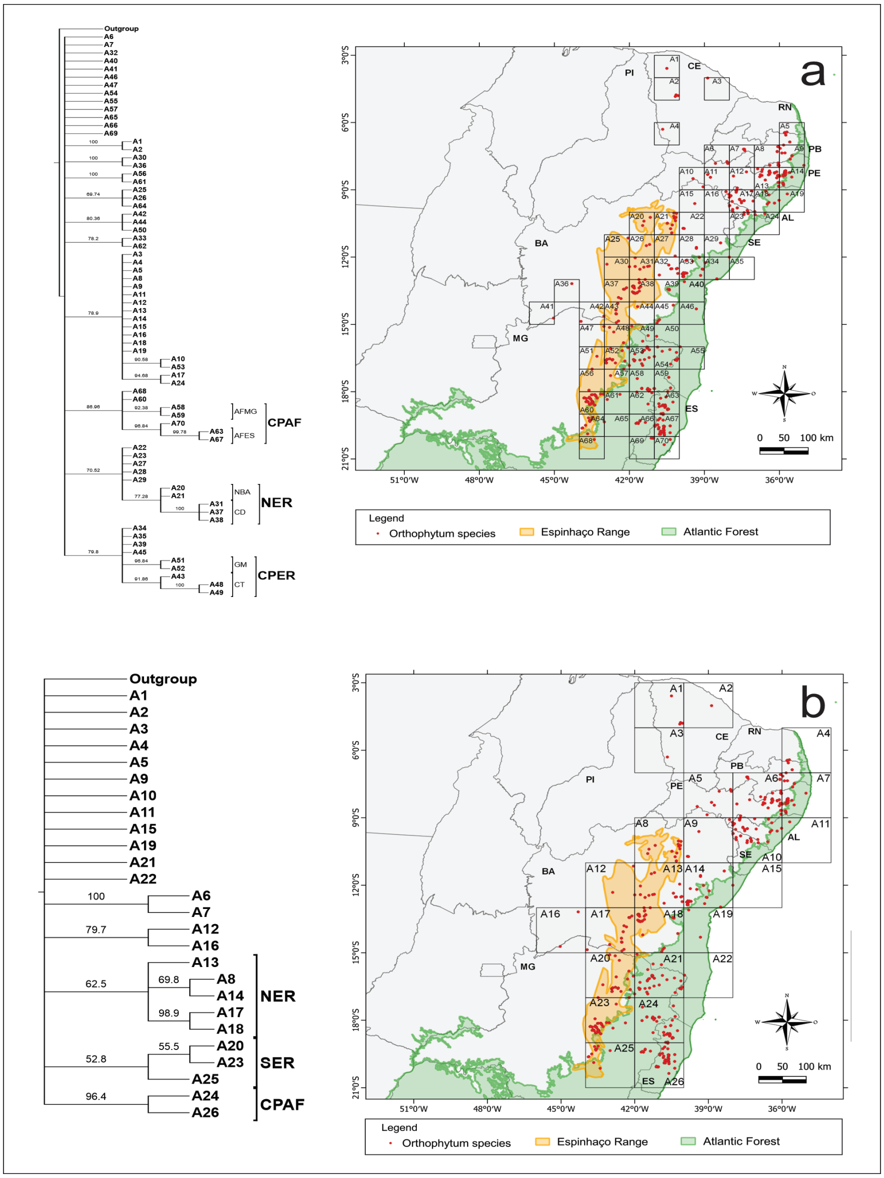

Figure 3. The majority rule consensus tree obtained with the 1-degree (a) and 2-degree (b) size cells analyses, showing the major and minor areas of endemism determined by PAE. Numbers under the lines indicate bootstrap proportions. AFMG: Atlantic Forest of Minas Gerais; AFES: Atlantic Forest of Espírito Santo; NBA: North of Bahia; CD: Chapada Diamantina; GM: Grão Mogol; CT: Caetité; CPAF: Central Portion of Atlantic Forest; NER: North of Espinhaço Range; CPER: Central Portion of Espinhaço Range; SER: South of Espinhaço Range; PI: Piauí; CE: Ceará; PB: Paraíba; PE: Pernambuco; AL: Alagoas; SE: Sergipe; ES: Espírito Santo; BA: Bahia; MG: Minas Gerais.

The results in both analyzes were similar, the 1-degree result shows a big basal polytomy, but recovered small clades that can be considered small endemism areas. The 2-degree result also shows a basal polytomy, but for being bigger quadrats, result in larger endemism areas. The areas NER and CPAF in both degrees are equivalent and the mainly difference between results analyses is in the areas CPER (1-degree) and SER (2-degree), southernmost areas of Espinhaço Range. The SER of 1-degree analysis covered areas even further south of Espinhaço Range than the CPER that covers the central region of Espinhaço Range, in the boundaries of Bahia and Minas Gerais states.

Therefore, as there were not so many significant differences between both analysis results, here, we will consider for purposes of description and discussion, the areas of endemism recovered from the 2-degree analysis: NER, SER and CPAF.

The first area considered is the northern region of the Espinhaço Range in Bahia State, formed by the grid groups A8, A13, A14, A17 and

A18, (with bootstrap = 62.5%) with five exclusive species. The second area is the South of Espinhaço Range in Minas Gerais, formed by the grid group A20, A23 and A25 (bootstrap = 52.8%), also with five exclusive species. The last area, with the highest number of exclusive species (13), is the Central Portion of the Atlantic Forest located in Espirito Santo and on the boundary with Minas Gerais, formed by the grid group A24 and A26 (bootstrap = 96.4%).

DISCUSSION

As previously mentioned, many authors define an area of endemism when the distribution of two or more species converge to the same region and do not occur anywhere else (Morrone 1994, Garcia-Barros et al. 2002, Platnick 1991). Such a region will evidence a higher-than-expected endemism when compared to adjacent regions (Crisp et al. 2001, Laffan & Crisp 2003). Due to the high number of microendemic species and species known for only one location, we decided to define here an endemism area when the clades resulted in the consensus area cladograms from PAE analysis received bootstrap support ≥ 50% and shared three or more species.

The identification of areas of endemism is important for reconstructing the historic and ecological biogeography of taxa, as well as for biodiversity conservation (Szumik 2002, Echternacht et al. 2011). This is because the delimitation of areas of endemism allows the identification of priority areas for conservation that harbor unique concentrations of biodiversity (Myers et al. 2000, Williams et al. 2002) and represent independent geographic units. The analysis of the relationships between those areas will generate information about the processes responsible for their formation (Anderson 1994, Morrone 1994, Laffan & Crisp 2003).

In this study, smaller grid sizes result in a finer resolution of distributional patterns and smaller individual areas of endemism but show a big basal polytomy (Fig. 3). Linder (2001) argues that the disadvantage of smaller grid sizes is that they would lead to an increase in the number of false absences. Nelson et al. (1990) showed that the detection of centers of endemic plant species in the Brazilian Amazon may be flawed due to collection errors. However, this distorting effect could be avoided if was used large grids sizes. In our case, the most of major patterns are recovered in both areas' cladogram, and the difference between both analysis results was not so significant (see in the Results section), so we choose to use the 2-degree results for purposes of description and discussion, and we believe that appears to be an adequate resolution to be explored in future research of secondary biogeographical homologies (Costa S.L. et al., unpublished data).

Thus, the present study identified and defined three large areas of endemism of *Orthophytum*: NER, SER, and CPAF (Fig. 3), with existing legally constituted conservation areas within them; the main conservation reserves in each area are listed in Table II.

The NER and SER together cover almost the entire Espinhaço Range, except for the region of Oliveira dos Brejinhos (corresponding to areas A12 in central Bahia – which had good support in together with A16, however have only one record and therefore were not identified as areas of endemism for *Orthophytum*). The NER is located in the Bahia portion of the Espinhaço Range, while the SER is in Minas Gerais portion of the Espinhaço Range. Both areas evidence high richness (36 and 22 species respectively), medium endemism (five exclusive species each), and medium to high diversity (NER: 0.89 – 2.19; SER: 0.88 – 2.19).

Table II. Main Conservation Units created within the areas of endemism identified by PAE of 2-degrees grid size and the grid/area in which each one occurs. Numbers in parentheses indicate the total number of conservation units within the grid/area. Bold indicates that there are *Orthophytum* species within these conservation units. RPPN: Reserva Particular do Patrimônio Natural; APA: Área de Proteção Ambiental; RVS: Refúgio de Vida Silvestre; PN: Parque Nacional; PE: Parque Estadual; RDS: Reserva de Desenvolvimento Sustentável; FN: Floresta Nacional; ARIE: Área de Relevante Interesse Ecológico; MN: Monumento Natural; RB: Reserva Biológica; ESEC: Estação Ecológica.

Endemism Areas	Area	Main Conservation Units	
		Sustainable Use Units	Integral Protection Units
North of Espinhaço Range	A8 (6)	RPPN Maria Maria, APA Lago de Sobradinho, RPPN Toca dos Ossos, **APA Boqueirão da Onça**;	RVS Riacho Pontal, **PN Boqueirão da onça**;
	A13 (22)	ARIE Serra do Orobó, **APA Marimbus**, APA Grutas dos Brejões, RPPN Ametista, RPPN Pau d'Arco;	**PN Chapada Diamantina**, **PE Morro do Chapéu**, PE Sete Passagens, MN Cachoeira do Ferro Doido;
	A14 (14)	**APA Baía de Todos os Santos**; RPPN Curió, RPPN Olho de Fogo, APA Plataforma Continental do Litoral Norte;	MN Cânions do Subaé;
	A17 (7)	APA Lajedão;	PE Serra dos Montes Altos, PE Verde Grande, **PE Caminho dos Gerais**, RVS Serra dos Montes Altos, **PE Mata Seca**, PE Lagoa do Cajueiro;
	A18 (17)	**ARIE Nascente do Rio de Contas**, FN Contendas do Sincorá, APA Serra do Barbado, APA da Serra do Ouro, **APA Serra do Barbado, RPPN Arco Verde**;	PN Boa Nova, **PN Chapada Diamantina**, RVS Boa Nova;
South of Espinhaço Range	A20 (10)	RDS Nascentes Geraizeiras, APA Serra do Sabonetal;	RB Jaíba, **PE Caminho dos Gerais**, PE Serra Nova e Talhado, PE Lapa Grande, PE Botumirim, **PE Grão Mogol**, RB Serra Azul, PE Montezuma;
	A23 (15)	**APA Águas Vertentes**, APA do Alto do Mucuri;	PE de Botumirim, PE Serra da Candonga, PE Serra do Intendente, **MN Estadual Várzea do Lageado**, PE Serra Negra, PE Pico do Itambé, **PN das Sempre Vivas**, ESEC Acauã, **PE Biribiri**;
	A25 (60)	APA da Perdição, APA Alto Taboão, APA Cachoeira das Andorinhas, **APA Córrego da Mata**, RPPN Mata dos Jaca, APA Carste de Lagoa Santa, **APA Sul-RMBH, RVS Macaúbas;**	MN Municipal Morro do Pires, PE do Rio Doce, **PE Serra do Sobrado**, PE Serra do Brigadeiro, PE Serra Verde, **PE Serra do Intendente**, PN da Serra do Gandarela, PE do Itacolomi, **PN Serra do Cipó;**
Central Portion of Atlantic Forest	A24 (8)	**APA Alto do Mucuri**, RPPN Córrego das Traíras, **RPPN Prati**, RPPN Antônio Lopes Merson, RPPN Lemke;	RB Córrego do Veado, RB Sooretama, MN Pico do Ibituruna;
	A26 (120)	FN Pacotuba, FN Goytacazes, APA Corredeiras, **RPPN Meu Cantinho, RPPN Bei Cantoni, RPPN Olho d'Água, RPPN Três Pontões, RPPN Boa Fé, RPPN Passos, RPPN Freisleben,** APA Lagoa Jacuné;	**MN Pontões Capixabas**, PE Mata das Flores, **PE Sete Salões**, PN Caparao, MN Pontões Capixabas, **MN Pedra do Monjolo,** MN o Frade e a Freira;

Both the NER and SER have a large extension of “Campos Rupestres” (rocky altitudinal fields) – a landscape composed mainly of grasslands and quartzite-sandstone rock outcrops above 900 masl. The Espinhaço Range represents approximately 1% of the total land area of Brazil, but shelters approximately 10% of the country’s plant diversity (Rapini 2010). Most of those species have restricted distributions, and the floristic compositions of the rocky fields of the Espinhaço Range are marked by rare species and high rates of endemism – perhaps the highest among Brazilian plant formations (Giulietti et al. 1987, 1997, Giulietti & Pirani 1988, Rapini 2010).

The geological origin of the constituent blocks of the Espinhaço Range is dated to the Pre-Cambrian period. The soil is characterized by being shallow, sandy, acidic, and nutrient-poor, which contributes to a phytophysiographic mosaic of rare species, due to the segmentation of the vegetation in different and small populations between rock outcrops (providing specific niches to the species) besides living in several locations with difficult to access, remaining undersampled or practically unexplored (Rapini 2010, Schaefer et al. 2016, Silveira et al. 2016), even being an area intensely researched (see Rapini et al. 2008, Borges et al. 2011, Echternacht et al. 2011, Bitencourt & Rapini 2013, Colli-Silva et al. 2019, Alves & Loeuille 2021, Alves & Buril 2022, Assunção-Silva & Assis 2022, Barros-Souza & Borges 2023).

The *Orthophytum* species of the NER occur on high elevation rock outcrops (more than 900 masl), while the species of the SER occur on lower elevation rock outcrops (less than 900 m). Echternacht et al. (2011) observed that the species that occur in the northern section of Espinhaço Range in Minas Gerais (corresponding to SER of our study) occur in lowlands with contrasting climatic and edaphic conditions that could represent barriers to many endemic mountain plants. These lowlands were also reported as probable geographic barriers for Harley (1988), Rando & Pirani (2011), and Alves & Buril (2022) in the dispersal of many mountain species and this could help to explain the distribution of the *Orthophytum* species that occur in SER and NER.

The third area of endemism of our study, the CPAF (areas A24 and A26), harbors the highest diversity, richness, and endemism, with 13 exclusive species, H’ = 1.76 - 2.19, and the highest support in PAE (96.4%). This area was previously indicated by Martinelli et al. (2008) as a possible center of diversity and endemism. The CPAF is located in northeastern Espírito Santo State and Minas Gerais State, which are covered by the Atlantic Forest domain and characterized by an evergreen tropical forest vegetation (Oliveira-Filho et al. 2006). In addition to forest physiognomies, the area holds mangrove swamps, shrubby Restinga (sandy coastal) vegetation, and patches of high-altitude grasslands and rock outcrops (Safford 1999, 2007, Scarano 2002).

The *Orthophytum* species that occur in the CPAF are found on inselbergs and on exposed rock outcrops in the Atlantic Forest domain. Several authors observed that naturally open formations (such as inselbergs and granite rock outcrops) found in high altitude montane areas of the Atlantic Forest harbor a highly endemic flora (over 20% of its species) that have strong floristic connections with other montane areas, such as those of the Andes and the Espinhaço Range (e.g., Safford 1999, 2007, Giulietti & Pirani 1988, Calio et al. 2008, Porembski 2007).

Not only *Orthophytum*, but also most of the Bromeliaceae family, demonstrate high diversity and endemism in the Atlantic Forest domain. Zizka et al. (2019) identified three large centers of endemism and diversity of the American Bromeliaceae: in the Atlantic Forest of southeastern Brazil, in the Central Andes,

Table III. Presence/absence matrix (area × species) used in parsimony analysis of endemicity of 1-degree grid size.

	Orthophytum alagoanum	Orthophytum alvimii	Orthophytum arcanum	Orthophytum argentum	Orthophytum atalaiense	Orthophytum boudetianum	Orthophytum braunii	Orthophytum buranhense	Orthophytum caraibense	Orthophytum cearence	Orthophytum cristaliense	Orthophytum conquistense	Orthophytum diamantinense	Orthophytum disjunctum	Orthophytum duartei	Orthophytum eddie-estevesii	Orthophytum elegans	Orthophytum erigens	Orthophytum estevesii	Orthophytum falconii	Orthophytum foliosum	Orthophytum fosterianum	Orthophytum glabrum	Orthophytum graomogolense	Orthophytum grossiorum	Orthophytum guaratingense	Orthophytum gurkenii	Orthophytum harleyi	Orthophytum horridum	Orthophytum jabrense	Orthophytum jacaraciense	Orthophytum lanuginosum	Orthophytum lemei	Orthophytum leprosum	Orthophytum macroflorum	Orthophytum magalhaesii	Orthophytum maracasense	Orthophytum mello-barretoi	Orthophytum minimum	Orthophytum piranianum	Orthophytum pseudostoloniferum	Orthophytum pseudovagans	Orthophytum riocontense	Orthophytum roseolilacinum	Orthophytum santaritense	Orthophytum santosianum	Orthophytum saxicola	Orthophytum schulzianum	Orthophytum sp.nov.	Orthophytum striatifolium	Orthophytum sucrei	Orthophytum triunfense	Orthophytum toscanoi	Orthophytum vasconcelosianum	Orthophytum zanonii
Out	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A4	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A8	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A10	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A11	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A12	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A13	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A14	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A15	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A16	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A17	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A18	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A19	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A20	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A21	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A24	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A31	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A32	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
A33	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
A38	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
A39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A41	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A45	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
A47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
A49	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
A50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A51	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A52	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
A53	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A54	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
A57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table III. Continuation.

A58	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A60	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
A61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
A62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
A64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A66	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0
A67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
A68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A69	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
A70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table IV. Presence/absence matrix (area × species) used in parsimony analysis of endemicity of 2-degree grid size.

	Orthophytum alagoanum	Orthophytum alvimii	Orthophytum arcanum	Orthophytum argentum	Orthophytum atalaiense	Orthophytum boudetianum	Orthophytum braunii	Orthophytum buranhense	Orthophytum caraibense	Orthophytum cearence	Orthophytum cristaliense	Orthophytum conquistense	Orthophytum diamantinense	Orthophytum disjunctum	Orthophytum duartei	Orthophytum eddie-estevesii	Orthophytum elegans	Orthophytum erigens	Orthophytum estevesii	Orthophytum falconii	Orthophytum foliosum	Orthophytum fosterianum	Orthophytum glabrum	Orthophytum graomogolense	Orthophytum grossiorum	Orthophytum guaratingense	Orthophytum gurkenii	Orthophytum harleyi	Orthophytum horridum	Orthophytum jabrense	Orthophytum jacaraciense	Orthophytum lanuginosum	Orthophytum lemei	Orthophytum leprosum	Orthophytum macroflorum	Orthophytum magalhaesii	Orthophytum maracasense	Orthophytum mello-barretoi	Orthophytum minimum	Orthophytum piranianum	Orthophytum pseudostoloniferum	Orthophytum pseudovagans	Orthophytum riocontense	Orthophytum roseolilacinum	Orthophytum santaritense	Orthophytum santosianum	Orthophytum saxicola	Orthophytum schulzianum	Orthophytum sp.nov.	Orthophytum striatifolium	Orthophytum sucrei	Orthophytum triunfense	Orthophytum toscanoi	Orthophytum vasconcelosianum	Orthophytum zanonii
Out	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A4	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A6	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A8	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A10	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A11	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A13	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
A14	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A16	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
A18	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0
A19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
A20	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
A21	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
A22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A23	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
A24	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
A25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A26	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1

and in Central America. Those authors also observed that the subfamily Bromelioideae was most species-rich and evidenced high endemism in the eastern Atlantic Forest of Brazil. The high occurrence of Bromeliaceae, especially Bromelioideae, in the Atlantic Forest is consistent with the extensive diversification of the family in eastern Brazil (Smith 1934, Smith & Downs 1974).

The Atlantic Forest of southeastern Brazil has been identified in many studies as a center of endemism, diversity, and richness for many groups of plants, and as one of the most important regions for the conservation of global biodiversity (see Zizka et al. 2019, Myers et al. 2000, Smith 1934, Smith & Downs 1974, Benzing 2000, Mori et al. 1981, Prance 1982, Cracraft 1985, Soderstrom et al. 1988, Costa et al. 2000, Silva et al. 2004, Santos et al. 2007).

According to Forza et al. (2020), 87% of all Bromeliaceae species within the Brazilian Atlantic Forest are endemic, and Zizka et al. (2019) and Martinelli (2000) observed that probably the most threatened Bromeliaceae species occur within that domain. The high level of habitat destruction in that region (only approximately 7.5% of the original vegetation remains) has indicated it as a priority site for global biodiversity conservation (Myers et al. 2000, Mittermeier et al. 2005). The creation of greater numbers of protected areas within the Atlantic Forest has accordingly been suggested to help assure the preservation of that biodiversity. It is worth mentioning that the A26 area alone (CPAF - which was identified as the most endemic area, with the greatest richness and diversity) already has more than 120 legally established conservation areas (Table II), which may have been one of the factors aiding the conservation of *Orthophytum* species – and demonstrates the importance of such conservation areas.

Distinct from the CPAF area, however, both the NER and SER regions (and the Espinhaço Range as a whole) have few established conservation areas, and those are not sufficient to protect the diversity found in the entire complex, requiring more parks and reserves to be created (Silva et al. 2008, Versieux & Wendt 2007). Additionally, the existing conservation areas in those regions lack government support, and without satisfactory physical and administrative infrastructures (Echternacht et al. 2011).

According to the *Red List* of the National Center of Flora Conservation (CNCFlora 2022, continuously updated) there are ten threatened species of *Orthophytum*. Louzada & Wanderley (2010), however, observed that there is insufficient information available concerning most of its species to be able to accurately determine their conservation statuses, mainly due to the scarcity of collection material (most are only known from the type collection and imprecise information in the literature and in herbaria collections – which leads us to believe that the number of threatened species is probably much higher. We observed that 44% (24 species) of the *Orthophytum* species evidence microendemic distribution patterns (Table I, Fig. 4–10), being restricted to, and exclusive to, a certain vegetation physiognomy found in only one grid square of the PAE, and with one to four known sites of occurrence. Many of those species are only known from the type collection – evidencing the necessity for more intensive floristic and geographic distribution studies within the family.

The concept of microendemism includes species with highly restricted and geographically proximate distributions (Townsend et al. 2011), as was also adopted by McCauley et al. (2010) for *Guaiacum unijugum* Brandegee (Zygophyllaceae), which occurs in less than 5% of the Baja California in Mexico. Giulietti et al.

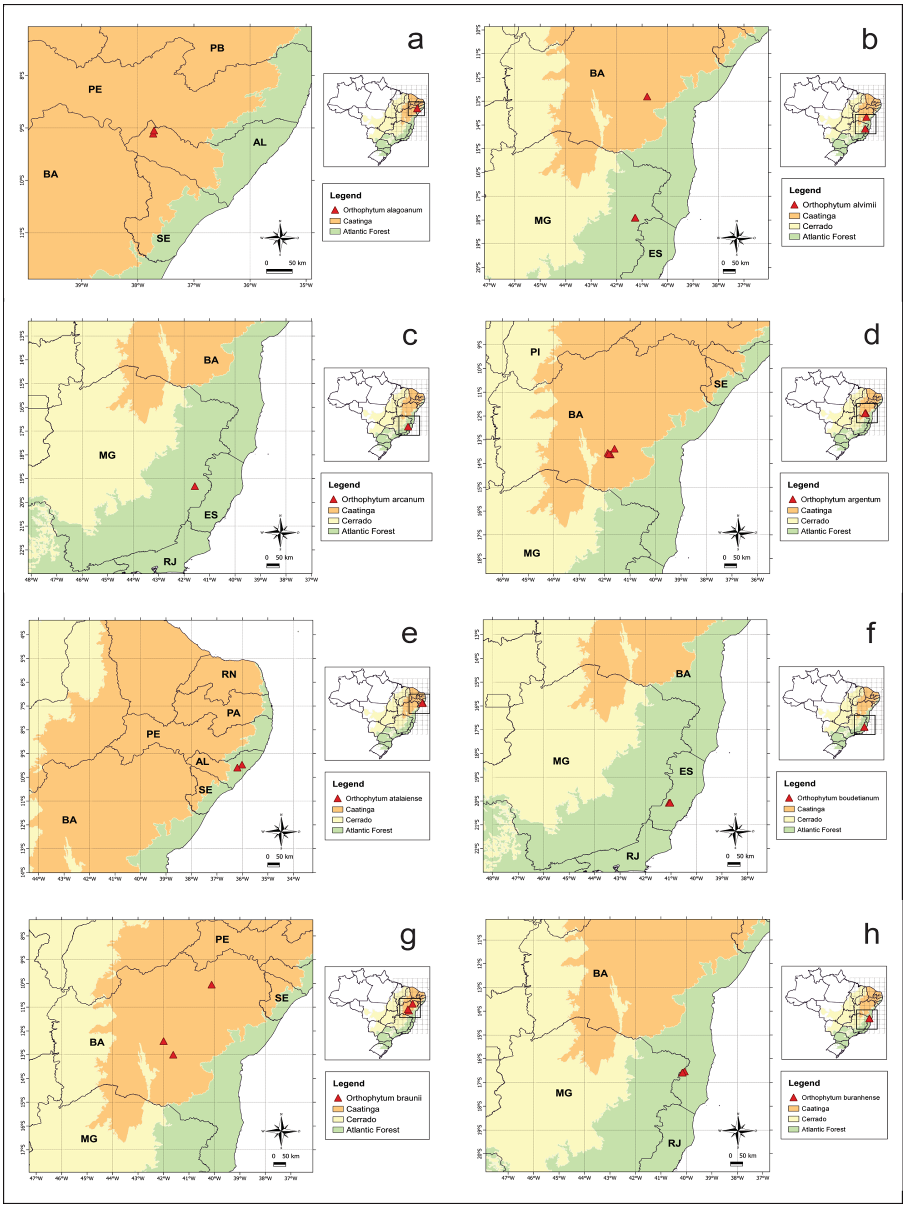

Figure 4. Distribution maps of *Orthophytum* species. a. *O. alagoanum*. b. *O. alvimii*. c. *O. arcanum*. d. *O. argentum*. e. *O. atalaiense*. f. *O. boudetianum*. g. *O. braunii*. h. *O. buranhense*.

(2005) also determined that approximately 96% of all Brazilian species of the Eriocaulaceae family are microendemic. Benzing (2000) and Martinelli et al. (2013, 2008) observed similar situations with other Bromeliaceae genera. Many *Aechmea, Hohenbergia*, and *Neoregelia* species characteristic of the Atlantic Forest have taxa occurring within just a few forest fragments or, in some cases, are restricted to only one protected area. Some *Cryptanthus* species are critically endangered, principally because they exist in only very small populations with reduced ranges in rocky fields, or are known only from their type collections.

Cox & Moore (2011) noted that there are two main factors influencing the degree of endemism in an area: isolation and stability, with isolated islands and mountains (such as inselbergs and rock outcrops) always being rich in endemic organisms. Inselbergs are isolated rock outcrops that harbor saxicolous vegetation and are inserted within landscapes of contrasting plant

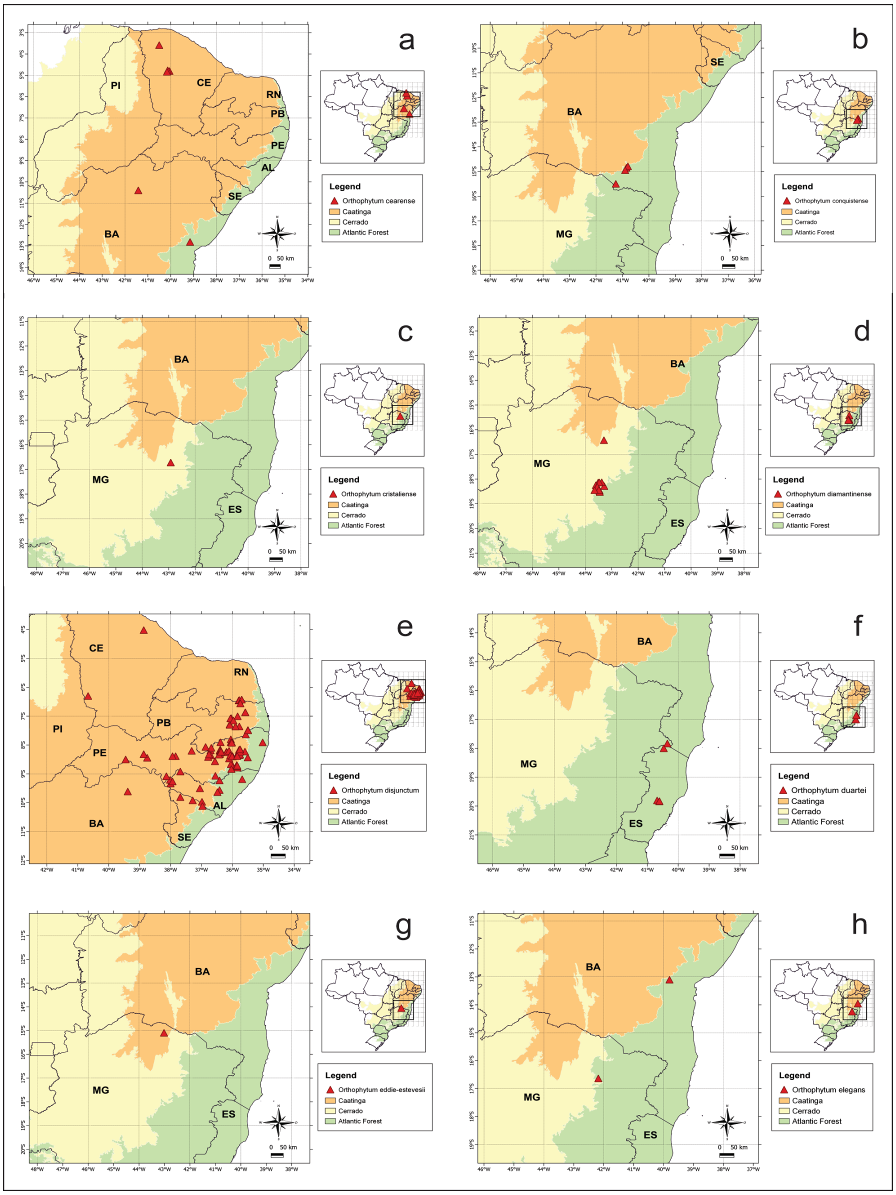

Figure 5. Distribution maps of *Orthophytum* species. a. *O. cearense.* b. *O. conquistense.* c. *O. cristaliense.* d. *O. diamantinense.* e. *O. disjunctum.* f. *O. duartei.* g. *O. eddie-estevesii.* h. *O. elegans.*

communities. Because they are geographically disconnected and show marked ecological isolation from their surrounding areas, inselbergs are often compared to oceanic islands and tend to maintain their typical attributes regardless of their geographic locations, occurring in areas with humid forests to dry environments (Porembski & Barthlott 2000).

Describing and recognizing geographic distribution patterns is one of the essential stages to delimit areas of endemism (Noguera-Urbano 2016, Morrone 1994), therefore, as endemic taxa are found exclusively in only a single region, that aspect of their distribution is highly important to their conservation, and the identification of neighboring areas of endemism with low floristic similarities can contribute to effective conservation planning. Benzing (2000) hypothesized that the high rates of endemism observed in some Bromeliaceae genera, mainly saxicolous taxa (e.g., *Orthophytum* and *Dyckia*), could be attributed to their morphologies and

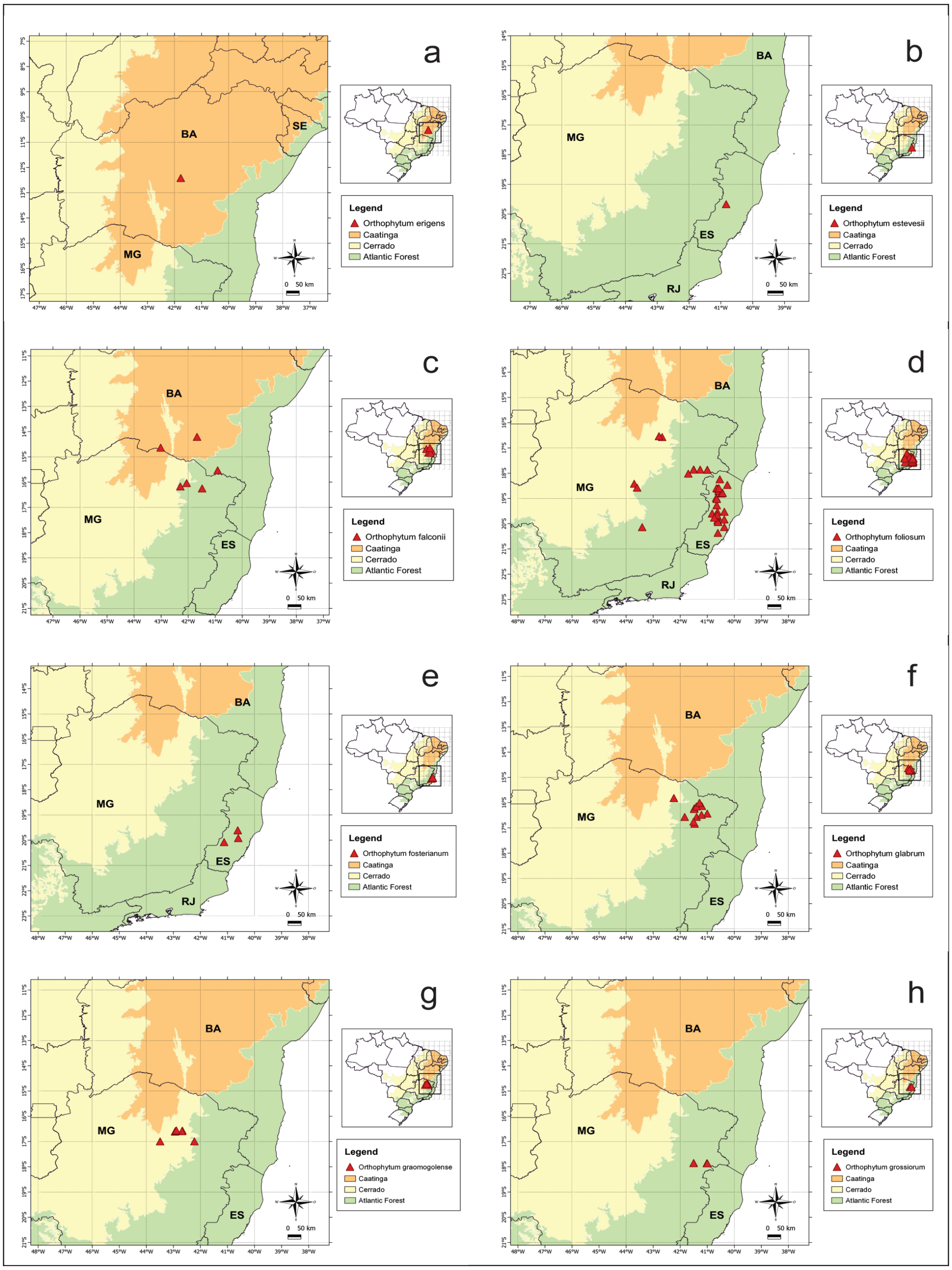

Figure 6. Distribution maps of *Orthophytum* species. a. *O. erigens.* b. *O. estevesii.* c. *O. falconii.* d. *O. foliosum.* e. *O. fosterianum.* f. *O. glabrum.* g. *O. graomogolense.* h. *O. grossiorum.*

to their lower dispersal capacities. Wanderley (1990) observed that the berry fruits and the bird (ornithophily) and insect (entomophily) dispersal observed in *Orthophytum* (and in the whole subfamily Bromelioideae), would limit the geographic distribution of its species in relation to the subfamily Tillandsioideae, whose seeds are widely dispersed by the wind.

Orthophytum is present in a diversity of spatially and ecologically isolated microhabitats (inselbergs and rock outcrops) that greatly restrict seed dispersal and migration, thus favoring the establishment of isolated populations and promoting speciation over successive generations. Studies of these types of islands have provided fundamental insights for understanding the ecological and evolutionary

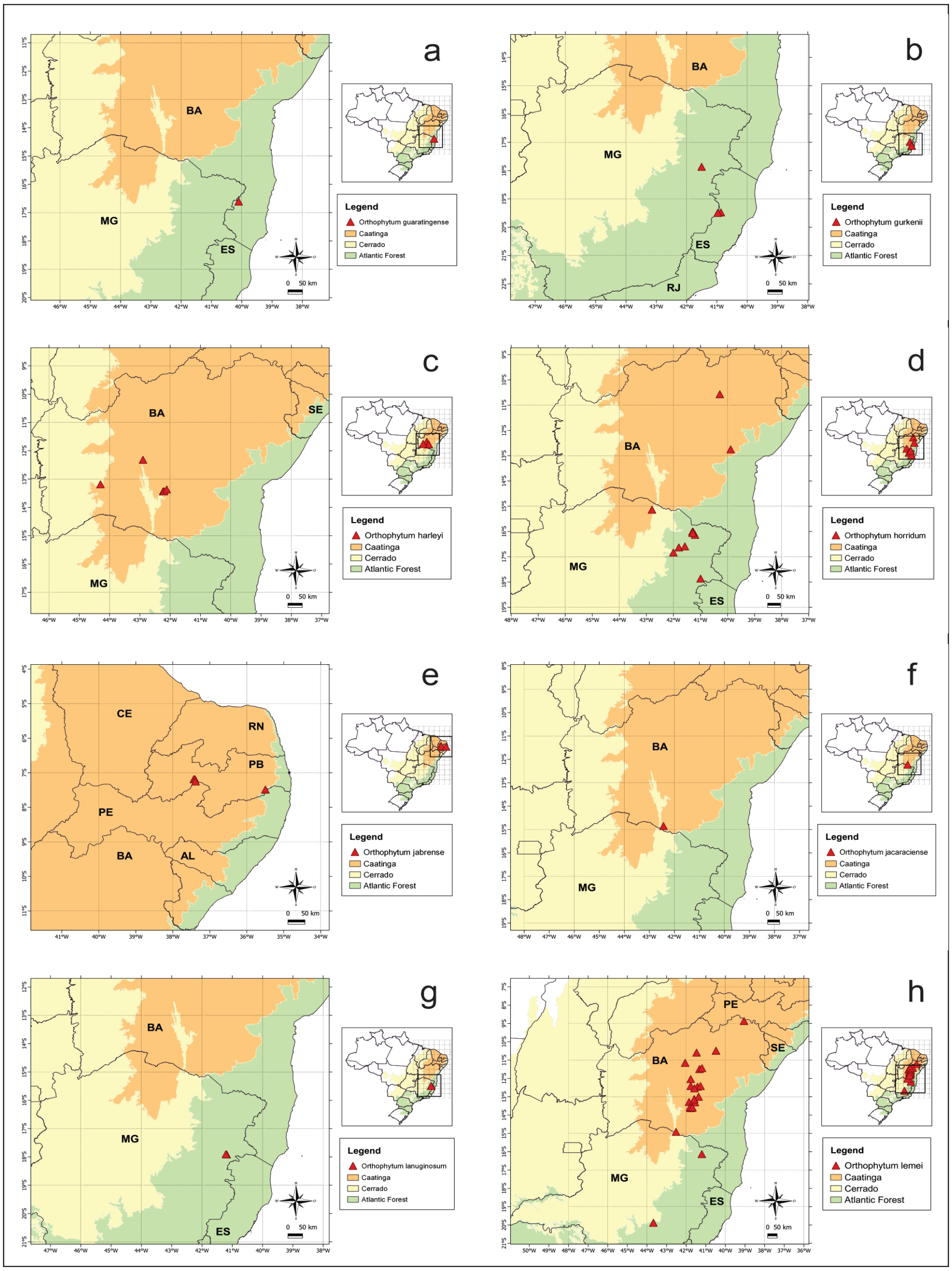

Figure 7. Distribution maps of *Orthophytum* species. a. *O. guaratingense*. b. *O. gurkenii*. c. *O. harleyi*. d. *O. horridum*. e. *O. jabrense*. f. *O. jacaraciense*. g. *O. lanuginosum*. h. *O. lemei*.

processes that affect the biodiversity of ecosystems (Porembski & Barthlott 2000), and the genus *Orthophytum* offers an interesting model system for examining speciation processes and endemism in neotropical habitats.

Studies like this provide a precise overview of species' distributions, and represent a step forward to understanding the historical processes involved in their current geographic placement. These results reinforce the importance of publishing complete lists of the materials examined in taxonomic reviews and making them available to scientists and herbaria to improve the representativeness of

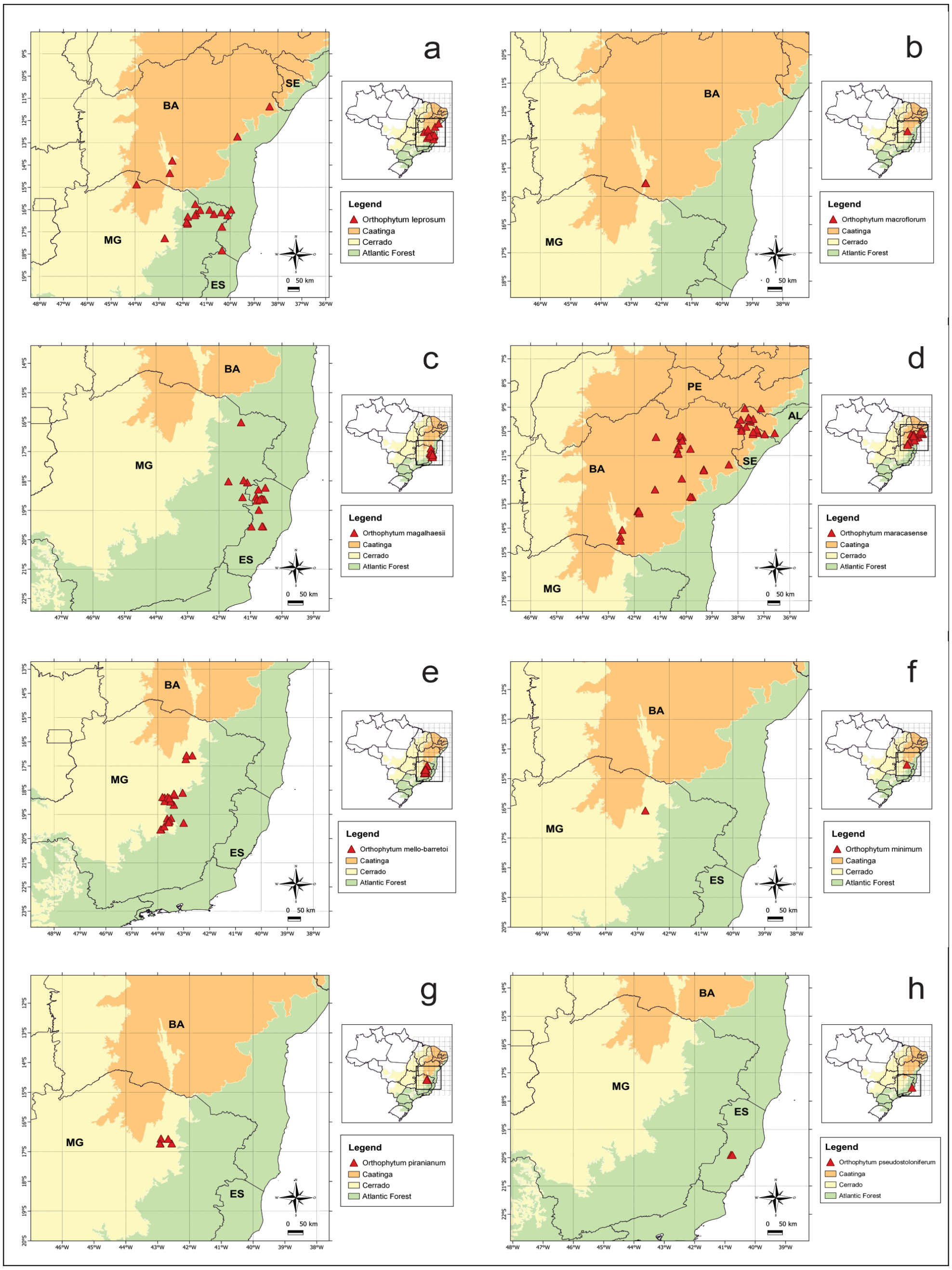

Figure 8. Distribution maps of *Orthophytum* species. a. *O. leprosum*. b. *O. macroflorum*. c. *O. magalhaesii*. d. *O. maracasense*. e. *O. mello-barretoi*. f. *O. minimum*. g. *O. piranianum*. h. *O. pseudostoloniferum*.

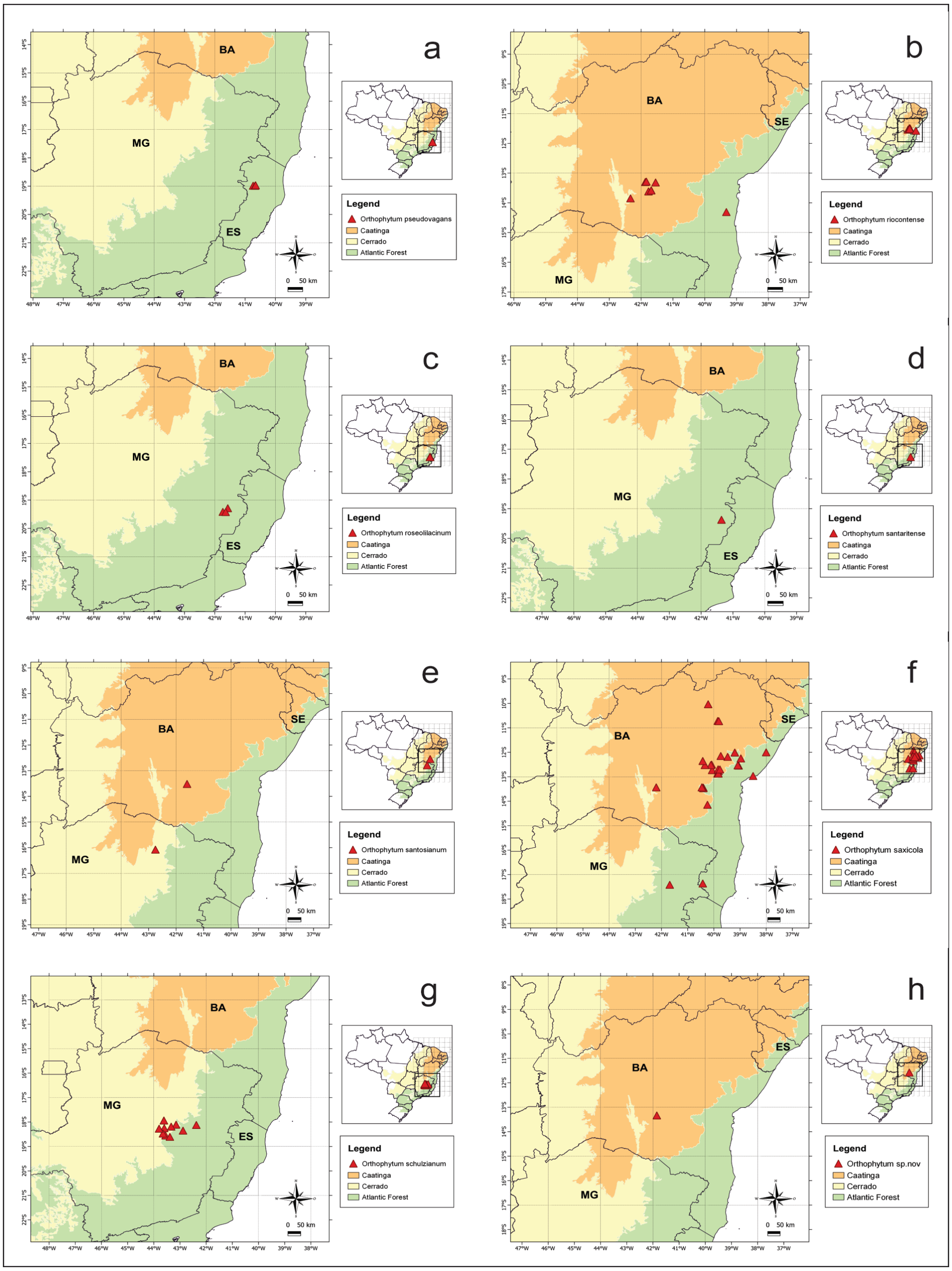

Figure 9. Distribution maps of *Orthophytum* species. a. *O. pseudovagans*. b. *O. riocontense*. c. *O. roseolilacinum*. d. *O. santaritense*. e. *O. santosianum*. f. *O. saxicola*. g. *O. schulzianum*. h. *O. sp. nov.*

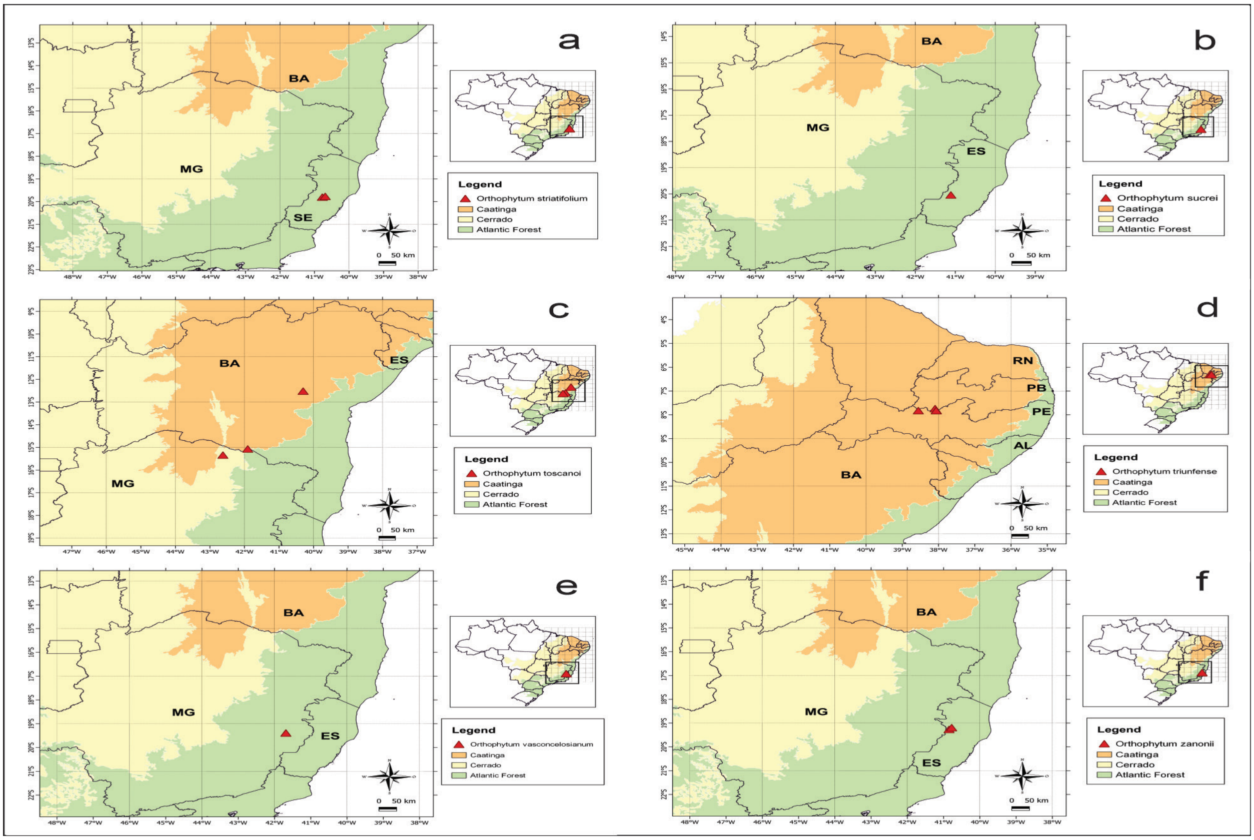

Figure 10. **Distribution maps of *Orthophytum* species. a. *O. striatifolium*. b. *O. sucrei*. c. *O. toscanoi*. d. *O. triunfense*. e. *O. vasconcelosianum*. f. *O. zanonii*.**

those collections. The results presented here and the identification of areas with high levels of endemism can act as a baseline to develop more detailed conservation assessments and assist public policies for preserving priority conservation areas.

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SLC contributed with data collection, analyses, statistical tests, data interpretation, and manuscript preparation. SCN and JVA contributed with analyses and statistical tests. RBL and MTB were responsible for designing the research, supervising the data analysis stages, and reviewing the manuscript. All authors participated in writing the final version of the manuscript.

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