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Global Biogeography of Predatory Stink Bugs (Pentatomidae: Asopinae): Richness, Endemism and Regionalization

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Asopinae is a globally distributed subfamily of Pentatomidae, encompassing 65 genera and over 300 known species. Most asopines are generalist predators, making them valuable for the biological control of agricultural pests. Although the subfamily has a wide global range, most genera are region-specific. To date, no database has consolidated collection sites or provided organized, updated distributional records for these predatory stink bugs. Here, we aim to build a web interactive database after compiling distribution data for Asopinae species across all continents except Antarctica, using taxonomic revisions, regional lists, catalogues, and specimen collections. Our study also examines global patterns of taxonomic richness using multiple analytical units, including political boundaries, biogeographic realms, ecoregions, and grid cells. The resulting database of 5,831 records for 298 species is now available on the "Asopinae of the World Database," an interactive, live website. Results indicate that the most species-rich countries are

predominantly the world's largest, with the exception of nations characterized by high proportions of deserts or extreme environments. Species richness across ecoregions exhibits discontinuous patterns, even between adjacent areas. Among biogeographic realms, the Neotropics host the highest richness, followed by Indo-Malay, Palearctic, Afrotropic, Nearctic, and Australasian regions. Furthermore, we identified 23 bioregions that align closely with classical biogeographical realms, and we recognized 14 key areas of endemism within the group. The extensive data presented in this study offer a valuable resource for future systematic, taxonomic, biological, and applied research on Asopinae.

Keywords: Biogeographical realms, Bioregion, Hemiptera, Insects, Entomological collection

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BACKGROUND

The predatory stink bugs (Asopinae) compose a relatively large, worldwide distributed subfamily of Pentatomidae with 65 genera and more than 300 known species (SM. 1). The asopines are commonly differentiated from other pentatomids by their predatory habits instead of phytophagy (Zhao et al. 2013a b; Salini 2016; Zhao et al. 2016 2018; Roca-Cusachs et al. 2018; Carpintero and Biase 2019; Roell et al. 2019). Most asopines are generalist predators, thus interesting for the biological control of agricultural pests (Salini and David 2023). Several morphological features are probably related to the asopines' alimentary habits, such as the large and strong labium and the presence of spines and leg projections. Other particular characteristics are found in the male genitalia, particularly the presence of pseudoclaspers connected to the parameres, and the aedeagus with a thecal shield (Gapud 1991; Gapon and Konstantinov 2006; Roell et al. 2020).

The monophyly of Asopinae has been speculated (Schouteden 1907; McDonald 1966; Thomas 1992; Gapon and Konstantinov 2006), and Pendergrast (1957) suggested that Asopinae, Discocephalinae, Podopinae (Graphosomatini) and Phyllocephalinae should form a natural group based on similarities in the male genitalia. McDonald (1966) also indicated that Asopinae, Podopinae and Pentatomini present the male genitalia similarly structured. Gapud (1991) proposed Asopinae as sister to a Pentatominae group formed by four Strachiini genera: *Eurydema* Laporte, 1833, *Murgantia* Stål, 1862, *Stenozygum* Fieber, 1860, and *Strachia* Hahn, 1833 (Rider 2024). More recent phylogenetic studies of Pentatomidae have been recovered the monophyly of Asopinae

and generally place the subfamily sister to Menidini (Pentatominae) (Lian et al. 2022; Roca-Cusachs et al. 2022; Ding et al. 2024; Genevcius 2024), but Luo et al. (2024) found Asopinae sister to the group Aeptini+Myrocheini.

Four tribes have already been proposed to classify the Asopinae genera based on morphological characteristics: Discoceraria Schouteden, 1907 (= Stiretrides Amyot & Serville, 1843), Asoparia Schoudeten, 1907 (= Asopides Amyot & Serville, 1843), Jallini Dupuis, 1949, and Stilbotini Gapud, 2015. However, this classification has not been used due to the lack of robust phylogenetic approaches evaluating the group's internal relationships and because these tribes were created for only a minority of the Asopinae genera.

In the last few years, some studies have sought to explore important taxonomic and morphological questions concerning asopines. Some genera were revisited and new species were described (*e.g.*, Zhao et al. 2016; Roca-Cusachs et al. 2018, 2019; Roell et al. 2019; Brugnera et al. 2020a b; Roell et al. 2021a b; Sampaio et al. 2023), morphological structures were evaluated from a comparative and evolutionary perspective (Brugnera et al. 2019a; Roell et al. 2020a, b), and a catalogue of type-specimens deposited in the Natural History Museum of London was presented (Roell et al. 2023). The phylogeny of Asopinae and its internal relationships is under study (Roell 2019).

Although the subfamily is largely distributed around the world, most genera are restricted to specific regions. Only *Andrallus* Bergroth is registered for all biogeographic regions (except Antarctica). Thomas (1992 1994) listed the occurrence countries for each Asopinae species based on literature data and museum specimens. The distributions of taxa described after 1994 were listed in the respective taxonomic treatments. To date, no database is available specifying the collection sites nor organizing and updating the distributional records of the predatory stink bugs. Furthermore, there are still no studies on endemism and regionalization for Asopinae, which is also quite scarce for Pentatomidae and even for Heteroptera (Poester-Carvalho et al. 2023).

Our primary goal in this study is to provide a web-based interactive database on the updated distribution records of the species in the subfamily Asopinae (Pentatomidae) across all biogeographic regions, and explore global taxonomic richness patterns considering a diversity of analytical units (political boundaries, biogeographic realms, and ecoregions and grid cells). Additionally, we aim to identify key areas of endemism and investigate global distribution patterns, proposing the first biogeographical regionalization scheme for the group.

MATERIALS AND METHODS

Distributional data and online database

We compiled distribution data for Asopinae species occurring in all continents except Antarctica (Fig. 1) from taxonomic revisions, biological treatments or catalogues of Asopinae that include collection site information about the specimens examined (published up to 2024), regional lists and catalogues of Hemiptera, Heteroptera or Pentatomidae (published up to 2019), and specimens deposited in collections. The identification of the physically examined specimens was verified through specific identification keys and consultation on type material. All sources used are available in SM. 2. For most of the specimen labels, the geographical coordinates of the collection site were unavailable; thus, we georeferenced the records using the locality indicated as the collection site. The geographic coordinates in decimal degrees were taken from the 'Google Maps' website (https://www.google.com.br/maps/) and the 'GeoNames' website (http://www.geonames.org). When localities for a given species provided limited information, such as solely the country name, we georeferenced them only if they represented the sole occurrence for that species within the respective country. We discarded records whose assigned localities were impossible to georeference due to missing or inconsistent information. For the final analysis, we also discarded duplicate records.

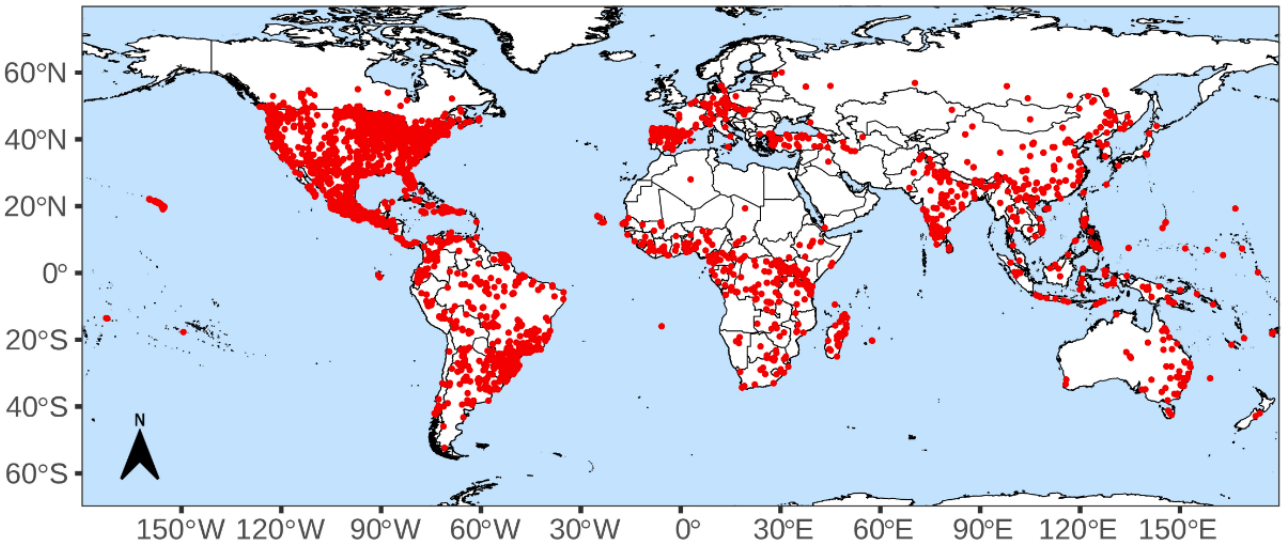

Fig. 1. World map showing all records gathered.

The specimens examined are deposited in the following collections, and please refer to the List of Abbreviations for the full names of units: AMNH; AMS; BHMH; CEIOC; CeNak; CERPE; CLEV; DARC; DZUP; NMPC; EMG; FSCA; HNHM; IAvH-E; ICN; INHS; INPA; MACN; MCNZ; MCPM; MCTP; MLPA; MNHN; MNRJ; MPUJ; MZLS; MZSP; NHMUK; NHRS;

OUMNH; RBINS; RMCA; SDEI; SIM; STRI; UFRG; UFRJ; UNAB; UMSP; USNM; VMNH; ZFMK; ZMHB; ZMUC.

Our final database is available on an interactive live website, accessible through the platform GitHub Pages (https://afonsopoester.github.io/asopinae_of_the_world/main.html). We built the website using the Quarto publishing system in the R Environment (R Core Team) and published it on Github. We wrote the code of the website using the Quarto Document, which allows for the creation of websites with interactive filters, maps and tables. The data used is the same for the analysis of species richness and endemic species. The code is available through the GitHub repository "asopinae_of_the_world" (https://github.com/afonsopoester/asopinae_of_the_world), with the respective packages used in the creation of the website. We used leaflet (Cheng et al. 2025) for maps; reactable (Lin 2025) for tables, crosstalk (Cheng and Sievert 2023) and bslib (Sievert and Cheng 2025) for filters, and also htmlwidgets (Vaidyanathan et al. 2023) and htmltools (Cheng et al. 2024).

Species richness and distributional patterns

Regarding the analysis in this section, we considered all 298 species in the database. We created richness maps to (1) World Administrative Division (GADM 2024, http://www.gadm.org/), (2) Ecoregions and (3) Biogeographical Realms (the latter two according to Dinerstein et al. 2017, https://ecoregions.appspot.com/). We also produced species richness maps using 2º grid cells, which allow for a better exploration of sample bias and discrepancies among the areas. We assessed species that are restricted to specific countries, continents, or biogeographical regions to generate summary statistics on the data. All maps and analyses were run in R Environment (R Core Team), using the packages *tidyverse* (Wickham et al. 2019), *sf* (Pebesma 2018) and *SpeciesGeoCodeR* (Toppel et al. 2016). We used the *SpGeoCod* function from the *SpeciesGeoCodeR* package to classify the records according to the GADM and Ecoregions datasets. We used the *sf* package to conduct multiple spatial data transformations and extract information from these data.

Infomap Bioregions analysis

Bioregions were defined through the bipartite network approach implemented in the web application Infomap Bioregions (Edler et al. 2017). For this analysis, we discarded species known only for the country level, leaving 268 species and 4,993 records. The method builds a bipartite network of grid cells and species, and searches for *clusters* of grid cells with the Infomap Algorithm

(Rosvall and Bergstrom 2008). The network clusters, identified by Infomap algorithm (Rosvall and Bergstrom 2008) to cluster bipartite networks, represent bioregions each presenting a species list along with their indicative scores for the respective bioregion. The grid cells use adaptive resolution to determine their sizes according to the number of records assigned per area. We selected a minimum cell size of 2º and a maximum cell size of 8º, providing a balance between a global scale representation and enhanced resolution in densely sampled areas. A minimum cell capacity of two records was established, leading to the exclusion of cells with only one record. Additionally, a maximum cell capacity of 20 was set, ensuring that regions with a higher concentration of records were subdivided into smaller cell sizes, thereby enabling greater resolution in densely sampled areas. All analyses were run with 10 trials. Infomap Bioregions also has the "Cluster Cost" parameter, which defines the time needed for a cluster to be defined during the search. The default value is 1.0. A smaller value will result in more bioregions, as opposed to a higher value, which will result in less bioregions. As a sensitivity criteria, we tested four values of "Cluster Cost", in four different analyses, keeping the other parameters the same. The values tested were: 0.8; 1.0; 1.2 and 1.4. The input files (.csv) used in Infomap Bioregions, as well as the results of the analyses and corresponding files, are available as sm. 3.

NDM/VNDM analysis

We performed an endemicity analysis using NDM/VNDM v. 3.1 (Szumik and Goloboff 2004) to identify Areas of Endemism (AEs) for Asopinae species. In the same way as the Infomap Bioregions analysis, we discarded species known only for the country level, leaving 268 species and 4,993 records. NDM searches for sets of grid cells which share two or more species, using an heuristic algorithm, based on an index of species distribution fit within a particular area (set of grid cells), where the endemism index of a given area is the sum of the fits of the species occurring there. In order to search for AEs across different scales, we used two grid cell sizes: 4º and 8º (latitude/longitude) The same grid origins were used in both analyses (X = -192.000 and Y = 66.000). We marked the options: "swap two cells at a time", and "use edge proportions". We set "Save up to 100,000 sets" - increasing memory -, "If memory is filled during search, clean up to 5 times", "Keep Overlapping Sets if 50% of Species Unique" - keeping overlapping areas only if half of species unique - and "Repeat Search 50 times". All the remaining search parameters were kept as default. After the search of Individual Areas, we applied a flexible consensus (Aagesen et al. 2013) to group Individual Areas into Consensus Areas (CAs), with a cut-off value of 50%. The input files

(.xyd) used in the NDM analysis, as well as the results of the analyses and corresponding files, are available as sm. 4.

Due to the large number of consensus areas (CA) identified at different spatial scales, we applied a metaconsensus criterion to group the CAs resulting from the NDM analysis (Hoffmeister and Ferrari 2016; Ferrari et al. 2022; Poester-Carvalho et al. 2023). This approach has been proven to be useful to group areas from multiple analyses with similar species composition. We used the beta-Simpson index of dissimilarity to calculate pairwise dissimilarity of species composition between the CAs and subsequently clustered them using UPGMA (unweighted pair-group method using arithmetic averages) algorithm. The resulting dendrogram was used to define Areas of Endemism Groups (AEGs). Some areas were not clustered, but we still used the term AEG, for the sake of simplicity. The metaconsensus analysis was run in the R Environment (R Core Team) using the *recluster* R Package (Dapporto et al. 2013) based on a presence/absence matrix of the CAs and the species of the dataset, using the *recluster_cons()* function. The R script and the presence/absence matrix are available as sm. 5.

RESULTS

The compiled database is available on the "Asopinae of the World Database" (https://afonsopoester.github.io/asopinae_of_the_world/). Interactive filters, tables and maps, and summary statistics are available on the website. A map with all records as points is available, and the user can select the species or genus of interest. The raw data contains latitude, longitude, continent and country of each record. There is also a complete list of the species and the respective continents and countries where each species was recorded. As new records and species are made available throughout the time, we intend to update the database.

Overall, we compiled records for 5831 specimens for 298 species, from 133 published papers (4260 records) and 44 scientific collections (1571 specimens). After the exclusion of duplicates, 5030 records remained (Fig. 1A), with an average of 16.82 records per species (standard deviation of 40.82). Singletons represent 31.2% of the dataset, totalising 93 species with only one locality recorded. *Podisus maculiventris* (Say), *Apoecilus bracteatus* (Fitch), *Podisus brevispinus* Thomas, *Podisus placidus* Uhler, and *Apoecilus cynicus* (Say) are the top five species in number of records (Fig. 2A; SM. 1 and 2).

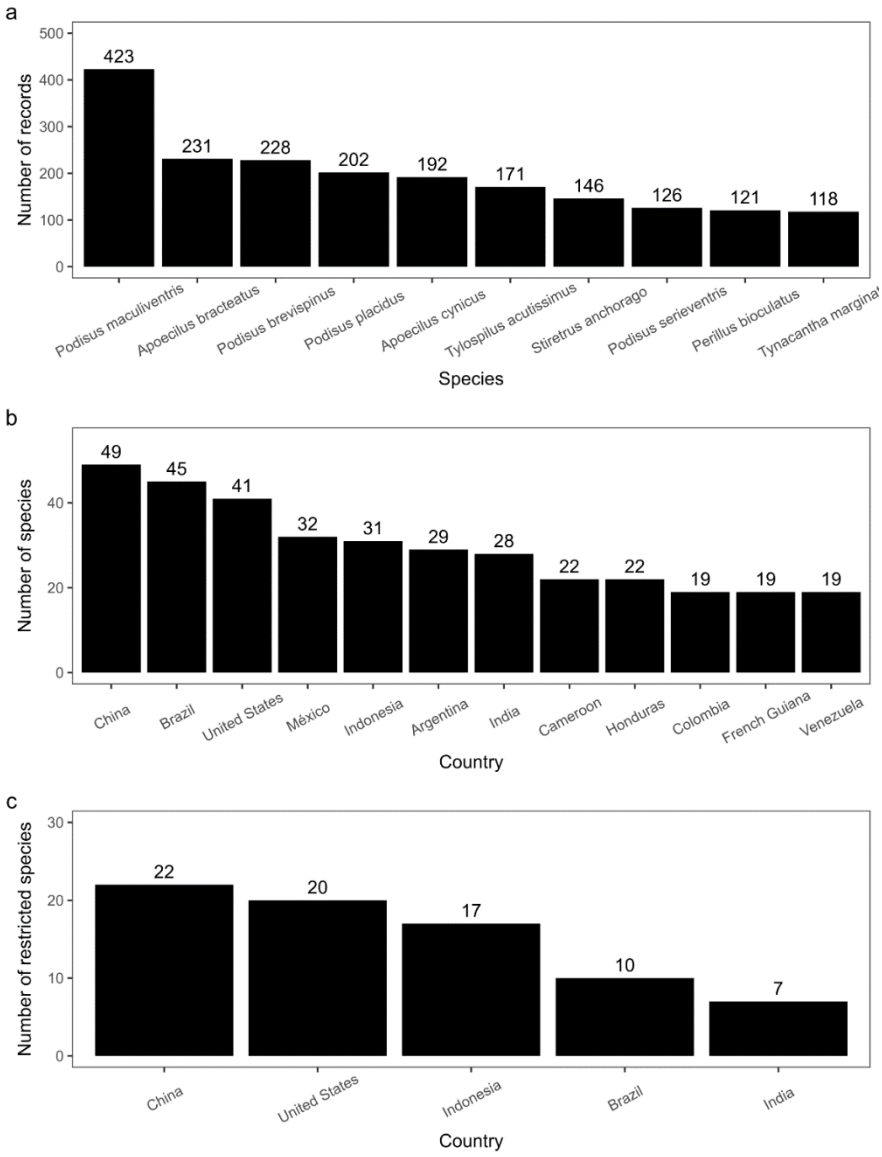

Fig. 2. A, Top 10 Asopinae species with the most records. B, Top 10 most speciose countries. C, Top 10 countries with most species restricted to.

We recorded information on Asopinae species for 129 countries or administrative regions (following the GADM classification) from all continents except Antarctica (Fig. 1). The southernmost record is located at -52.36º Latitude, in Chile, while the northernmost is located at 60.05º Latitude, in Russia (Fig. 1A). A large number of species, 263 out of 298 (87.96% of the dataset), occur in only one continent. Considering the political units, 154 species (51.50% of the dataset) occur in only one country or administrative region.

As shown in figure 2B and figure 3, the most species-rich countries are mainly the largest countries of the world. However, large countries with high proportions of deserts and extreme environments, such as Australia and Russia, are not so speciose. Diversity across countries is unevenly distributed, with noticeable gaps (*e.g.*, the northeastern region of Brazil).

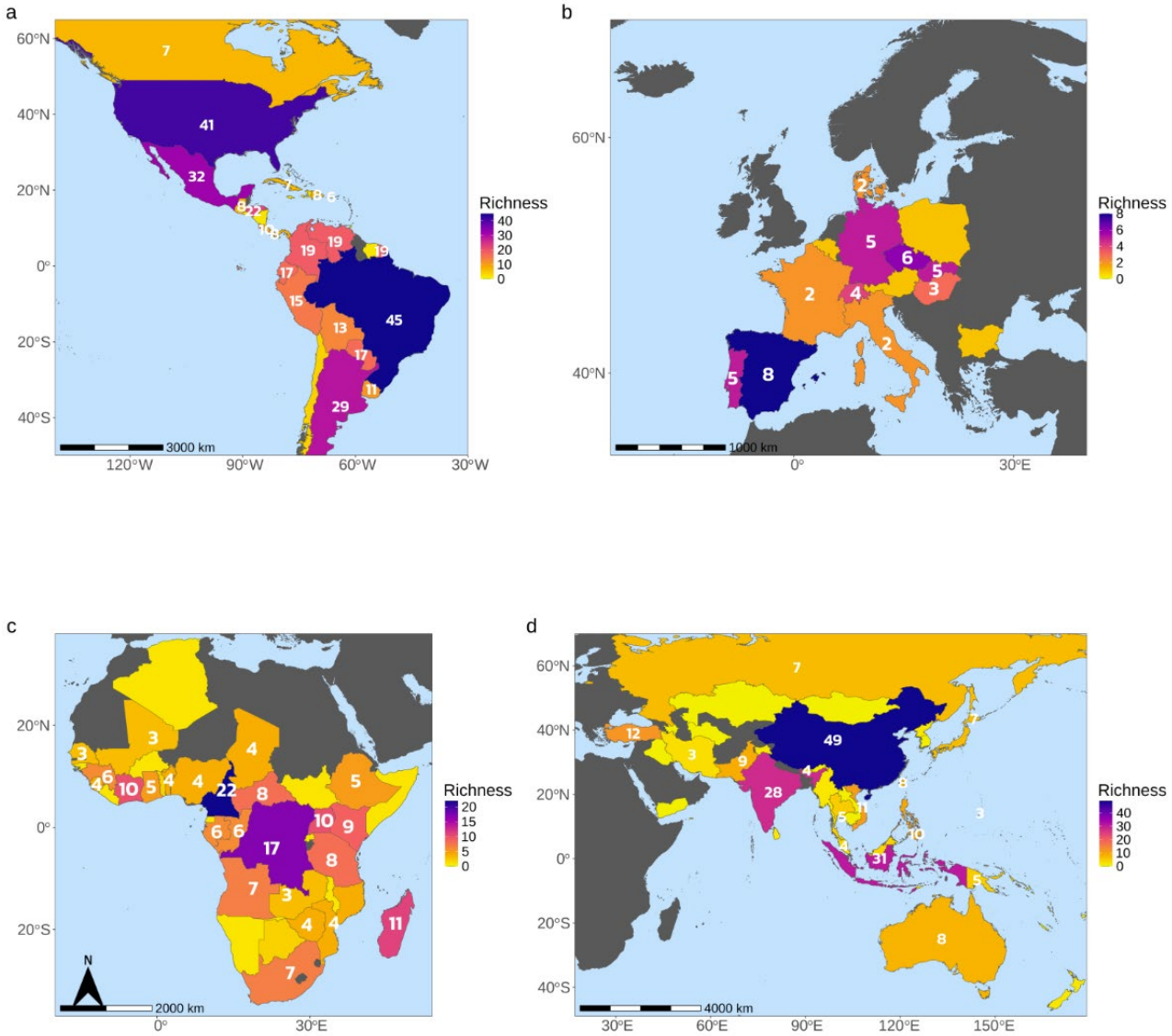

Fig. 3. Number of Asopinae species in each political unit, for different regions of the World: A, Americas. B, Europe. C, Africa. D, Asia and Oceania.

All the top 10 most recorded species (Fig. 2A) are restricted to the American continent, mainly distributed in North America - with the exception of *T. marginata* Dallas, restricted to South America. *Alcaeorrhynchus grandis* (Dallas) and *Apateticus lineolatus* (Herrich-Shaffer) are distributed across the Americas. There are 36 species occurring in more than one continent. We highlight some of the most widely distributed species of our dataset: *Andrallus spinidens* (Fabricius) and *Zicrona caerulea* (Linnaeus) both occur widely, across the Americas, Africa and Eurasia. *Picromerus bidens* (Linnaeus) also occurs both in the Americas and Eurasia.

The patterns of species richness across ecoregions (Fig. 4) exhibit discontinuous patterns between nearby areas. In South America (Fig. 4A), the highest richness is found in the South and Southeast ecoregions of Brazil, particularly in the Alto Paraná Atlantic forests, southern Atlantic Forest, and also Pampa, with the Cerrado showing high richness as well. The Amazon region shows very unequal and discontinuous richness among the ecoregions, with the highest richness in the

Guianan lowland moist forests. In the northern limit of the Neotropics, the Petén-Veracruz moist forests and Trans-Mexican Volcanic Belt pine-oak forests stand out, while in the southern part of the Nearctic region, the Chihuahuan desert and Western shortgrass prairie are notable. In the Nearctic region, the areas of the Temperate Broadleaf and Mixed Forests biome exhibit greater richness compared to the West Coast (Fig. 4A).

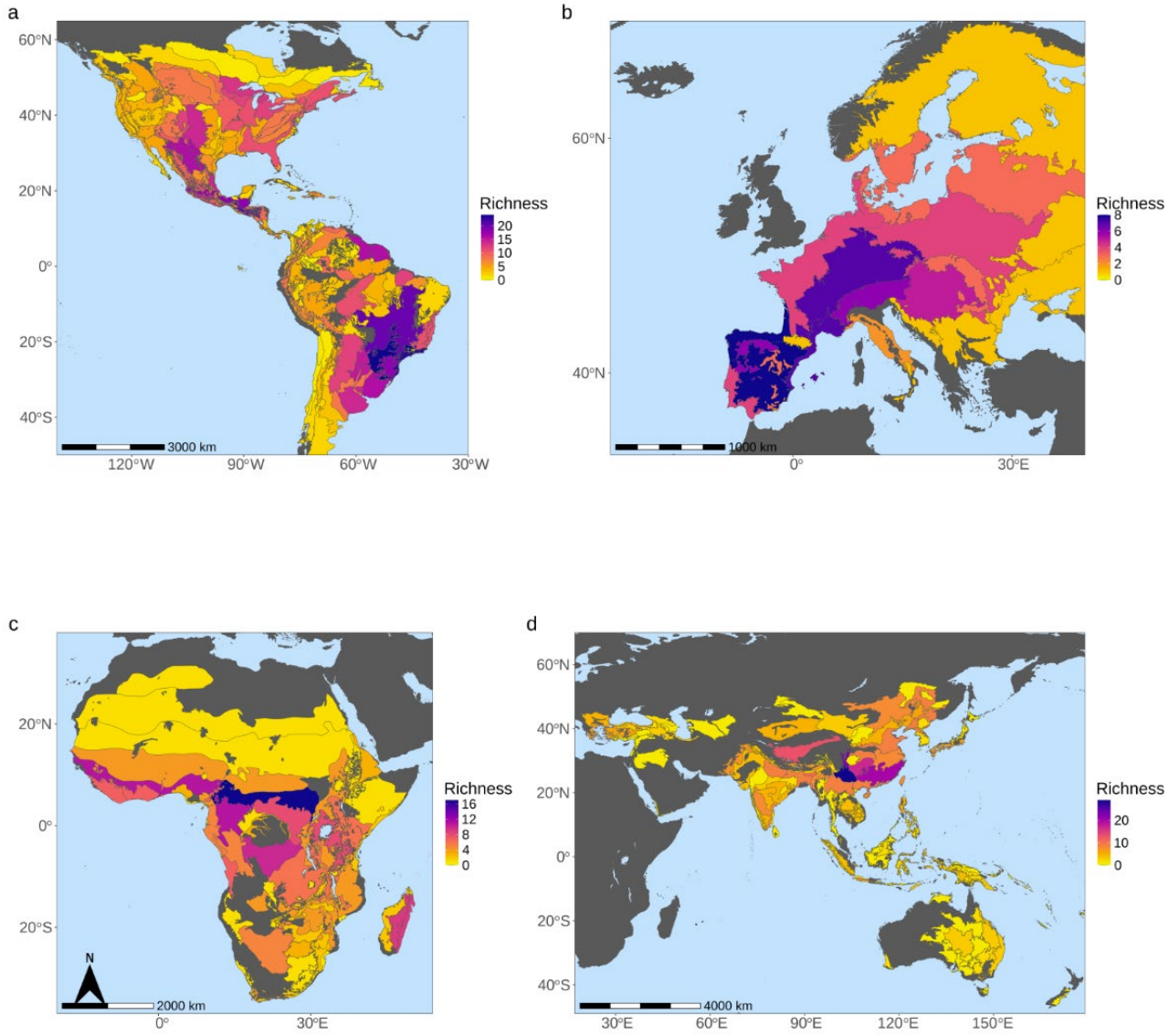

Fig. 4. Richness of Asopinae species in each WWF Ecoregion, for different regions of the World: A, Americas. B, Europe. C, Africa. D, Asia and Oceania. The original ecoregions map can be accessed in: https://ecoregions.appspot.com/

In the west of the Palearctic region (Fig. 4B), the highest richness is concentrated in the Iberian Peninsula, particularly in the Iberian sclerophyllous and semi-deciduous forests and the Cantabrian mixed forests. Near the southeastern limits of the Palearctic region (Fig. 4D), richness is concentrated in areas such as the Yunnan Plateau Subtropical Evergreen Forests, Jian Nan Subtropical Evergreen Forests, Guizhou Plateau Broadleaf and Mixed Forests, and Central Tibetan

Plateau Alpine Steppe. In the Indomalayan region, the richness is not high, and homogeneous species distribution is observed across nearby ecoregions. In the Afrotropical region (Fig. 4C), the highest richness is found in tropical forest ecoregions, particularly in the Northern Congolian Forest-Savanna, Guinean Forest-Savanna, and Northeast Congolian Lowland Forests. The lack of species records for several ecoregions or the reduced number of species in areas close to regions with considerable richness is evident.

Considering the biogeographic realms (Fig. 5a), the Neotropics present the greatest richness, followed by the Indo-Malay, Palearctic, Afrotropic, Nearctic and Australasia (Fig. 5b).

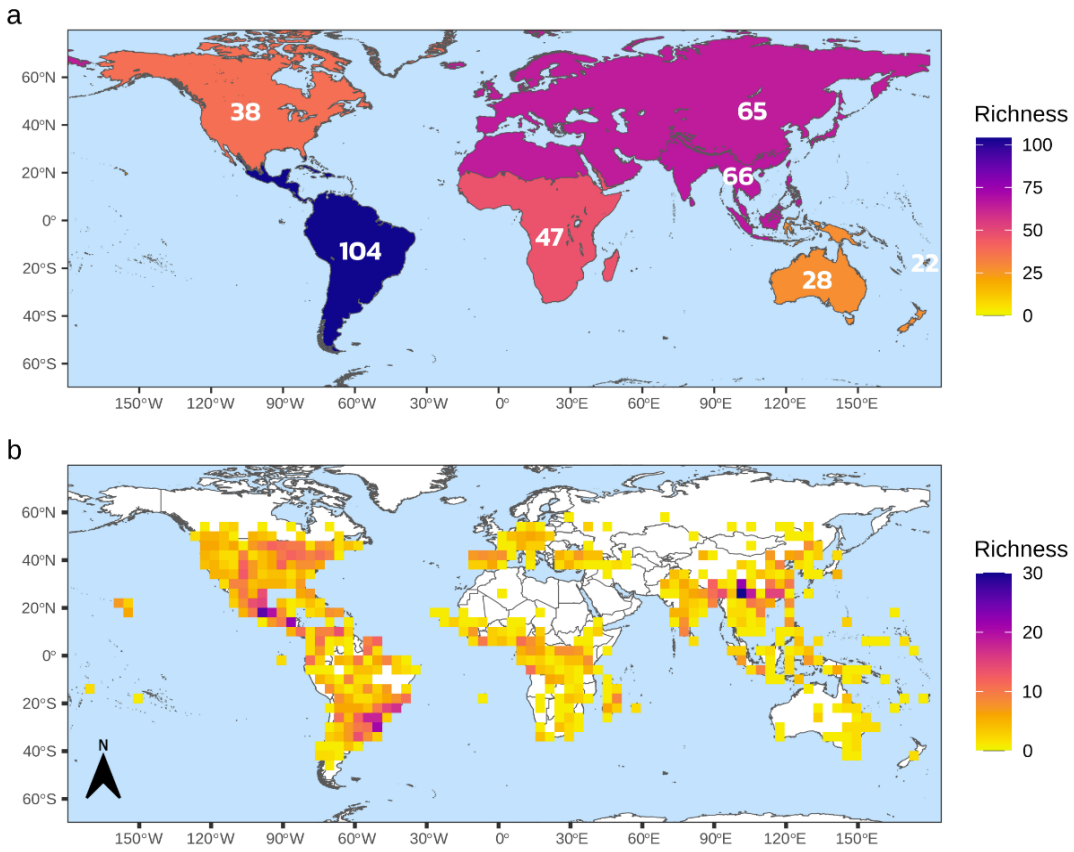

Fig. 5. A, Number of Asopinae species in each WWF Biogeographical Realm. B, Richness map for a 4º Latitude/Longitude quadrat grid.

Bioregions

The resulting bioregionalization of the analysis with a Cluster Cost of 1.0 is shown in Figure 6, while the results of the remaining analyses with Cluster Costs of 0.8, 1.2, and 1.4 are available in figures S1, S2 and S3 in sm. 6. Table 1 shows the number of clusters resulting from the four Infomap Bioregions analyses, which varied from 37 clusters with a lower cluster cost to 12 clusters with a higher cluster cost. The species composition of each bioregion from each analysis is detailed

in sm. 3. The top Indicator Species (see Edler et al., 2016) of each bioregion is available in each Figure (Fig. 6B; Figs. S1b; S2b; S3b). In the analysis with a Cluster Cost of 1.0, Bioregion 1, located in the Neotropical region, has the highest number of species, totalling 67 (Fig. 6).

Table 1. Number of clusters resulting from the Infomap Bioregions analyses

Cluster	Bioregions
0.8	37
1.0	19
1.2	14
1.4	12

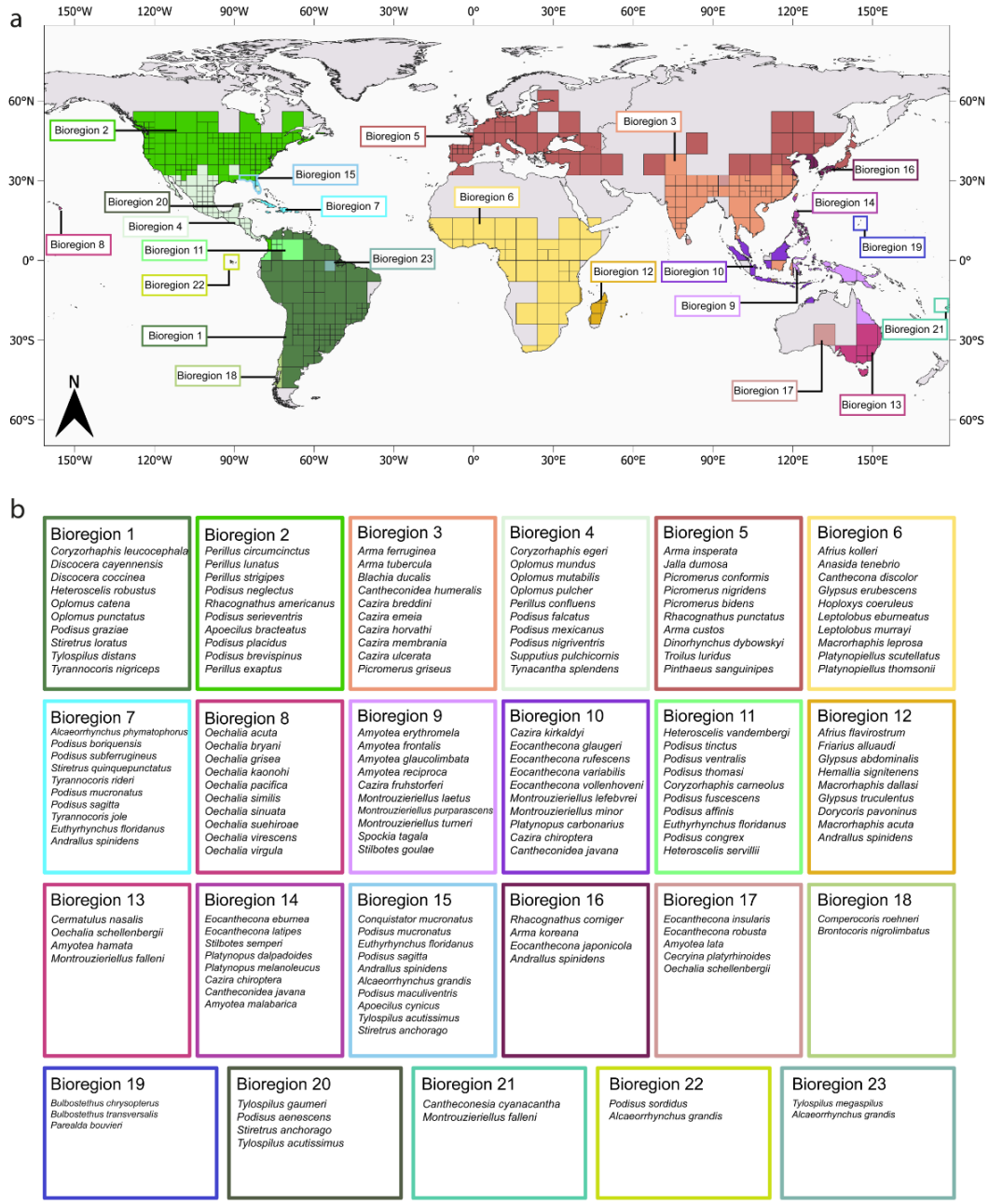

Fig. 6. A, Bioregionalization from the Infomap Bioregions analysis, with a cluster cost of 1.0. Color scheme classifies the bioregions according to their resemblance to previous biogeographical realms schemes. B, The species composition of each Bioregion.

The bioregionalizations with different cluster values show similar patterns with different levels of aggregation (Fig. 6, SM. 6). The Nearctic and Neotropical regions were recovered, as well as the Mesoamerican Region, all in separate Bioregions across all analyses (Fig. 6, SM. 6). Also, the Mexican Transition Zone was not recovered separately from the Nearctic, Mesoamerica and Neotropical. The Afrotropical region appeared as a distinct region (*i.e.*, Bioregion 6; Fig. 6), bounded north by the Sahara Desert and distinct from Bioregion 12, which identified a region over Madagascar. The Palearctic region (Bioregion 5) was recovered as a distinct area, bounded southeast by the Indomalayan region (Bioregions 3, 10, 14). The insular regions of the Indomalayan

realm were recovered as distinct areas (Bioregions 9, 10, 14, 19), but are limited to the southeast by the Australasian region, recovering the limits of the Wallace Line. The Australasian region was recovered as two bioregions: the insular areas correspond to Bioregions 9 and 21, with the latter covering the northeastern part of the Australian continent, and Bioregions 13 and 17, which encompass the southern and southeastern regions of Australia. Generally, the bioregions largely correspond to the Wallacean biogeographical realms, especially with higher cluster cost (SM. 6, Fig. S2 and S3).

The Americas are divided into at least three major bioregions, resembling the Nearctic and Neotropical Regions, and Mesoamerica. With a lower cluster cost, small areas appear in the Amazonian Forest. Hawaiian Islands, the Galapagos Islands and the Antilles are consistently recovered as regions separate from the continental areas. Florida is also recovered separately from the Nearctic Region. The European and Asian continents are united in the higher cluster cost, overlapping the Palearctic region. As the cluster cost gets lower, this region is separated from the Oriental Region (Fig. 6), and further divided into India and Indo-China (SM. 6). The Afrotropical region and Madagascar appear separated in all cluster costs. The Wallace Line appears dividing the Bioregions 9 and 10. The Mariana Islands and Guam, as well as Fiji, appear as distinct units (Bioregions 19 and 21, respectively).

Finally, still considering the 1.0 cluster cost Analysis, 68 species contributed to more than two Bioregions. *Andrallus spinidens* Fabricius contributed to more bioregions (11) than any other species, being widely distributed across the globe.

Areas of endemism

The resulting CAs were grouped into 14 Areas of Endemism Groups (AEGs) (Fig. 7) according to the metaconsensus criterion based on the UPGMA dendrogram (Fig. 7A). The number of species contributing and not contributing to the analysis, number of IAs and CAs, and maximum Index of Endemism (IE) of each analysis are available in table 2. The species composition of each AEG is provided in figure 7C and as sm. 4. Less than half of the species of the dataset contributed to the NDM analyses (Table 2).

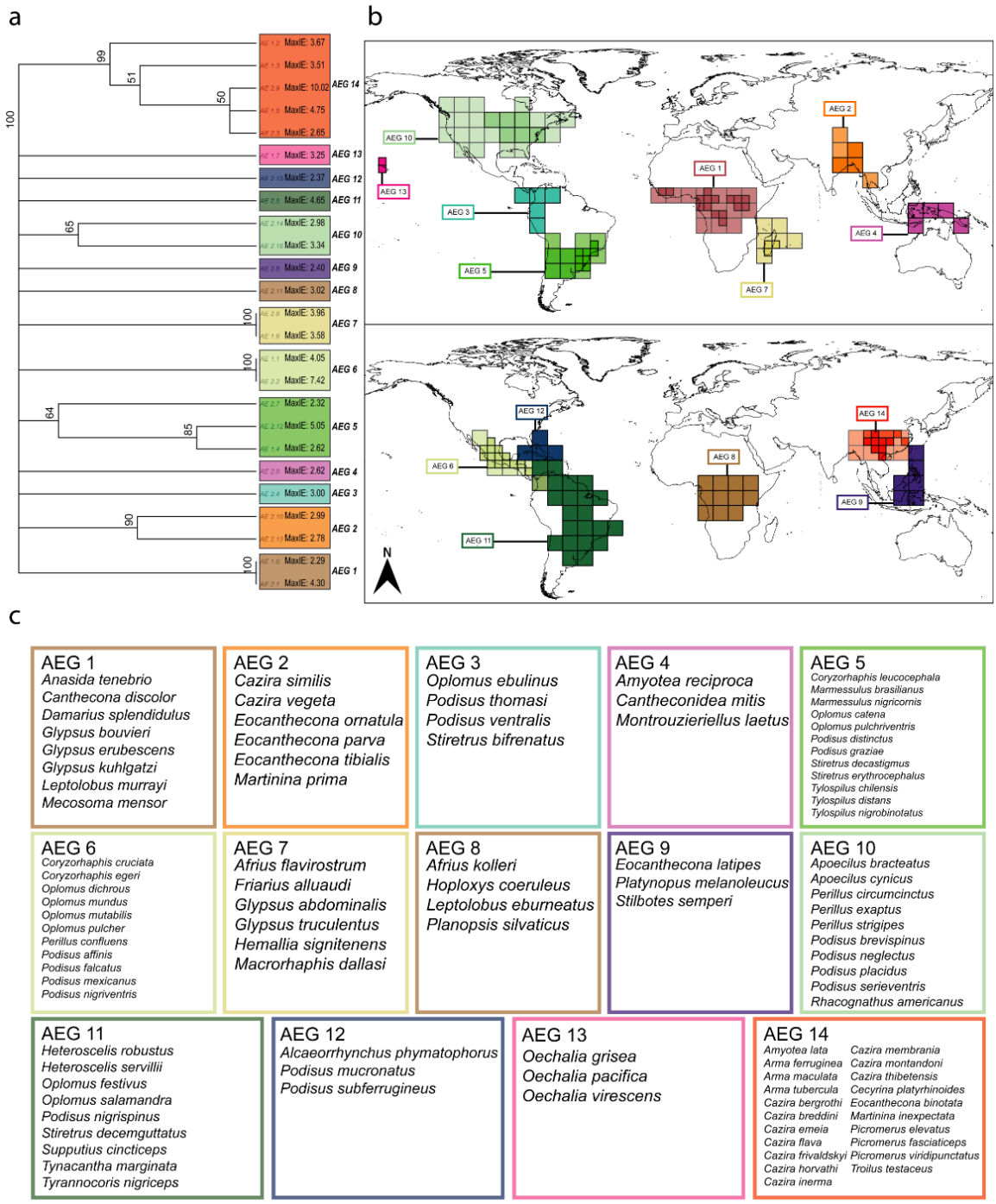

Fig. 7. A, Resulting dendrogram from the metaconsensus analysis, showing how the Areas of Endemism from the NDM analysis were clustered into AEGs. B, The resulting AEGs from the metaconsensus analysis. C, The species composition and Index of Endemicity (IE) of each AEG.

Table 2. Endemicity analyses: number of species contributing and not contributing to the analyses, number of IAs and CAs, and maximum Index of Endemism (IE) of each analysis

	4x4 Grid	8x8 Grid
IAs	15	49
CAs	8	17

IE (max)	4.75	10.02
Species contributing	37	98
Species not contributing	231	170

We identified areas of endemism that contain portions of the Neotropical region (AEG 3, AEG 5, AEG 6, AEG 11, and AEG 12), the Nearctic region (AEG 10), the Afrotropical region (AEG 1, AEG 7, and AEG 8), the Palearctic and Indo-Malayan/Oriental region (AEG 2, AEG 9, and AEG 14), the Australasian region (AEG 4) and an additional area with occurrence in Hawaii (AEG 13).

AEG 14, overlapping the Oriental Region, is the AEG with the highest number of species (21 species), followed by AEG 5 - Southern Neotropic - and AEG 6 - Mesoamerica, with 12 and 11 species, respectively. Of the 268 species, 103 species contribute to one the two analyses. Of these 103 species, only two are singletons, (*i.e.*, *Cazira bergrothi* (Breddin) and *Martinina prima* (Distant)). However, considering the whole dataset, 93 species are singletons, illustrating singleton species contributed much less to the endemicity analysis.

In the Americas, AEG 11 contains most of the Neotropical portion of South America, including widely distributed species such as *Tynacantha marginata* Dallas, and *Podisus nigrispinus* Dallas. AEG 5 represents a more restricted area in the Neotropic, namely the Chacoan Subregion and adjacent areas, also having a high IE - CA 2.12. AEG 3 overlaps the Northern Andes, characterized by different biogeographic dominions (Pacific, Boreal and South Brazilian) and the South American Transition Zone, supported by three medium ranged species. AEG 6 - CA 2.2 has the second highest IE, overlapping both the Neotropical and Mexican Transition Zones and extending to the southern edge of the Nearctic region. This area hosts 11 species confined to the zone where Neotropical and Nearctic biotas converge. AEG 10 represents the Nearctic region as a whole, overlapping both the Western and Alleghany Subregions, revealing ten species restricted to a large-scale pattern, from small ranged (*e.g.*, *Rhacognathus americanus* Stål) to wide ranged species (*e.g.*, *Podisus brevispinus* Thomas).

A portion of the Afrotropical region is contained in AEG 1, supported by 8 species, restricted to the central portion of Africa, matching the West African Subregion and adjacent areas. Most species of AEG 1 are widely distributed in Central Africa, while some are more concentrated in Western Africa. AEG 8 also appears in Central Africa, but with a different composition, and only four species, which do not occur throughout Western Africa.

Two AEGs (AEG 2 and AEG 14) overlap with the Oriental Region, although some of the records of endemic species are also found in the Palearctic Region. AEG 14 has the highest IE, and

is composed of 21 species, some of them with records restricted to Central China, such as *Amyotea lata* Zhao and *Arma maculata* Zheng. AEG 2 is more associated with Central and Central-Western China, while AEG 14 is mostly contained in Eastern China. *Cazira* Amyot & Serville, *Arma* Hahn, and *Eocanthecona* Bergroth are the main genera composing these AEGs.

AEGs 4 and 9 are contained in the Australasian region, which is associated with the Wallace Line region. AEG 4 species occur mainly in the Sulawesi and New Guinea Islands in Indonesia as well as neighboring islands. AEG 9 is supported by three species mainly occurring in the Philippines, and also Taiwan and Sulawesi Island. The Hawaii Islands were recovered as Areas of Endemism (AEG 13), supported by three species of the genus *Oechalia*, a genus originally restricted to the Oceania and Australasian Realms.

DISCUSSION

The online database and studies on Asopinae

The global distribution of Asopinae species provides valuable insights into their habitat preferences and range limits, supporting studies in taxonomy, biogeography, ecological niche modeling, and conservation. By compiling an extensive, globally accessible database, we aim to address significant gaps in our understanding of Asopinae distribution. This resource allows researchers to navigate records by genus or species, helping identify biogeographic patterns and informing more targeted conservation strategies, for instance enabling a prompt visualization of endemism areas with high species richness. While our dataset is extensive, substantial gaps remain, particularly in under-sampled regions and within museum collections. For this reason, our database is designed to evolve, enabling updates as new records are documented. Over time, this iterative process can help fill knowledge gaps and broaden our understanding of Asopinae diversity across various global bioregions, supporting future studies and applications in these fields.

Our dataset includes numerous records sourced directly from collections, many of which were previously unavailable in the literature or existing databases. Alongside previously published records, which also originated from collections, this substantial volume of data underscores the critical role of Natural History Collections and Museums. These institutions serve as vast repositories of information but are increasingly threatened by significant budget cuts in recent decades (*e.g.*, Kemp 2015; Funk 2018; Löbl et al. 2023). Furthermore, the accessibility and

accuracy of these resources are exposed to several circumstances. Although multiple initiatives are emerging to digitize data associated with collections (e.g., Tegelberg et al. 2014; Hudson et al. 2015; Hedrick et al. 2020), care must be taken with the quality of this kind of data, particularly regarding taxonomic identification. Identifying any specimen is the first step in conducting biological research, and accurate species identification can significantly impact monitoring and conserving biodiversity (Graham et al. 2004). During the development of this work, the identification of the physically examined specimens was verified through specific identification keys and consultation on type material. This thorough procedure was crucial since many specimens were not previously identified or were misidentified. Only after such verification can these records be helpful in systematic, taxonomic, and biological assessments and even in applied approaches.

Regarding fundamental taxonomic research, such as generic revisions, taxonomists will find our database helpful in locating catalogued specimens and suitable areas for field surveys, thereby expediting specimen and data collection. Concerning more applied studies, especially in conservation, ecology, and evolution, our tool provides species occurrence records that can be used, for instance, to model species distribution, evaluate niche or lineage spatial evolution (*e.g.*, Bloom et al. 2017; Spalink et al. 2018), and benefit other fields of study.

Our work also provides insight into the state of knowledge on Asopinae. Some groups have been more studied and collected, while others remain poorly understood. Among the less studied groups, singletons account for a large portion of our dataset. This pattern is common among arthropods (Lim et al. 2012; Hoffmeister and Ferrari 2016; Poester-Carvalho et al. 2023). Several factors contribute to this scenario. The rarity of specimens may be linked to the solitary behavior of Asopinae (Gapud 2015). There is also limited biological knowledge for most species (Plata-Rueda et al. 2022), which hinders our understanding of their habitats and the development of effective collection methods. Moreover, few taxonomists are dedicated to the group, and most comprehensive studies have been carried out by a small number of researchers from South and North America, Asia, and Europe (*e.g.*, Thomas 1992, 1994; Zhao et al. 2013 a b; Lupoli 2019; Roca-Cusachs et al. 2019; Roell 2019; Brugnera et al. 2020b; Roell et al. 2023). As a result, the Asopine investigated, particularly in the last 30 years and in these continents, are better known in both taxonomic and distributional terms. Additionally, many species described long ago are now difficult to recognize. Often, they were examined only once at the time of their description, with type material now lost or inaccessible.

The existing gaps in species distribution lead to what is known as the Wallacean shortfall (Lomolino 2004), which could affect our results. These gaps may arise from uneven records between different regions within the same country, or across different countries and continents. Various factors contribute to these gaps, including historical influences, sociological aspects, and

differences in accessibility to areas. Such discrepancies can introduce bias into the results (Hortal et al. 2015) and hinder the accurate identification of distribution patterns (e.g., Oliveira et al. 2016). For instance, we observed discontinuous species richness of Asopinae in the Amazon region, with the highest richness recorded in the Guianan lowland moist forests. This discontinuity may be attributed to sampling biases, as there is more comprehensive data on asopines in French Guiana than in other Amazonian regions. A significant portion of this data was extracted from Lupoli (2019), who catalogued the Asopinae of French Guiana based on recently collected specimens and previously unpublished data. The 'Our Planet Reviewed' expedition, organized by the Muséum national d'Histoire naturelle (MNHN, Paris, France) and Pro-Natura International NGO (France) (Touroult et al. 2018), played a crucial role in collecting numerous species of Asopinae in French Guiana, updating existing records and identifying new ones (Lupoli 2019). This highlights how focused collection efforts, similar to those in other tropical regions like Mexico (Ortega-León 1997), can shape biodiversity data. In Brazil, most data on Amazonian asopines are stored in local museums, such as INPA (see SM. 2). However, the focus of sampling efforts on specific projects or heavily impacted regions can lead to biases in biodiversity records. Moreover, insufficient resources for taxonomic studies and ongoing ecosystem destruction exacerbate knowledge gaps, contributing to a large number of undescribed species (Linnaean shortfall) and limited knowledge of species' geographic distributions (Wallacean shortfall), as well as their responses to environmental conditions (Hutchinsonian shortfall) (Lomolino 2004; Whittaker et al. 2005; Hortal et al. 2015; Oliveira et al. 2016; Andrade-Silva et al. 2022).

While biases in distribution data are potentially present for many species in sampling reports, compiling distribution data for a particular group allows, on the one hand, to measure which regions exhibit greater sampling bias and, on the other, to identify priority areas for planning new collection efforts. Our analyses do not circumvent nor solve the bias problem in distributional data. They are prone to the influence of such bias in that more even data coverage may allow the identification of more areas because more continuous distributions in space influence both NDM and Infomap results. Additionally, sampling bias may have led to identifying relatively restricted endemism areas to some species that could be more extensive with better sampling coverage.

Examining our database, one might wonder why citizen science data was not incorporated into this study to help complete some occurrence points. While platforms for sharing biodiversity data have indeed become valuable for studying organisms, our choice to rely exclusively on bibliographic information was due to challenges in curating citizen science data. First, the sheer volume of records poses a hurdle; for instance, iNaturalist hosts over 40,000 records for Asopinae, but a preliminary review revealed frequent misidentifications, such as individuals from other subfamilies labeled as Asopinae. This issue makes it difficult to extract reliable distribution lists, as

ideally, each record would need individual verification. Second, species identification from photos is often challenging; while some Asopinae species can be identified visually, others require more detailed examination that photos alone cannot provide. The identification of some species requires analyzing morphological details such as features of the pronotum, legs, and genitalia (*e.g.*, Brugnera et al. 2019b; Roell et al. 2021; Sampaio et al. 2023). Therefore, reviewing each photo individually would be essential for using these occurrences. Third, most Asopinae species lack detailed descriptions of their nymphal stages; in the Neotropics, for instance, only about 1% of immature stages of predatory stink bugs have been documented to date (Brugnera et al. 2019c). This is problematic because many records on citizen science platforms consist of immature individuals, making precise species-level identification challenging. Despite these limitations, citizen science data holds significant potential for expanding our understanding of Asopinae distribution and could help fill existing knowledge gaps. With careful curation and validation, these data may prove invaluable for future research.

Bioregions

The bioregions identified in this work largely correspond to classical zoogeographic regions (Wallace 1876) (Fig. 6). In the New World, our results delineate the Nearctic and Neotropical regions, as well as the Mesoamerican Region. Holt et al. (2013), analyzing data from over 21,000 mammal, bird, and amphibian species, reported similar divisions, designating these regions as the Nearctic, Panamanian, and Neotropical. From Morrone (2014), we also recognized the Antillean subregion (Bioregion 7) and a small Amazonian area (Bioregion 11), which includes parts of the Pacific and Boreal Brazilian dominions. Additionally, we recovered sections of the Southeastern Amazonian dominion (Bioregion 23) and the South American transition zone (Bioregion 18).

The Afrotropical region (Bioregion 6) is similarly consistent with previous findings from other animal groups (*e.g.*, Holt et al. 2013). We found an endemic group (AE7) and a bioregion (bioregion 12) of Asopinae for Madagascar. Madagascar is home to a remarkable diversity of unique taxa and ecosystems, recognized as one of the world's "hottest" biodiversity hotspots. Over millions of years, complex speciation and extinction patterns have enriched its terrestrial and freshwater biodiversity (Myers et al. 2000; Antonelli et al. 2022). Some Madagascar-endemic Asopinae species share genera with Afrotropical species, though the dispersal patterns and evolutionary history of asopines in this region would benefit from phylogenetic studies with biogeographical reconstructions.

The Palearctic region (Bioregion 5) is delineated as a distinct area, bordered to the southeast by the Oriental region (Bioregions 3, 10, 14) and a small portion of the Chinese transition zone

(Bioregion 16) *sensu* Morrone & Ebach (2022). These patterns align with regionalizations likely driven by orographic features formed through the collision of the African, Arabian, Eurasian, and Indian tectonic plates. This collision not only created physical barriers but also influenced climate transitions (Ficetola et al. 2017).

The insular Indo-Malayan transition zones also appeared as distinct regions (Bioregions 9, 10, 14, 19), bounded to the southeast by the Australasian region, thereby defining the limits of the Wallace Line. In the Australian region, we identified two primary bioregions: the insular zones (Bioregions 9 and 21), including northeastern Australia, and Bioregions 13 and 17, covering the southern and southeastern areas of the continent.

Distribution patterns

We found a range of diverse distribution patterns between species groups in Asopinae. Some species are very restricted, such as those on small islands. *Oechalia* Stål is a remarkable group with most species endemic to the Hawaiian archipelago (SM. 2). The origins and dispersal patterns of the Hawaiian fauna have been explored for different taxa in the literature. Although some progressive patterns of speciation occurring from older to newer islands have been hypothesized, the diversification of Hawaii's fauna appears to present much more complex patterns related to the species' dispersal potential (Cowie and Holland 2008; Hembry et al. 2021). The lack of recent collections and studies on *Oechalia*, especially phylogenetic studies, prevents us from making broad inferences about the history of the group in the archipelago of Hawaii. However, some observations may contribute to future studies: six species occur in Hawai'i, the larger and more recent island of the archipelago, five of which are possibly endemic to this region; eight species are distributed in the north-western islands Maui, O'ahu, and Kaua'i forming together the bioregion 8 (Fig. 6). Besides, the range of the genus must be much broader beyond the Hawaiian archipelago, since *O. schellenbergii* (Guérin-Méneville) is recorded in several regions of Oceania, mainly Australia and its surroundings. Many Hawaiian insect lineages originated in several locations of the Pacific Basin (Hembry et al. 2021), and a phylogeographic investigation could elucidate some aspects of the origin and diversification of *Oechalia*. However, the taxonomy of the genus should be explored with caution before any broad investigation. Usinger (1941) indicated several morphological variants of *O. schellenbergii* that may occur in areas not recorded in our work. Because of these variations, we preferred to use geographic records taken from museum specimens instead of the literature. We encourage future investigations on *Oechalia* biogeography, systematics, and taxonomy.

Bulbostethus Ruckes, *Parealda* Schouteden, and *Ponapea* Ruckes are also endemic taxa from volcanic islands distributed along Micronesia, forming the bioregion 19 (Fig. 6). Unfortunately, the scarcity of specimens makes it challenging to study the morphological and biological aspects of this group. *Ponapea arachnoides* Ruckes is known only from the holotype and a single nymph from the Caroline Island Ponape (Ruckes 1963). *Parealda bouvieri* Schouteden, *Bulbostethus chrysopterus* (Herrich-Schaeffer), and *B. transversalis* (Ruckes) are endemic to the Mariana Islands (Ruckes 1963).

Areas of endemism

Restricted co-occurrence patterns confined to specific regions, i.e., areas of endemism, were identified for most regions of the globe, with the exception of polar regions, the Palearctic, and Australia. The metaconsensus criterion enabled the identification of regions less sensitive to the effects of analysis scale (i.e., grid size), thereby representing more robust areas compared to individual areas. The highest endemism indices were recovered in regions composing AEG14, with maximum endemism in one of the areas of 10.02 and overlapped with the Oriental region. AEG 6 also deserves to be highlighted with a maximum IE of 7.42 (composed of 11 species) and AEG 5 with a maximum IE of 5.05 and composed of 12 species. A large region across South America also emerged as an AE with an I.E. of 4.65 (AEG11), although smaller areas were also identified within South America (AEG3 and AEG5). It is worth noting that, out of a total of 298 species analyzed in our database, only 27 and 98 species contributed to the areas identified in the analyses using 4-degree and 8-degree cells, respectively.

A reduced number of species contributing to areas of endemism can result from several factors, including biological, methodological, and data-related issues. Biologically, species with highly restricted distributions or rarity are less likely to overlap with others in the same region, limiting their contribution to co-occurrence patterns. Methodologically, the use of large grid sizes or coarse resolution can obscure fine-scale patterns of endemism, while small grids may fragment data and reduce detectable overlaps (Daru et al. 2020; Dolores et al. 2009). Additionally, biases in sampling, such as the Wallacean shortfall, where knowledge of species' distributions is incomplete, can further restrict the pool of species included in analyses (Hortal et al. 2015; Oliveira et al. 2016). In some ways, data limitations (Wallacean shortfall) become difficult to distinguish from biological constraints of the taxa (*e.g.*, microendemism). Given the scarcity of data for the group, it is more parsimonious to assume that the limited number of endemic species in the areas identified here is primarily due to the restricted number of co-occurrences, resulting from sampling issues.

Nonetheless, the areas of endemism identified here align with regions traditionally recognized for insects and other organism groups. The Nearctic region was recovered in AEG10 at two scales, one corresponding to the eastern portion of the region, an area also identified for other Pentatomidae not belonging to Asopinae (Poester et al. 2023). An area of endemism was identified in the Mesoamerican region (AEG6, Fig. 7), which aligns with AEG1 and AEG2 reported by Poester et al. (2023). The Antilles (AEG12, Fig. 7), however, were not identified as an isolated area of endemism for Pentatomidae in the analysis by Poester et al. (2023), nor in the analysis of Triatominae by Ferrari et al. (2022). The northern Andes (AEG3 Fig. 7) is corroborated in Ferrari et al. (2022), as is the broad region encompassing the Atlantic Forest, Pampas, and Chaco (AEG5, Fig. 7).

The Afrotropical region was also identified in two clusters, AEG1 and AEG8, as well as the Madagascar region (AEG7). The Oriental region was represented by two areas, AEG2 and AEG14. Additionally, two geographically proximate areas of endemism, AEG9 and AEG4, align with the boundaries between the Oriental and Australasian faunas respectively, coinciding with the limits of the Wallace Line. Although there is partial overlap between an AEG4 and AEG9 cell, the species records from these areas do not overlap, and only *Platynopus melanoleucus* occurs below the Wallace Line. However, the composition of these areas is entirely distinct. This pattern has been corroborated by several studies on insects. De Boer and Duffels (1996) highlighted the restricted distribution of cicadas in Wallacea and adjacent regions. Similarly, Holloway and Jardine (1968) emphasized the zoogeographic discontinuities across Wallace's Line based on butterfly distribution. Bell et al. (2004) demonstrated how phylogenetic and biogeographic studies of the dung beetle genus *Temnoplectron* reveal lineage diversification constrained by Wallace's Line. The *Crematogaster inflata* group (Hymenoptera: Formicidae) also supports this pattern, with most species confined to the Sundaic region, reflecting the Wallace Line’s role in limiting gene flow and promoting diversification through geographic isolation (Hosoishi et al. 2023). Furthermore, Condamine et al. (2015) provided robust evidence through the study of birdwing butterflies (*Papilionidae*), showing how this biogeographical barrier influences dispersal and speciation patterns. Collectively, these findings reinforce the ecological and evolutionary significance of Wallace's Line in shaping insect distributions.

Ecoregions

The patterns of species richness found in this study reveal an heterogeneous distribution across adjacent ecoregions. In the Neotropical region, the high richness observed in southern and southeastern Brazil, particularly in the Alto Paraná Atlantic Forest and other Atlantic Forest

ecoregions, is consistent with previous studies identifying these areas as entomological diversity regions. This is largely attributed to their habitat heterogeneity, structural complexity, and temperature seasonality (Brown and Freitas 2000; Antonio et al. 2025). We also found high richness for the Cerrado; this region is an important reservoir of insect diversity, with many species presenting seasonal patterns (Silva et al. 2016). In contrast, Amazonian ecoregions exhibited uneven species richness, with the Guianan lowland moist forests standing out. Insect diversity across the Amazon can vary greatly, influenced by factors such as soil type, geological history, vegetation cover, and vertical forest stratification. Quantifying the abundance and species richness of megadiverse insect groups in tropical forests remains a major challenge and requires diverse strategies to effectively access the full range of microhabitat diversity (Basset et al. 2012; Amorim et al. 2022).

In the transitional zone between the Neotropical and Nearctic regions, areas such as the Petén-Veracruz moist forests and the Trans-Mexican Volcanic Belt pine-oak forests showed remarkable richness. Similar patterns were found for fruit-flies and leafhoppers (Berrones-Morales et al. 2019; Pinedo-Escatel et al. 2020). These transition zones, where both tropical and temperate faunas coexist, are supported by steep altitudinal and climatic gradients (Morrone 2010).

According to Sánchez-Fernández et al. 2021, knowledge about insect distribution in the Iberian Peninsula remains incomplete, largely due to uneven sampling efforts across different insect groups. We found high Asopinae richness for this region, particularly in the Iberian sclerophyllous and semi-deciduous forests and the Cantabrian mixed forests, which could be useful in future assessments. High richness in the Iberian Peninsula has also been documented for other insect groups such as Lepidoptera and Hymenoptera, and is often attributed to refugium areas, climatic diversity, and historical evolutionary processes (Romo and García-Barros 2010; Tinaut and Ruano 2021).

In the Indomalayan region, Asopinae richness and distribution appeared relatively homogeneous across ecoregions, while in the Afrotropical region, richness was higher in tropical forest ecoregions, particularly in forest–savanna mosaics in the Congo and Guinean regions. Several factors may influence insect diversity in African landscapes, including both tropical forests and savannas. Studies on other insect groups suggest that these factors include human disturbance (Landmann et al. 2023), climatic conditions and environmental characteristics (Axmacher et al. 2009; Habel et al. 2021), habitat heterogeneity at the local scale (Yeo et al. 2017), as well as latitude, paleo-history, and forest size (Swart et al. 2021).

CONCLUSIONS

In summary, this study provides a comprehensive and up-to-date database on the distribution and diversity of Asopinae, bridging significant gaps in our understanding of the group's global distribution patterns. By examining Asopinae richness across political, biogeographic, and ecological boundaries, we identified key areas of high diversity and endemism, particularly within the Neotropics. The insights from this database offer a valuable foundation for future research in systematics, taxonomy, and applied biological control, highlighting regions and taxa that merit further exploration. The 'Asopinae of the World Database' represents a crucial tool for ongoing studies, enabling better-informed conservation strategies and facilitating access to data for the scientific community.

List of abbreviations

AMNH, American Museum of Natural History (New York, United States of America).
AMS, Australian Museum (Sydney, Australia).
BHMH, Universidade Federal de Minas Gerais, Museu de História Natural (Belo Horizonte, Brazil).
CEIOC, Instituto Oswaldo Cruz, Coleção Entomológica (Rio de Janeiro, Brazil).
CeNak, Center for Natural History of the University of Hamburg (Hamburg, Germany)
CERPE, Coleção Entomológica da Universidade Federal Rural de Pernambuco (Recife, Brazil).
CLEV, Cleveland Museum of Natural History (Cleveland, United States of America).
DARC, David A. Rider collection (Fargo, United States of America).
DZUP, Museu de Entomologia Padre Jesus Santiago Moure, Universidade Federal do Paraná (Curitiba, Brazil).
NMPC, National Museum (Prague, Czech Republic).
EMG, Entomologisches Museum Geyer, Insekten Dauerausstellung (Geyer, Germany).
FSCA, Florida State Collection of Arthropods (Gainesville, United States of America).
HNHM, Natural History Museum (Budapest, Hungary).
IAvH-E, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (Villa de Leyva, Colombia).
ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia (Bogota, Colombia).
INHS, Illinois Natural History Survey (Champaign, United States of America).
INPA, Instituto Nacional de Pesquisas da Amazônia, Coleção Sistemática da Entomologia (Manaus, Brazil).

MACN, Museo Argentina de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina).
MCNZ, Museu de Ciências Naturais da Secretaria do Meio Ambiente e Infraestrutura (Porto Alegre, Brazil).
MCPM, Milwaukee City Public Museum (Milwaukee, United States of America).
MCTP, Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, Brazil).
MLPA, Universidad Nacional de La Plata, Museo de la Plata (La Plata, Argentina).
MNHN, Muséum National d'Histoire Naturelle (Paris, France).
MNRJ, Universidade do Rio Janeiro, Museu Nacional (Rio de Janeiro, Brazil).
MPUJ, Pontificia Universidad Javeriana, Museo Javeriano de Historia Natural, Laboratorio de Entomología (Bogota, Colombia).
MZLS, Musée Zoologique (Lausanne, Switzerland).
MZSP, Museu de Zoologia da Universidade Federal de São Paulo (São Paulo, Brazil).
NHMUK, The Natural History Museum (London, United Kingdom).
NHRS, Naturhistoriska riksmuseet (Stockholm, Sweden).
OUMNH, Oxford University Museum of Natural History (Oxford, United Kingdom).
RBINS, Royal Belgian Institute of Natural Sciences (Brussels, Belgium).
RMCA, Musée Royal de l'Afrique Centrale (Tervurem, Belgium).
SDEI, Senckenberg Deutsches Entomologisches Institut (Müncheberg, Germany)
SIM, Staten Island Museum (Staten Island, United States of America).
STRI, Smithsonian Tropical Research Institute (Balboa, Panama).
UFRG, Universidade Federal do Rio Grande do Sul (Porto Alegre, Brazil).
UFRJ, Universidade Federal do Rio de Janeiro (Rio de Janeiro, Brazil).
UNAB, Universidad Nacional, Facultad de Agronomía (Bogota, Colombia).
UMSP, University of Minnesota (St. Paul, United States of America).
USNM, National Museum of Natural History (Washington D.C., United States of America).
VMNH, Virginia Museum of Natural History (Martinsville, United States of America).
ZFMK, Zoologisches Forschungsmuseum "Alexander Koenig" (Bonn, Germany).
ZMHB, Museum für Naturkunde (Berlin, Germany).
ZMUC, University of Copenhagen, Zoological Museum (Copenhagen, Denmark).

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Supplementary materials

SM 1. Asopinae genera and species (Table). (download)

SM 2. Raw data with locations, coordinates and references. List containing all the data sources used for the database (Papers and Collections). (download)

SM 3. Input files for Infomap Bioregions analyses. All output files of the Infomap Bioregions analyses. (download)

SM 4. Input files for the NDM analyses. All resulting files from the NDM analyses and species composition. (download)

SM 5. Input files and code used to run the metaconsensus analysis. (download)

SM 6. Figures showing the resulting bioregionalization of the Infomaps Bioregions analyzes with 0.8; 1.2 and 1.4 Cluster Cost parameter. Figure S1, Figure S2, Figure S3. Output files from the Infomap Bioregion Analysis. (download)

SM 7. Input data and code for the figures. (download)