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Conservation of Paraguay's floristic biodiversity: a biogeographical analysis with a multi-scale spatial approach for the identification of priority areas

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SUMMARY

Areas of endemism are defined as regions where two or more species share congruent distributions, representing primary homologies in historical biogeography. These areas are critical for conservation efforts. This study identified areas of endemism in Paraguay using an endemicity analysis (EA) with NDM/VNDM software, based on 2,587 records of 106 plant species. We used grids of 0.5° and 0.6° latitude and longitude to evaluate the stability of these areas across different spatial scales. Sixty areas of endemism were identified and grouped into seven consensus areas. Two of these areas, located in the Dry Chaco and the Alto Paraná Atlantic Forest (BAAPA), were consistent across both scales. No endemism areas were found in the Humid Chaco or Pantanal regions. In the Cerrado, two consensus areas overlapped with those of the BAAPA. Additionally, a consensus area was identified in the Cordillera de los Altos and the southern BAAPA region, highlighting a biogeographic transition and the ecotonal nature of the area.

INTRODUCTION

Paraguay is a landlocked country covering 406,752 km² in the heart of South America. It borders Brazil to the east and north, Bolivia to the northwest, and Argentina to the south and west. The Paraguay River divides the country into two main geographic regions: the Eastern Region and the Western Region, also known as the Chaco.

Biogeographically, Paraguay spans several domains, including the Amazonian Domain (comprising the Paranaense and Cerrado Provinces), the Chacoan Domain (with the Chaco Province), and the Neotropical Seasonally Dry Forest Domain, which includes the Misiones and Chiquitanía nuclei (Cabrera and Willink, 1973; Mogni et al., 2015; Oakley and Prado, 2011). Avila et al. (2018) classified Paraguay into seven distinct ecoregions (Fig. 1), influenced by the Cerrado province, Chaco province, Parana Forest province and Madeira province (Morrone et al., 2022).

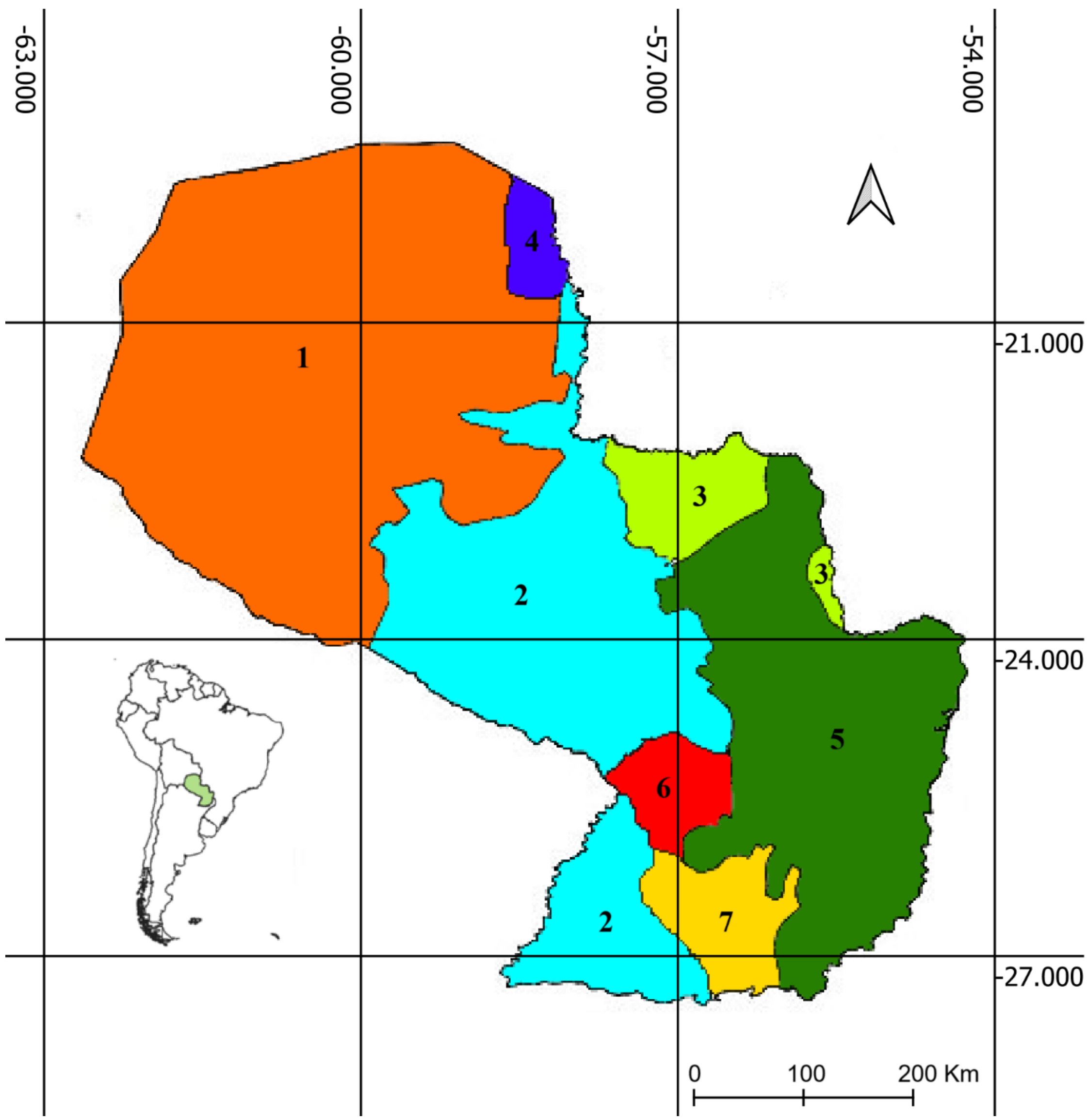

Figure 1. Ecoregions of Paraguay according to Avila et al., (2018).1. Dry Chaco, 2. Humid Chaco, 3. Cerrado, 4. Pantanal, 5. Atlantic Forest of the Upper Paraná, 6. Cordillera de los Altos and 7. Mesopotamian Savanna.

Importance of Geographic Distribution in Biogeography

Understanding the geographic distribution of organisms has multiple applications in biogeography. From an ecological perspective, one of the goals of biogeographic analysis are to create maps representing natural areas (Espinosa et al., 2001). In contrast, historical biogeography focuses on uncovering patterns of taxon distribution across space and time (Morrone, 2012; Zunino and Zullini, 2003). The distribution of a species is shaped by both historical and contemporary factors. When two or more species share distributional congruence, it may indicate common factors that influenced their speciation and distribution (Morrone, 2012). This congruence can define areas of endemism, where species exhibit similar responses to shared environmental or historical influences (Noguera-Urbano, 2017).

Identifying patterns of taxon distribution and areas of endemism is not only critical for historical biogeography but also essential for informing public policies on the prioritization and selection of protected areas (Avila et al., 2023; Mendoza-Fernández et al., 2014; Vieira-Guimarães et al., 2024). Giraudo and Arzamendia (2018) highlight that biogeographic principles and methods are crucial for designing protected areas, including the prioritization and selection of optimal locations. Bioregionalization serves as a key component in conservation strategy development, laying the groundwork for evaluating the representativeness and effectiveness of protected areas in conserving biodiversity.

Areas of Endemism

Areas of endemism are defined as geographic regions where two or more taxa are exclusively found (Szumik and Goloboff, 2004). These areas represent congruent species distributions, whether the species are phylogenetically related, and indicate primary biogeographic homologies suggesting a shared biogeographic history (Deo and Desalle, 2006; Noguera-Urbano, 2016; Noguera-Urbano and Escalante, 2015). Identifying such areas is a key objective in historical biogeography, as they are fundamental units of study (Sánchez et al., 2019).

According to Martínez-Hernández et al. (2015), identifying areas of endemism is essential for selecting priority areas for biodiversity conservation. When endemism is restricted to a specific country or geographic region, it holds considerable value for species richness analysis and conservation efforts. The occurrence of patterns formed by species that are both restricted to and sympatrically distributed within these areas, as noted by Noguera-Urbano (2017), provides a reference framework for identifying regions with unique biota. These studies offer practical criteria for defining priority conservation areas and targets.

Background on Paraguay's Phytogeography

The first phytogeographic studies in Paraguay date back to the pioneering works of Tortorelli (1967), Cabrera (1970), Ferreiro (1981), and Sanjurjo (1989), who described the country's forest regions. Later, Spichiger et al. (1995) proposed a more detailed regionalization, including various types of flora and ecotonal zones. Oakley and Prado (2011) focused on forest species in the Neotropical Seasonally Dry Forests, outlining their biogeographic areas of influence in both regions of the country. Additionally, Spichiger et al. (2006) conducted an analysis of the distribution of 39 tree species, providing valuable insights into the regionalization of Paraguay's forest flora.

Several studies have focused specifically on the vegetation of the Paraguayan Chaco. Ramella and Spichiger (1989), Spichiger et al. (1991), and Prado (1993) analyzed the vegetation of the region, while Mereles (2005) offered a synopsis of the Paraguayan Chaco's vegetation formations, emphasizing hydrological and edaphic factors. Mereles

(2013) and Mereles et al. (2013) further complemented these works by providing detailed descriptions of the Chaco's vegetation.

Together, these studies have significantly advanced our understanding of Paraguay's floristic diversity and distribution. The present study continues this line of research by identifying areas of floristic endemism using a matrix of botanical species records. This approach aims to pinpoint priority areas for the conservation of native botanical species, thus contributing to the preservation of Paraguay's rich biodiversity.

MATERIALS AND METHODS

This study collected data on the presence of native plant species in Paraguay from various sources, including the herbarium of the Faculty of Exact and Natural Sciences of the National University of Asunción, online databases (www.ville-ge.ch/cjb/fdp/publications/familias_publicadas.html and www.tropicos.org/), the database of the National Forestry Institute, and scientific literature (Gauto, 2015; Gauto, Spichiger, & Stauffer, 2011). This study exclusively utilized records that were georeferenced. Data without geographic coordinates were excluded from the analysis to ensure the accuracy and reliability, resulting in a dataset of 2,587 records representing 106 botanical species (Supplementary Table 1).

The study covered the entire territory of Paraguay. Endemism analysis (EA) was conducted using NDM/VNDM software version 3.0, as proposed by Szumik et al. (2002) and optimized by Szumik and Goloboff (2004). The software was used with its default configuration parameters, which include predefined settings for the analysis of species distribution and endemism patterns. Specifically, no modifications were made to parameters such as random seed, fill radius, or assumed radius of grids. Two grid cell sizes were applied: 0.5° x 0.5° and 0.6° x 0.6° in geographic latitude and longitude. Smaller grid sizes were tested to improve the geographic resolution of the results, but these did not produce identifiable areas of endemism. A multi-scale approach was implemented to evaluate the consistency of endemism areas across different spatial scales. The results from each scale were compared to identify consistent patterns, ensuring the stability of the identified endemism areas.

Areas of endemism were defined by considering overlapping regions that shared 30% or more species. These were classified as consensus endemism areas, following the protocol established by Casagranda and Szumik (2009), facilitating the synthesis of overlapping patterns into coherent consensus areas. Spatial comparisons of the areas were carried out using QGIS software.

RESULTS

A total of 60 areas of endemism were identified. Using a grid size of 0.5° × 0.5°, the NDM/VNDM software identified 28 areas of endemism (Supplementary Figure 1), and with a grid size of 0.6° × 0.6°, 32 areas of endemism were identified (Supplementary Figure 2). All of them were summarized into seven consensus areas (Fig. 2). Two of these areas were consistent across both spatial scales: one in the Dry Chaco (Figs. 2C, 2G, and 3A), defined by eight species (Table 1), and another in the Atlantic Forest of Alto Paraná (BAAPA) (Figs. 2A, 2F, and 3A), which was supported by 12 endemic species (Table 2).

In the Cerrado ecoregion, two consensus areas were identified that overlapped with those of the BAAPA (Figs. 2B, 2D, and 3B). Additionally, a consensus area was identified at the 0.6° x 0.6° scale in the Cordillera de los Altos, the Mesopotamian Savanna, and the central and southern BAAPA regions (Fig. 1E).

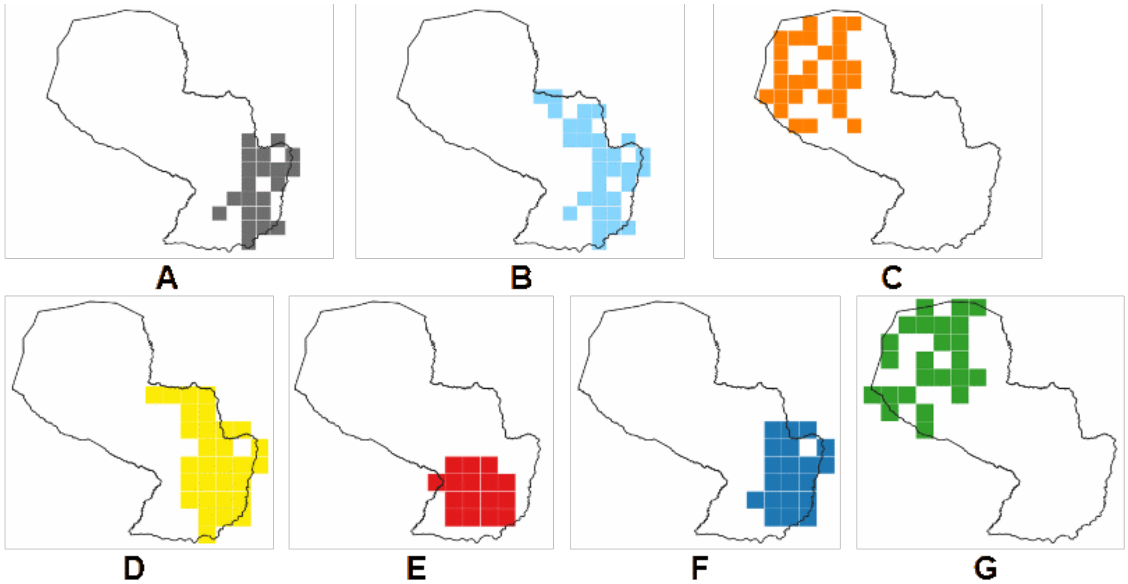

Figure 2. Areas of consensus endemisms. Grid 0.5º x 0.5º lat and long: A, B and C. Grid 0.6º x 0.6º lat and long: D, E, F and G.

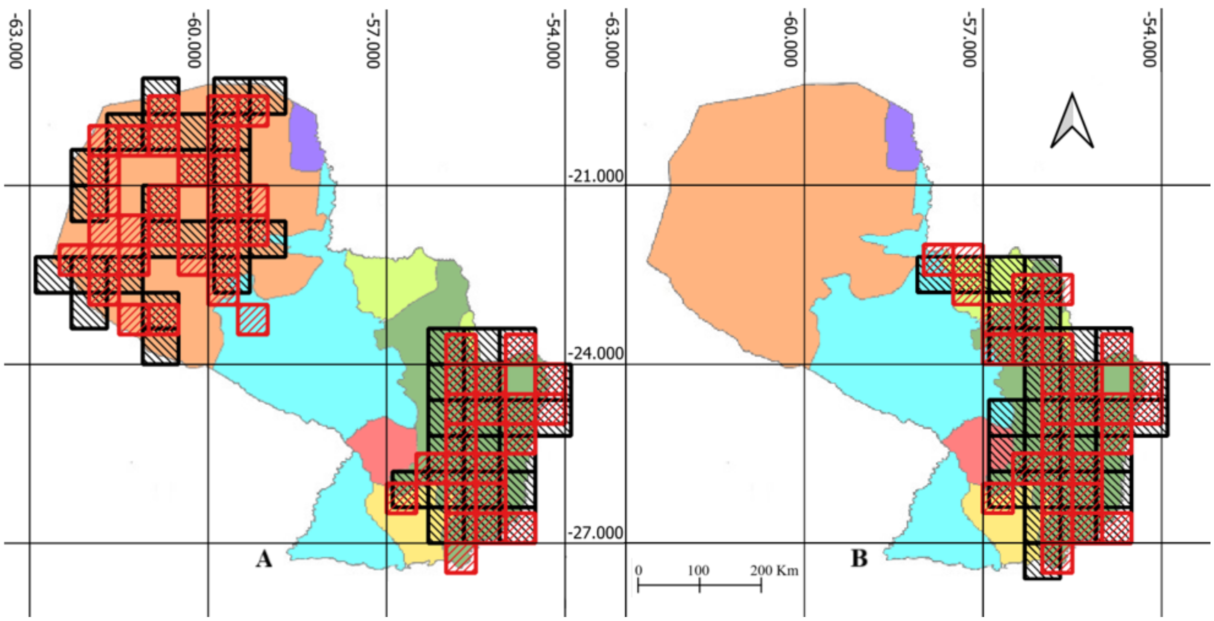

Figure 3. Consensus areas. A: Consensus areas coinciding at both study scales, corresponding to the Chaco Seco and BAAPA. B: Consensus areas coinciding at both study scales, corresponding to the Cerrado and BAAPA together. Red grids: 0.5º x 0.5º and black grids: 0.6º x 0.6º geographical latitude and longitude. Ecoregions of Paraguay: Dry Chaco: orange, Humid Chaco: light blue, Cerrado: light green, Pantanal: lilac, Atlantic Forest of the Upper Paraná: green, Cordillera de los Altos: red and Mesopotamian Savanna: yellow.

Table 1. Species found at different scales sharing the area corresponding to the Chaco Seco.

Chaco Seco Species	0.5° x 0.5	0.6° x 0.6
Sideroxylon obstusifolium (Roem. and Schult.)	X	X
Parkinsonia praecox (Ruiz and Pav. ex Hook) Hawkin	X	X
Schinopsis lorentzii (Griseb.) Engl.	X	X
Cereus forbesii Otto ex. C.F. Först.	X	X
Senegalia praecox (Griseb.) Seigler and Ebinger	X	X
Aspidosperma quebracho-blanco Schltdl.	X	X
Aspidosperma triternatum Rojas Acosta	X	
Gonopterodendron sarmientoi (Lorenz ex Griseb.) Godoy-Bürki	X	

Table 2: Species found at different scales sharing the area corresponding to the Upper Paraná Atlantic Forest (BAAPA).

BAAPA species	0.5° x 0.5	0.6° x 0.6
Inga laurina (Sw.) Willd.	X	X
Bastardiopsis densiflora (Hook and Arn.) Hassl.	X	X
Alchornea triplinervia Müll. Arg.	X	X
Cupania vernalis Cambess.	X	X
Cabralea canjerana (Vell.) Mart.	X	X
Allophylus edulis (A.St.-Hil., A.Juss. and Cambess.) Hieron. ex Niederl.	X	X
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. and Wess. Boer	X	X
Guarea kunthiana A. Juss.	X	X
Diatenopteryx sorbifolia Radlk.		X
Plinia rivularis (Cambess.) Rotman		X
Muellera campestris (Mart. ex Benth.) M.J. Silva and A.M.G. Azevedo		X
Euterpe edulis Mart.		X

DISCUSSION

The endemism analysis conducted in this study revealed key patterns in the distribution of endemic species in Paraguay, contributing significantly to our understanding of the country's biogeography. The identification of endemism areas in the Dry Chaco (Fig. 2C, Fig. 2G) and the Atlantic Forest of Alto Paraná (BAAPA) (Fig. 2A, Fig. 2F) highlights the importance of these ecoregions as centers of floristic diversity, reinforcing their conservation value.

A biogeographic analysis of endemism areas, as defined by Platnick (1991), explores the extent to which different taxonomic groups coexist within these regions. Typically, one or more factors, whether historical or ecological, influence taxon distribution. However, these causal factors do not necessarily affect the entire biota uniformly, as species have distinct attributes and ecological requirements, resulting in different distribution patterns. Any repetitive patterns not attributable to sampling artifacts are likely the result of some shared factor (Szumik et al., 2012).

This study focuses exclusively on Paraguay to identify areas of endemism and prioritize conservation efforts within the country's borders. While Paraguay is not an isolated biogeographic unit and shares ecological and biogeographical connections with its neighboring countries, the scope of this analysis was determined by the practical need to inform national conservation policies. As Martínez-Hernández et al. (2015) highlighted, identifying endemism restricted to a specific geographic region holds considerable value for guiding local conservation efforts and optimizing resource allocation.

The repetition of areas of endemism across both scales of analysis (0.5º and 0.6º) (Fig. 3A, Fig. 3B), suggests that common historical factors have shaped species distribution over time. However, the absence of endemism areas in the Humid Chaco and Pantanal raises important questions. While these regions may be biologically rich, they may not exhibit significant levels of endemism due to their floristic heterogeneity or different biogeographic processes, such as the influence of adjacent ecoregions. Alternatively, limited data or even the grid size used could have impacted the detection of endemism in these regions.

The detection of an ecotonal zone in the Cordillera de Los Altos, Mesopotamian Savannas and southern BAAPA regions (Fig. 2E), likewise, the Cerrado and northern BAAPA areas (Fig. 2D), emphasizes the biogeographical importance of transition zones, where species from different ecoregions intermingle. These ecotones highlight the need to protect these areas for their biodiversity and their potential role in ecological resilience amidst environmental changes.

The multi-scale approach employed in this study allowed for the identification of more robust endemism patterns, underscoring the importance of using multiple spatial scales to better understand ecological interactions within each ecoregion.

Noguera-Urbano and Escalante (2015) refer to these overlapping areas as unions or transitions, resulting in patterns with diffuse boundaries. This finding aligns with the concept of biogeographic transition zones, geographical areas characterized by species overlap, partial segregation, and gradients of replacement (Ferro and Morrone, 2014). Ecologically, transition zones correspond to ecotones, where both ecological interactions and historical relationships among species are shared (Acha et al., 2015; Brown et al., 1996; Noguera-Urbano and Escalante, 2015; Yackulic and Ginsberg, 2016).

The results suggest a biogeographic transition and an ecotonal character from the Amambay and Ybyturuzú mountain systems toward the Paraguay River floodplain in the western part of Paraguay’s Eastern Region, consistent with what was postulated by Spichiger et al. (2006), who consider the Paraguay River floodplain as an ecotone between Chacoan communities and other communities in the Eastern Region. Mereles (2013) also points out that there is an ecotonal zone between the dry Chaco vegetation formations and the humid forests of the east.

The Dry Chaco and Atlantic Forest are two well-supported ecoregions by endemic flora species. Moreover, this analysis shows the ecotonal character of the Paraguay River floodplain, which forms the Cordillera de Los Altos and Cerrado ecoregions, where endemism areas were found but with species shared with the BAAPA (Fig. 2D, Fig. 2E). These results are consistent with those reported by Avila et al. (2023).

The findings of this study may be used for planning conservation strategies that prioritize the detected areas of endemism. However, they also underscore the importance of continuing research in regions where endemism was not detected, such as the Pantanal and the Humid Chaco, as well as in ecotones that may be key to ecological resilience in the context of climate change. Future studies should include additional records, species, and taxonomic groups to provide a more comprehensive view of Paraguay's biogeographical patterns.

While the species analyzed in this study are not strictly endemic to Paraguay and their distributions extend beyond the country's political borders, this research adopts a perspective that considers Paraguay as a biogeographic "island." This approach, although artificial, is necessary to identify priority areas for conservation within the national territory. By focusing on species overlap and endemism patterns within Paraguay, this study aims to provide actionable insights for conservation planning and policymaking at the national level. We recognize that expanding the scope of future studies to include transboundary analyses would provide a more comprehensive understanding of biogeographical patterns and connections across South America. However, the current study emphasizes the importance of addressing conservation challenges within Paraguay's borders, where critical biodiversity hotspots remain underrepresented in conservation efforts.

CONCLUSION

This study identified two key floristic endemism areas in Paraguay across different spatial scales: one in the Dry Chaco and another in the Atlantic Forest of Alto Paraná (BAAPA), underscoring their biogeographic importance for biodiversity conservation. The endemism areas in the Cerrado and Cordillera de los Altos further highlight the critical role of ecotones and biogeographic transitions in fostering diversity and speciation.

The absence of detectable endemism in the Humid Chaco, Mesopotamian Savannas, and Pantanal regions suggests the need for further research to investigate historical, ecological, or sampling factors that might explain these results. While these regions did not show endemism in this study, they may still hold important biological value, which should be explored using other approaches or taxonomic groups.

The results of this analysis provide a solid foundation for prioritizing conservation efforts, especially in response to threats like deforestation, agricultural expansion, and climate change. Strengthening protection in the BAAPA, Dry Chaco, and identified ecotonal zones will be essential for ensuring long-term ecological resilience.

Future studies should incorporate additional taxonomic groups to further validate and refine these endemism patterns. Expanding our understanding of Paraguay's biogeography will significantly enhance conservation planning, resulting in more comprehensive and effective strategies to protect the country's biodiversity.

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SUPPLEMENTARY MATERIALS

Supplementary Figure S1. Maps of areas of endemism reported by the NDM/VNDM program on the scale 0.5 x 0.5 degrees of geographic latitude and longitude.

Supplementary Figure S2. Maps of areas of endemism reported by the NDM/VNDM program on the scale 0.6 x 0.6 degrees of geographic latitude and longitude.

Supplementary Table S1. Record table of all species with latitude and longitude coordinates.

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