

# Where are they from and where are they going?: detecting areas of endemism, distribution patterns and conservation status of the order Spirostreptida in Brazil (Diplopoda, Juliformia)

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# Abstract

Millipedes are well-known for their limited dispersal abilities with species restricted to mountains, islands, and patches of forest being important models for formulating and testing biogeographic hypotheses. The order Spirostreptida is composed of nearly 1,300 species distributed across the Afrotropical, Oriental, and Neotropical regions. The order is divided into the suborders Cambalidea and Spirostreptidea with the families Pseudonannolenidae (Cambalidea) and Spirostreptidae (Spirostreptidea) occurring in Brazil. To date, there have been no studies on the biogeography of Neotropical Spirostreptida. We employed a multi-approach analysis with Parsimony Analysis of Endemicity, Endemicity Analysis, and Infomap, to detect areas of endemism and patterns of distribution of the order in Brazil. Six areas of endemism are proposed for the 133 Brazilian species: Northern Serra Geral, Southeastern mountain ranges, Cerrado and Atlantic Forest zone, Eastern Cerrado and Serra do Espinhaço, Pantanal, and Southern Amazon and Cerrado zone. Most endemic areas fall within the Atlantic Forest, which has been previously shown to be an important area of endemism for many invertebrate taxa. The richest biomes are the Atlantic Forest with 75 species and the Cerrado with 55 species, while the least rich biomes are the Caatinga with six species and the Pampa with three species. Although the southeastern region of Brazil has the highest species richness, it also has the highest concentration of threatened species. Based on International Union for Conservation of Nature (IUCN) criteria, most Brazilian Spirostreptida are either endangered or critically endangered, with the highest concentration of endangered taxa occurring in the Atlantic Forest biome.

# Introduction

The recognition of areas of endemism is essential for the understanding of historical biogeography and for determining conservation policies of specific regions (Myers et al. 2000; Casagrande and Grosso 2013; Martínez-Hernández et al. 2015). Areas of endemism correspond to regions which share a common history mainly as results of historical events (e.g. vicariance) and ecological factors acting to delimit the distribution of local species (Nelson and Platnick 1981; Rosen 1988; Hovenkamp 1997; Szumik et al. 2002, 2012; Morrone 2009). Different methods, such as Parsimony Analysis of Endemicity (PAE), Endemicity Analysis (EA), Brooks Parsimony Analysis (BAP), Paralogy-free subtree analysis, and Vicariance Events Analysis, have been used to identify such areas (Rosen 1988; Morrone 1994; Szumik et al. 2002, 2012; Hausdorf and Hennig 2003; Szumik and Goloboff 2004; Aagesen et al. 2013; Edler et al. 2017). Also, numerous studies have been conducted using these methods to detect areas of endemism in the Neotropical region based on the distribution of insects (Domínguez et al. 2006; Sigrist and Carvalho 2009; Ferrari et al. 2010; Silva and Vaz-de-Mello 2020), spiders (Sigrist and Carvalho 2009; Oliveira et al. 2015), and harvestmen (DaSilva et al. 2017).

Millipedes (class Diplopoda) are known for their low vagility and limited distributions with species often restricted to mountains, islands, and patches of forest (Golovatch and Kime 2009; Enghoff 2015). In some cases, species occur exclusively in a single cave and possess unique morphological adaptations as consequence of their restriction to subterranean environments (Golovatch and Kime 2009; Iniesta and

Ferreira 2015; Shear et al. 2016; Enghoff and Reboleira 2020). Members of the class have been used as important models for formulating and testing biogeographic hypotheses (Simonsen 1992; Enghoff 1993, 1995, 2015; Wesener and VandenSpiegel 2009; Suzuki et al. 2012; Means and Marek 2017; Reip and Wesener 2018). Moreover, millipedes are recognized for their important role as detritivores, playing a crucial role in the decomposition of plant matter and nutrient cycling (Schubart 1942; Crawford 1992; Golovatch and Kime 2009; Suzuki et al. 2013; David 2015; Nsengimana et al. 2018; Potapov et al. 2019). More recently, studies have focused on the relation between microclimatic factors and the distribution and life cycle of millipedes (David and Vannier 1997; Ott and Van Aarde 2014; Bogyó et al. 2015; Lazorík and Kula 2015), especially in regards to global change (David 2009; Gilgado et al. 2022).

The order Spirostreptida Brandt, 1833 comprises nearly 1,300 described species commonly found in tropical, subtropical, and temperate forests (Shear 2011; Enghoff et al. 2015). The distribution of the order corresponds to the classic Gondwana pattern with members occurring throughout the Afrotropical, Oriental, and Neotropical regions (Hoffman 1980; Jeekel 1985; Enghoff et al. 2015). Historically, a number of biogeographic hypotheses have been proposed regarding dispersion events of spirostreptidan groups towards the southeastern United States and northern Africa (see Jeekel 1985). The order is divided into the suborders Cambalidea and Spirostreptidea, each containing five families (Shear 2011; Enghoff et al. 2015). The families Pseudonannolenidae (Cambalidea) and Spirostreptidae (Spirostreptidea) are the dominant groups in the Neotropical region occurring from the Mexican to the South American transition zones (Enghoff et al. 2015; Iniesta et al. 2020). Although Brazil stands out in terms of high levels of species richness and endemism the distribution patterns and areas of endemism of the group in the country are poorly known (Schubart 1945a, 1950; Hoffman 1980; Krabbe 1982). Worldwide, members of Spirostreptida have received little attention concerning their conservation status although some taxa, such as Pseudonannolenidae from subterranean habitats, have been included in Red List categories (e.g. vulnerable, endangered, and critically endangered) according to IUCN criteria (Karam-Gemael et al. 2018, 2020).

In the present work, we investigate the biogeographic patterns of Spirostreptida in Brazil to address the following questions: (1) what are the areas of endemism for the order? (2) what are the species distribution patterns for the group and how are these patterns spatially arranged? (3) what is the conservation status of these species according to IUCN criteria? These questions were addressed using a multi-approach analysis, including distribution patterns and conservation statuses of native species from a biogeographical perspective.

## Material and methods

*Data collection.* The study group comprised 133 species from 21 genera in two families (Pseudonannolenidae and Spirostreptidae) (Fig. 1). Non-native species or species with doubtful records were excluded from the analyses. Distribution data were collected through a series of literature queries and supplemented with data from the following Brazilian institutions (curators in parentheses): **ABAM**, Coleção Biológica do Sul da Amazônia, Universidade Federal do Mato Grosso, Sinop, Mato Grosso (L. D.

Battirola); **CZUFMT**, Coleção Zoológica da Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso (A. Chagas Jr.); **IBSP**, Instituto Butantan, São Paulo (A. D. Brescovit); **ISLA**, Invertebrados Subterrâneos de Lavras, Lavras, Minas Gerais (R. L. Ferreira); **MCN**, Museu de Ciências Naturais, SEMA, Porto Alegre (R. Ott); **MNRJ**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (A. B. Kury); **MZSP**, Museu de Zoologia, Universidade de São Paulo, São Paulo (R. Pinto da Rocha); **UFPB**, Coleção de Invertebrados Paulo Young, Universidade Federal da Paraíba, João Pessoa, Paraíba (M. B. da Silva).

Data were checked to eliminate repetitive samples, and any samples with imprecise or incongruent locality information were not included in the analyses. All species described by 2020 were included in the dataset. Location information and geographical coordinates were verified in Google Earth Pro (Alphabet, California, USA, v.7.1). All map scales are given in kilometers. For this work, we employed the six Brazilian terrestrial biomes according to Coutinho (2006), *viz.*, Amazon Forest (*Amf*); Atlantic Forest (*Atf*); Caatinga (*Ca*); Cerrado (*Ce*); Pampa (*Pap*); and Pantanal (*Pat*).

*Areas of endemism.* To address the first question (what are the areas of endemism for the order?), we carried out two analyses of endemism based on distribution data. For the Parsimony Analysis of Endemism (PAE) (Rosen 1988; Morrone 1994; Nihei 2006) the entire region was divided into 1600 quadrats plotted on a map with grid size of 1°. Each species was coded according to its absence (0) or presence (1) in each quadrat. A hypothetical ancestral area (all-zero) was added to the matrix to root the tree (Rosen 1988). Quadrats without recorded species were omitted from the analysis. The dataset was analyzed under the parsimony criterion using TNT 1.5 (Goloboff et al. 2008; Goloboff and Catalano 2016). New Technology Search was performed under equal weights with the following parameters: random seed 0, sectorial search in default mode, and tree-fusing with five rounds until the most parsimonious tree was reached 50 times independently (Goloboff, 1999).

The same dataset was analyzed in an Endemism Analysis (EA) under NDM using the program VNDM ver. 3.0 (Szumik and Goloboff 2004) with grid sizes of 1°, 2°, and 3°. Approaches with different grid sizes were conducted to check the effect of this parameter on patterns of endemism based on distribution data (Aagesen et al. 2009; Escalante et al. 2010, 2013). The searches were conducted to retain areas with scores equal to or above 2.0 and containing at least two endemic species. The searches were repeated 100 times, keeping overlapping areas only if 90% of the species in each area were unique. Consensus areas of endemism using a cut-off of 100% similarity and strict consensus were computed (Szumik et al. 2002; Szumik and Goloboff 2004). As PAE and EA have different premises and parameters, we selected the final areas of endemism based on the outputs of both analyses, with the limits of the areas of endemism (totally or partially overlapping) drawn based on the clades and quadrats recovered in PAE and EA.

In addition to PAE and EA, analyses of bioregions were conducted using Infomap Bioregions (Vilhena and Antonelli 2015; Edler et al. 2017). This analysis is a network-based method which provides bipartite networks of species using a clustering algorithm based on geographical data, so that grid cells merge into different clusters, and thus, into distinct bioregions. We performed the analysis with the following

parameters: cell size (minimum = 1°, maximum cell size = 4°), cell capacity (minimum = 10, maximum = 100), and grid resolution of 1°. We used the following cluster parameters: number of trials = 1, cluster cost = 1.00, and with false weight on abundance.

*Patterns of richness and distribution.* To answer the second question (what are the species distribution patterns for the group and how are these patterns spatially arranged?), the species richness was calculated separately for all terrestrial Brazilian biomes. To examine the patterns of Spirostreptida distribution, we performed an analysis delimiting the range extension of each genus with a grid size of 1° (for more details see Lennon et al. 2004; Colli-Silva and Pirani 2019), with three different distribution categories defined according to the number of grids containing at least one record: narrow (2 or fewer grids), medium (3–9 grids), and widespread (10 or more grids). The analysis was conducted at the generic level due to the paucity of species-level taxonomic treatments for most genera within the order. The turnover of species proposed by Whittaker (1960) was calculated in order to measure the rate at which species assemblages change by grid. All these analyses were performed with DIVA-GIS ver. 7.5.0. (Hijmans et al. 2001).

In addition, we used the “Betapart” package in R (Baselga and Orme 2012) to assess the beta-diversity of all taxa. This analysis computed the total dissimilarity using Sørensen index, turnover, and nestedness components according to the distribution of the order across all biomes (Baselga 2010, 2012).

*Conservation status.* The third question (what is the conservation status of these species according to IUCN criteria?) was addressed via the R package “ConR v. 1.2.2” (Dauby et al. 2017) computing the extent of occurrence (EOO) and area of occupancy (AOO) of all species. This package generated automated conservation assessments (AA) according to IUCN Red List categories: Least Concern, Near Threatened, Vulnerable, Endangered, and Critically Endangered. These analyses are focused on providing tools for conservation policies based on a biogeographical approach. In addition, we assessed all occurrences and distribution categories for each genus throughout the Brazilian biomes. Data were plotted using the R package “ggplot2” (Wickham2016).

## Results

We compiled 545 occurrence points of Brazilian Spirostreptida. The PAE, EA, and Infomap analyses, carried out to detect endemic areas of Spirostreptida in Brazil, reflected the same pattern of biogeographical units: Pantanal, southern Amazon rainforest, eastern Cerrado, and central Atlantic Forest (mainly the mountain ranges of Serra da Mantiqueira and Serra do Mar) (Figs. 2–3). A summary containing all endemic areas recovered convergently in all analyses is presented in Fig. 8.

The PAE resulted in 196 trees, with 197 steps, consistency of 68, and retention of 62. Four areas were recovered with at least one quadrat containing exclusive species: area 1 (blue) – two grids in the Amazon River and Marajó Bay; area 2 (yellow) – six grids in the southern Amazon Rainforest, southern Pantanal, and western Cerrado (Araguaia River); area 3 (red) – one grid in the southern Caatinga; area 4 (green) –

six grids in the central Atlantic Forest (Mantiqueira and Mar mountain ranges) (Fig. 2). The values obtained in this analysis with species recovered by grid are presented in Supplementary material 1.

The EA recovered seven consensus areas with endemism indices (EI) ranging from 2.0 to 5.19 (grid size of 1°), six consensus areas with EI ranging from 2.0 to 6.98 (grid size of 2°), and eight consensus areas with EI ranging from 2.04 to 9.94 (grid size of 3°). The endemic areas recovered were the Atlantic Forest and southern Cerrado (in green), and the Pantanal, eastern Cerrado, and southern Amazon Rainforest (in yellow) (Fig. 3a). The number of consensus areas by each grid size and number of endemic species are presented in Supplementary material 2.

The Infomap analysis resulted in eight bioregions (Fig. 3b), with the number of species records by cell varying in relation to each bioregion. Bioregions 1 and 3–8 correspond to the Atlantic Forest and (partially) the Cerrado, with the most common species being *Pseudonannolene robsoni* Iniesta & Ferreira, 2014, *Pseudonannolene microzoporus* Mauriès, 1987, and *Plusioporus setiger* (Brölemann, 1901). Bioregion 2 corresponds to the Pantanal, eastern Cerrado, and southern Amazon Rainforest, with *Trichogonostreptus (Oreastreptus) mattogrossensis* (Silvestri, 1902) being the most common species. Sixty-one species of Pseudonannolenidae and Spirostreptidae were recovered with a single record across all bioregions. A summary table for all bioregions identified in this analysis is presented in Supplementary material 3.

The regions with the highest species richness of Pseudonannolenidae and Spirostreptidae are located primarily in the Atlantic Forest, with a maximum of 11 species by grid across both families (Fig. 4a). A similar trend is observed for the turnover of species, with 12 turnovers for Pseudonannolenidae and 16 for Spirostreptidae (Fig. 4b). The Atlantic Forest contains at least six exclusive genera, followed by the Amazon Forest with four genera, and the Pantanal with a single genus. The Cerrado, Caatinga, and Pampa did not contain any exclusive genera. The richest biomes are the Atlantic Forest with 75 species (46 Pseudonannolenidae and 29 Spirostreptidae) and the Cerrado with 55 species (35 Pseudonannolenidae and 20 Spirostreptidae), while the least rich biomes are the Caatinga with six species (three Pseudonannolenidae and three Spirostreptidae) and the Pampa with three species (one Pseudonannolenidae and two Spirostreptidae) (Fig. 5a). Eleven genera occur only in a single biome. Of the 21 genera, six are classified as widespread (occurring in at least 10 grids), seven as having a medium distribution (between 3–9 grids), and eight as having a narrow distribution (less than or equal to 2 grids) (Fig. 5b). The values of Sørensen dissimilarity, nestedness of species assemblages, and spatial turnover are 0.912, 0.128, and 0.784, respectively, with the highest values found between the Amazon Forest-Caatinga, Amazon Forest-Pampa, Caatinga-Pantanal, Caatinga-Pampa, and Cerrado-Pampa (Fig. 6).

Regarding the conservation assessments according to the IUCN Red List categories, most Brazilian Spirostreptida are classified as either critically endangered or endangered in terms of the number and proportion of species (Fig. 7a). The highest concentration of endangered species based on the proportion and number of species by grid, and number of records by grid, is in the Atlantic Forest, specifically the same region that was recovered as endemic (*i.e.* Cerrado and Atlantic Forest; Fig. 7b).

## Discussion

# Endemic areas and distribution patterns of Spirostreptida

The spirostreptidan fauna of Brazil is largely unknown primarily due to the scarcity of trained taxonomists in the country, with new records often turning out to represent undescribed taxa (Hoffman et al. 1996, 2002). The areas of endemism detected in this study were recovered at different levels of geographical congruence, and as such, we delimited them on the basis of their contiguous grids and number of shared species. Six endemic areas are herein proposed for the Brazilian Spirostreptida: Northern Serra Geral (**NSG**), Southeastern mountain ranges (**Smm**), Cerrado and Atlantic Forest zone (**CAF**), Eastern Cerrado and Serra Espinhaço (**ECS**), Pantanal (**Pt**), and Southern Amazon and Cerrado zone (**SAC**) (Table 1).

Table 1

Areas of endemism of Brazilian Spirostreptida. See Fonseca (1985), Lorenzi (1992), Coutinho (2006), Colombo and Joly (2010), and Alvares et al. (2013) for details of the biomes and ecoregions.

Endemic Area	State	Biome	Ecoregion	Features
Northern Serra Geral (NSG)	Santa Catarina, Paraná, São Paulo	Atlantic Forest	Araucaria Forest, Atlantic provinces	The Serra Geral is a mountain range located in southern Brazil, delimited by the Paraná Basin, and drained by tributaries of the Uruguay River. The region runs parallel to the Atlantic coast in its eastern portion and includes a narrow coastal plain connected to the southern Serra do Mar system. Its topography ranges from 900 to 1,200 meters a.s.l. with large canyons in the eastern portion. The annual mean temperature ranges from 10 to 22°C with temperatures reaching from 0 to 36°C in some areas), annual rainfall ranges from 1300 to 2200 mm. The area is characterized by largely subtropical vegetation.
Southeastern mountain ranges (Smm)	Mostly São Paulo	Atlantic Forest	Araucaria Forest, Paraná Forest, Atlantic provinces	The region includes three of the main mountain ranges in southeastern Brazil, the Serra da Paranapiacaba (ca. 1,000 meters a.s.l.), Serra da Mantiqueira (ca. 2,800 meters a.s.l.), and Serra do Mar (ca. 2,200 meters a.s.l.). The region has a variety of climates with annual mean temperature ranging from 10 to 26°C and annual rainfall ranging from 1000 to 2500 mm. The vegetation is composed of tropical rainforests and patches of forests of Brazilian pine <i>Araucaria angustifolia</i> (Bertol.) Kuntze (Araucariaceae) and <i>Podocarpus lambertii</i> Klotzsch (Podocarpaceae).
Cerrado and Atlantic Forest zone (CAF)	Mosly Goiás, Minas Gerais, São Paulo	Cerrado, Atlantic Forest	Paraná Forest, Cerrado provinces	The zone may be viewed as an ecotone between the southeastern Cerrado and the western Atlantic Forest. The region is characterized by a variety of climates, with annual mean temperature ranging from 18 to 26°C and annual rainfall ranging from 1000 to 1900 mm. Elevation ranges from 250 to 3,000 meters a.s.l. The area is composed of a shifting mosaic of habitats, with both biomes occurring in well-drained areas primarily along the Grande, Paranaíba, and Tietê rivers, located between strips of gallery, deciduous, and semideciduous seasonal forests.

## Figures.

Endemic Area	State	Biome	Ecoregion	Features
Eastern Cerrado, Serra do Espinhaço (ECS)	Bahia, Minas Gerais	Cerrado, Caatinga, Atlantic Forest	Cerrado province	The region includes the Serra do Espinhaço mountain range (ca. 2,000 meters a.s.l.), which runs through the states of Minas Gerais and Bahia, and the mineral-rich “Iron Quadrangle” (Quadrilátero Ferrífero) area, composed of meta-sedimentary rocks. The region is primarily drained by the São Francisco and Doce rivers. The annual mean temperature ranges from 20 to 26°C and the annual rainfall ranges from 700 to 1600 mm. The vegetation of the region is typical of the Cerrado, represented by a shifting mosaic of habitats, including rupestrian grasslands, and gallery forests.
Pantanal (Pt)	Mato Grosso, Mato Grosso do Sul	Pantanal	Rondônia province	The area corresponds to the Pantanal biome: a tropical wetland area interspersed with flooded grasslands. The annual mean temperature ranges from 22 to 26°C and the annual ranges from rainfall 1000 to 1900 mm. The region includes tropical grasslands, dry forests, and semiarid lowlands with a mosaic of rainforest and semiarid woodland plants.
Southern Amazon and Cerrado Zone (SAC)	Mato Grosso, Amazonas (in part)	Cerrado, Amazon Forest	Cerrado, Xingu-Tapajós provinces	The zone may be viewed as an ecotone between the Cerrado and the southern Amazon. The annual mean temperature ranges from 24 to > 26°C, and the annual rainfall ranges from 1900 to 3100 mm. The elevation ranges from 200 to 800 meters a.s.l. The heterogenous vegetation is represented by a mosaic of habitats including rainforests, transitional, and semi deciduous forests.
<b>Figures.</b>				

Most of these endemic areas are contained within the Atlantic Forest biome (Fig. 10a–e), which has been previously shown to be an area of endemism for many invertebrate and vertebrate species (Silva et al. 2004; Sigrist and Carvalho 2009; Bispo and Lecci 2011; Mendes and Sebastiani 2012; Trevine et al. 2014; DaSilva et al. 2017; Tonetti and Cavarzere 2017). Overall, two regions in the biome are highlighted in relation to their geological aspects and endemic species assemblages, the Atlantic coastal region and its continental islands, (e.g. Alcatrazes, Anchieta, Ilhabela, Moela, and Queimada Grande) and the mountain ranges in the eastern part of the region.

Historically, the Atlantic coastal region has received considerable attention due to its very restricted millipede fauna (Brölemann 1909; Schubart 1945a, 1949, 1950), and more recently for the common occurrence of non-native species (Bouzan et al. 2018; Iniesta et al. 2020, 2021, 2022a). Most of the continental islands in the biome were connected to the continent by a land bridge during the recession of

seawater at the time of the Last Glacial Maximum (~ 85,000–15,000 years ago), with many vertebrate and invertebrate populations remaining isolated from each other and the continent (Martin et al. 1986; Fleming et al. 1998). Schubart (1949: 239) suggested this scenario for some millipede species when comparing their wide variation in body size and patterns of coloration between continental and insular populations. The presence of continental islands, large rivers (e.g. Tietê and Paraná), and mountain ranges (e.g. Serra do Mar, Serra de Paranapiacaba, and Serra da Mantiqueira) is a significant factor affecting the distributional patterns and endemism of Spirostreptida in the Atlantic Forest, specifically following the climatic changes during the Pleistocene (see Cabanne et al. 2016). Studies have shown that some mountain ranges in the Atlantic Forest (e.g. the **Smm** area) correspond to routes of species diversification, leading to higher rates of endemism as compared to surrounding areas (Grazziotin et al. 2006; Bragagnolo et al. 2015; DaSilva et al. 2015; Oliveira et al. 2015; Lago-Barcia et al. 2020).

Historical processes, such as climatic events during the last ~ 2 M.Y., along with corresponding alterations of the phytophysiology of tropical forests due to fluctuations in wet and dry climates have been demonstrated to have influenced the spatial distributions of birds (Cabanne et al. 2016), beetles (Silva and Vaz-de-Mello 2020), and harvestmen (DaSilva et al. 2017) in the Atlantic Forest (Haffer 1969; Ledru et al. 2005; Silveira et al. 2019; Rodríguez-Zorro et al. 2022). Similarly, Walker et al. (2009) revealed that the broad distribution of some millipede species of *Narceus* Rafinesque, 1820 (Juliformia, Spirobolida) in the Appalachian Mountains is a result of a complex evolutionary history with multiple refugia in southeastern North America and population expansions in the north during the Pleistocene. Decker (2016) suggested that paradoxosomatid species (Polydesmida, Paradoxosomatidae) in Australia have high genetic variability as consequence of multiple Pleistocene refugia in the southeastern Australian mainland. In fact, historical climatic events in the Atlantic Forest may partially explain the pattern of distribution of Spirostreptida species, especially considering the relevance and influence of environmental conditions on the distribution of low vagility millipede taxa (David 2009; Gilgado et al. 2022).

The highest species richness is primarily found in the states of São Paulo and Rio de Janeiro (Figs. 4a, b, 5a). This is not unexpected, as most of our knowledge regarding Brazil's millipede fauna is a result of extensive studies by the European naturalists O. Schubart and H. W. Brölemann at the beginning of the 19th century, which resulted in the description of a large number of species and distributional data from these states (Brölemann 1904, 1909; Hoffman 1980; Bouzan et al. 2018; Iniesta et al. 2021). Since these early studies, however, few others have focused on the taxonomy of Brazilian Spirostreptida (see Krabbe 1982).

The endemic pattern of Spirostreptida in the Cerrado (areas **CAF**, **ECS**, and **SAC**) may be best explained by the physiognomically heterogeneous vegetation of the biome (Lorenzi 1992) (Fig. 10f). Overall, these areas present a composition typical of a semi-humid tropical climate (Alvares et al. 2013) with a shifting mosaic of relatively well-drained gallery forest habitats along streams (e.g. São Francisco and Paraná rivers). Due to the low vagility of millipedes, it is plausible that many species have very limited distributions in specific areas across the biome (e.g. eastern portion of the Cerrado in **CAF**, or western

portion of the Cerrado in **SAC**) resulting in a distinctive faunal composition. The expansions and contractions of woodlands under cool and moist conditions in the Cerrado during the Last Glacial Maximum may have been influential in the diversification of species (Oliveira et al. 2020), although this has not been well documented for millipedes.

Most studies in the Pantanal have revealed high species richness influenced by a local mosaic of forests and savannas in extensive floodplains (Marques et al. 2016; Martins et al. 2021). The composition of millipedes shows high dissimilarity and high turnover of species as compared to other Brazilian terrestrial biomes (Fig. 6). The spatial distribution of Spirostreptida is largely concentrated in the northern part of the region and in the Cáceres and Poconé subregions (Fig. 4a, b) where extensive faunal surveys have been conducted during the last two decades (Golovatch et al. 2005; Battirola 2009, 2017; Santos-Silva 2019; Iniesta et al. 2022b). Most Spirostreptidae found in the Pantanal migrate along the surface following the flood line during high water periods (Battirola 2017). The same activity has been observed in some Central Amazonian millipede species (Adis 1981, 1992) in areas close to the Araguaia and Amazon rivers (Schubart 1947a). Most populations found in these areas are composed of large-bodied individuals with relatively high mobility (Santos-Silva, 2019) as compared to species from other endemic areas (e.g. **Smm**).

Most species recovered in the **SAC** endemic area are concentrated in the southern Amazon and in the northern Cerrado, a transitional zone partly composed of open ombrophylous forest with spaced vegetation and characterized by long periods of drought. The low species richness of the Amazon forest, as compared to the transitional area to the Cerrado, is likely a result of the limited number of taxonomic studies on the millipede fauna of the region (Brölemann 1904; Hoffman et al. 1996, 2002).

In general, little is known regarding the ecological drivers affecting the distributional patterns of Spirostreptida at small and medium scales. Nonetheless, average temperature and humidity have been recognized as important bioclimatic variables in determining the occurrence of millipede species around the world (David 2015; Gilgado et al. 2022; Iniesta et al. 2022a). Some spirostreptidans have a low ecological demand regarding their occurrence and abundance in old growth forests or in poly/monocultures of *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae), *Eucalyptus* L'Hér. (Myrtaceae), *Coffea* L. (Rubiaceae), *Zea mays* L., *Citrus reticulata* Blanco (Rutaceae), *Nicotiana* L. (Solanaceae), and beans (Fabaceae) depending only on relative humidity and availability of organic resources (Schubart 1942, 1945b, 1949, 1955). In addition, some synanthropic species found in close proximity to residential areas are known for their occasional population outbreaks (Schubart 1944, 1945b, 1947b, 1958).

## Conservation status of Spirostreptida

Most Brazilian Spirostreptida occur in areas that have not been designated as conservation units or do not have conservation policies in place. To date, five spirostreptidan species are classified as either endangered or critically endangered according to the most recent list of threatened species provided by Brazilian authorities (Fig. 9). All of these taxa occur in subterranean environments and represent

troglophobic species with specialized morphological traits, such as *Pseudonannolene ambuatinga* Iniesta & Ferreira, 2013, *P. lundi* Iniesta & Ferreira, 2015d *spelaea* Iniesta & Ferreira, 2013 (Pseudonannolenidae) (see Sket 2008).

In Brazil, since the publication of the Federal Decree n°6640/2008 and the Normative Instruction MMA 02/2017, subterranean environments are protected by law according to geological and biological attributes (e.g. presence of troglomorphic species), so that only caves of maximum relevance are fully protected (Brasil 2008, 2017). As a result, most of the Brazilian cave fauna has been extensively studied in the last two decades, resulting in the description of species, habitats, and biological attributes. With the exception of *P. lundi*, which occurs in a single, relatively well-preserved, rarely visited cave, the remaining species occur in areas which are at least partially impacted by anthropogenic activities. The caves where *P. ambuatinga* occurs are the focus of an intense investment in mining operations of carbonate rock to produce cement, lime, and soil correctives, directly affecting the subterranean environment and cave communities (Iniesta and Ferreira 2013a). Other impacts observed in the surrounding areas include deforestation, agropastoral practices, and construction in close proximity to drainages and/or cave entrances (Cavalcanti et al. 2012). *Pseudonannolene spelaea* is regarded as an Amazon Rainforest relict, occurring only in caves of the Serra do Carajás located in the region of the Floresta Nacional de Carajás (FLONA-Carajás), an Amazonian landscape composed of large plateaus of ferruginous outcrops (Iniesta and Ferreira 2013b). This region has experienced intensive exploration of its vast iron ore deposits, which has influenced the local economy and increased environmental pressures (Palheta et al. 2017). Other endemic invertebrates, such as beetles, crickets, flies, centipedes, spiders, and terrestrial isopods, are also found in these ferruginous outcrops, reinforcing the urgency of additional studies to understand the impacts of mining operations on species distribution and conservation (Iniesta et al. 2012; Brescovit et al. 2018; Campos-Filho et al. 2020; Chagas-Jr and Bichuette 2018; Bouzan et al. 2019; Asenjo et al. 2019; Junta et al. 2020; Teodoro et al. 2021). Although no apparent morphological features indicate the restriction of *P. imbiensis* to caves, all known specimens have been collected from caves or cave entrances (Fontanetti 1996; Gallo and Bichuette 2017; Bichuette et al. 2019). Populations of *P. imbiensis* from the Angélica, São Bernardo II, and São Vicente II caves have been considered as troglobitic, while those from the Terra Ronca II cave have been considered as troglophilic by Gallo and Bichuette (2017). Among the five IUCN threatened spirostreptidan species, *P. tocaiensis* is a typical troglophilic species known only from its type locality, Toca cave (Itirapina, São Paulo state), which has a fairly well-preserved surrounding area (Fontanetti 1996; Freitas et al. 2004). Importantly, the most recent presidential decree (decree n°10.935, January 12, 2022) is currently allowing the destruction of even the most conservation relevant caves in Brazil, and represents a serious threat to all Brazilian subterranean biodiversity (see Ferreira et al. 2022).

Although the southeastern region has the highest spirostreptidan species richness in Brazil (Figs. 4a, 5a), it also has the highest concentration of threatened species (Fig. 7b). The distribution of species in the Atlantic Forest has been severely altered by accelerated deforestation and subsequent fragmentation effects, medium to large-scale farming activities (e.g coffee, orange, and sugar cane), and by indiscriminate urban expansion and industrialization since the beginning of the 20th Century (see

Fonseca 1985; Lembi et al. 2020). Only approximately 10% of the original area of the Atlantic Forest (once covering 16% of Brazil) remains, represented by small forest patches and regenerating areas (Colombo and Joly 2010; Joly et al. 2014; Rezende et al. 2018). A similar situation can be seen in the Pantanal and the Cerrado, in which a number of endemic areas were recovered during this work. Studies have shown that there is a high potential for loss of biodiversity in these regions through deforestation due to extensive cattle farming, agricultural activities, wildfire, hunting, and unregulated tourism (Ratter et al. 1997; Durigan et al. 2007; Alho et al. 2019; Berlinck et al. 2022).

This is the first study focused on exploring the distribution of Spirostreptida in the Neotropics based on analytical methods, with six areas of endemism proposed for the 133 Brazilian Spirostreptida species. Most endemic areas fall within the Atlantic Forest biome, an extremely biodiverse Neotropical area harboring an abundance of invertebrate and vertebrate taxa. Although the southeastern region of Brazil (including the Cerrado and Atlantic Forest endemic areas) has the highest recorded Spirostreptida species richness, it also has the highest concentration of threatened species. In recent times, anthropogenic activities, such as farming practices and urban expansion, leading to an accelerated deforestation and habitat fragmentation, have greatly affected the flora and fauna of the region. The majority of Brazilian Spirostreptida, likely also true for other groups with low vagility, are either endangered or critically endangered, with the highest concentration of endangered species occurring in the Atlantic Forest. Our study demonstrates that species assemblages of Spirostreptida are largely restricted to small and medium scale areas (e.g. islands, mountain ranges, and caves) susceptible to human impacts. Moreover, these areas are severely threatened by the lack of comprehensive conservation strategies, especially those containing caves, which are continually threatened by mining and development operations. Increased taxonomic efforts coupled with in-depth exploration of biogeographic patterns may reveal detailed local patterns, such as in the Amazon and the Caatinga, which are largely unknown regarding Spirostreptida and Diplopoda as a whole.

## **Declarations**

## **Declarations**

### **Competing Interests**

The authors have no relevant financial or non-financial interests to disclose.

## **Author contributions**

LFMI and RSB developed the idea of the manuscript, collected the data, and performed the analyses. LFMI designed the figures and graphs. LFMI, RSB, JCM, KI interpreted the results. All authors contributed equally to the text.

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