FRONTIERS OF BIOGEOGRAPHY
The scientific journal of
The International Biogeography Society

Frontiers of Biogeography 19, 2026,
e155940 | DOI 10.21425/fob.19.155940

RESEARCH ARTICLE

Biogeographical patterns of the genus *Plectostoma* H. Adams, 1865 (Mollusca, Gastropoda) in Sundaland's limestone ecosystems

Thor-Seng Liew[1], Ayu Savitri Nurinsiyah[2], Mohammad Effendi Marzuki[3], W. K. Fletcher[4], Junn-Kitt Foon[5], Nur Atirah Bian[1], Yansen Chen[6], Mohd Zacaery Khalik[3], Jaap J. Vermeulen[7], Menno Schilthuizen[8]

1 *Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia*
2 *Museum Zoologicum Bogoriense, Research Center for Biosystematics and Evolution, National Research and Innovation Agency, 16911 Bogor, Indonesia*
3 *Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, 94300, Kota Samarahan, Sarawak, Malaysia*
4 *Earth, Ocean and Atmospheric Sciences, University of British Columbia, Vancouver, Canada*
5 *School of Science, Western Sydney University, Hawkesbury Campus, Richmond NSW 2753, Australia*
6 *Medan, North Sumatra, Indonesia*
7 *JK art and science, Lauwerbes 8, 2318 AT, Leiden, Netherlands*
8 *Naturalis Biodiversity Center, P.O. Box 9517, Leiden 2300 RA, Netherlands*

Corresponding author: Thor-Seng Liew (thorseng@ums.edu.my)

Editors Sérgio Ávila
Received 8 October 2025 ◆ **Accepted** 10 February 2026 ◆ **Published** 9 March 2026

Abstract

Sundaland's limestone ecosystems are biodiversity hotspots facing increasing threats from habitat fragmentation and human activities. Our study examines the biogeographical patterns of the limestone-obligate land snail genus *Plectostoma* across Sundaland to identify the drivers of species richness and endemism. Using 771 georeferenced records of 84 species, we delineated 33 bioregion (biogeographical region) areas based on species composition through Infomap Bioregions analysis. We then examined the effects of integrated island biogeography variables (limestone area, number of hills, isolation), MaxEnt-derived climate suitability, and landscape features such as topography and drainage networks on biogeography patterns and species diversity. Bioregion boundaries were best explained by elevation barriers, drainage basins, and river network connectivity, highlighting the importance of geomorphological and hydrological structure over geographic distance. Generalised linear mixed models revealed that larger limestone areas significantly predicted greater species richness than did higher climate suitability. Canonical Correspondence Analysis showed that endemism composition was primarily driven by the number and total area of limestone hills, while hill isolation and broad-scale climate variables played lesser roles. Most species (87%) were restricted to a single bioregion, with over half qualifying as short-range endemics (<10 km distribution range), underscoring strong spatial turnover. These patterns suggest that ancient geological connectivity, followed by progressive karst fragmentation, shaped current diversity. Future phylogenetic and multi-taxon studies will enhance the understanding of evolutionary processes and conservation strategies in Sundaland's limestone habitats.

Highlights

- We delineated 33 distinct bioregions for *Plectostoma* land snails across Sundaland.
- Precipitation defines the broad habitable envelope determining the occurrence of the genus, while drainage basins and elevation barriers (>250 m) serve as the primary determinants of bioregional boundaries.
- We established that the species richness and endemism of *Plectostoma* are primarily driven by the total area and total number of limestone hills within a bioregion, rather than broad-scale climatic suitability.
- Our results support a landscape-evolution model for diversity patterns, linking biological distribution to karstification stages where species dispersed across continuous surfaces during the early (Fengcong) stage of karstification before becoming isolated on "island" towers during the remnant (Fenglin) stage.

PENSOFT.

Keywords

fragmentation, Indonesia, island biogeography, Kalimantan, land snail, limestone-obligate species, Malaysia, Southeast Asia, spatial analysis, Sumatra

Introduction

Sundaland, the biogeographical region encompassing Peninsular Malaysia, the islands of Borneo, Java, Sumatra, and their surrounding islands (Fig. 1A), is recognised as one of Earth's biodiversity hotspots. This region harbours a significant number of endemic species that are threatened by habitat degradation (Myers et al. 2000; Sheldon et al. 2015). Geologically, Sundaland comprises a mosaic of terranes and blocks, each contributing distinct biogeographic attributes. The older inner core of Sundaland comprises the Indochina and Sibumasu Terranes, derived from Gondwana in the Devonian and Permian, respectively, with the Sukhothai Arc between them (Metcalfe 2013, 2017). The Southwest Borneo (SWB) and West Burma (WB) Blocks separated from Gondwana in the Triassic: SWB accreted to Sundaland in the Late Cretaceous whereas the WB remained an island in the Tethys Ocean until the Early Miocene (Advokaat and van Hinsbergen 2023).

The biogeographic patterns of Sundaland's species distributions are shaped by complex palaeogeographical events, including the emergence of land areas due to geological processes, Pleistocene climatic oscillations, and sea-level changes (De Bruyn et al. 2014; Sheldon et al. 2015; Atkins et al. 2020; Liew et al. 2020; Garg et al. 2022; Hosoishi et al. 2023). Within Sundaland, limestone ecosystems are globally recognised as habitat islands which, being naturally fragmented in this tropical region, support limestone-dependent biodiversity (Clements et al. 2006). Their isolated nature makes limestone outcrops ideal for investigating biogeographic principles, particularly drivers of species richness, endemism, and species composition (Gittenberger 2007; Clements et al. 2008; Azevedo et al. 2024; Clegg et al. 2025).

Previous studies have demonstrated that factors like isolation, area size, and microclimate influence species assemblages of land snails on limestone outcrops in this region (Clements et al. 2008; Foon et al. 2017). However, the effects of island biogeography variables, such as habitat isolation and size, are often difficult to disentangle from other ecological or historical factors, particularly when studying species assemblages of diverse taxa (e.g., different genera or families). Each taxon within an assemblage may have unique ecological preferences, such as specific requirements for microclimate or substrate type, and distinct evolutionary histories or distribution patterns shaped by past geological or climatic events. These factors can influence how species respond to biogeographical variables, often resulting in highly species-specific patterns.

By focusing on a single genus, it is possible to develop a more robust framework for isolating the specific effects of island biogeographical variables and climate suitability on biodiversity (Webb et al. 2002; Wiens and Graham 2005). This approach serves as a foundational first step toward understanding limestone biogeography, as it allows for the identification of clear environmental signals that might otherwise be obscured by the varied ecological preferences of a multi-taxa assemblage. The genus *Plectostoma* H. Adams, 1865, which currently includes 82 recognised species and subspecies and several other undescribed species, is predominantly endemic to the Sundaland biogeography region and its adjacent areas (MolluscaBase eds. 2024; Liew et al. *unpublished data*). These micro-snails, measuring between 1.5 mm and 4 mm, exhibit high microhabitat specificity and are restricted to the surfaces of geographically isolated limestone outcrops (Schilthuizen 2003; Schilthuizen et al. 2003a). All these characteristics limit their dispersal ability and have contributed to this species-rich snail genus exhibiting distinctive distribution patterns encompassing a gradient of endemism levels; from widespread species, wide-range to mid-range endemics, to highly localised, short-range endemics (Vermeulen 1994; Liew et al. 2014a). These characteristics, together with the relict origin crown age dated back to the early Paleocene (~ 65 Ma) (Köhler 2024), make them ideal candidates for the study of the biogeography, evolution, and diversification of limestone-obligate species in this region (e.g. Schwendinger 2020; Derkarabetian et al. 2021).

Out of the 40 *Plectostoma* species on the IUCN Red List, many face significant threats; one is classified as Extinct, 13 as Critically Endangered, four as Endangered, and four as Vulnerable (IUCN 2024a). Hence, studying *Plectostoma* is important to provide critical insights into how habitat isolation and fragmentation drive species endemism, richness, and vulnerability in limestone ecosystems, offering broader implications for conservation efforts. In this study, we aim to identify the primary determinants of *Plectostoma* diversity and provide insights into the ecological and evolutionary processes shaping the distribution of limestone-obligate species in Sundaland.

We delineate bioregions of *Plectostoma* across Sundaland and quantify patterns of species richness and endemism. We test the relative influence of island-biogeographical variables (e.g., limestone area, number of hills, and isolation) and ecological factors (e.g., climate suitability and variability) on biodiversity patterns, focusing on Malaysia, where high-resolution limestone maps are available. We further examine how species' distributional range categories relate to these predictors and assess the role of geological and geomorphological history in shaping species diversity and biogeographic patterns of the genus, providing a framework for understanding the drivers of limestone-obligate biodiversity in Sundaland.

Methods

We assigned specific spatial units (i.e. cells) to bioregion (biogeographical region) cells based on the occurrence data of *Plectostoma* species in Sundaland. Groups of adjacent cells with the same bioregion identity were then aggregated to represent a “bioregion area” with a cluster of limestone hills with similar species composition. Biodiversity variables, including species richness and endemism, were tabulated for each bioregion cell and bioregion area. We then assessed the effects of island-biogeographical variables—including the number of limestone hills, total limestone area size, and degree of isolation of limestone outcrops—and ecological variables such as climate suitability and variability at both the bioregion cell and area levels on species richness. This analysis focused on bioregions in Malaysia due to the availability of high-resolution limestone hill maps. Then, we explored the relationships between species distributional range categories (i.e., endemism categories) and the same set of biogeographical and ecological variables, using the bioregion cells and areas as above. Finally, we qualitatively assessed the association between geological and geomorphological history, including topography and drainage patterns, and the bioregion’s location and boundaries on biodiversity patterns.

Limestone hills and areas mapping

For Malaysia, detailed information on limestone hills is available from Liew et al. (2021), who mapped the 1,393 limestone hills of the Malay Peninsula and Malaysian Borneo (i.e., Sarawak and Sabah) (Fig. 1A). The precise mapping of each limestone hill, with clear demarcation of boundaries, allows more information to be extracted such as total limestone area sizes, number of hills, and the degree of isolation of limestone hills (see Island biogeography variables section).

For the limestone hill distribution in other areas of Sundaland or Southeast Asia, we digitised the limestone area map based on Laumanns and Price (2010a, 2010b). This map indicates the general distribution of limestone areas in a region, without the exact documentation of limestone hills in terms of the outline and location of each hill. Therefore, we could not obtain detailed geographical attributes of the limestone hills for other regions as we could for Malaysia. However, this general limestone area map is still useful to illustrate the distribution of the genus *Plectostoma* in association with the availability of limestone habitats over a larger geographical extent.

Collection of *Plectostoma* species distribution data

The presence data of *Plectostoma* spp. in the form of point occurrences were obtained from previously published sources (Vermeulen 1994; Clements et al. 2008; Liew et al. 2014a; Foon et al. 2017; Phung et al. 2018) and specimens deposited in the following collections: the BORNEENSIS collection at Universiti Malaysia Sabah (BORMOL), Jaap Vermeulen private collection (JJ), the Yansen Chen private collection (YSC), the Naturalis Biodiversity Center Collection (RMNH/ZMA), the Museum Zoologicum Bogoriense, National Research and Innovation Agency at Bogor, Indonesia (MZB), Zoological Museum UNIMAS (MZU), and Mohammad Effendi Marzuki private collection (ME). In addition, we included *Plectostoma* records from the unpublished land snail inventory data from 52 limestone hills in the Malay Peninsula that were collected between 2018 and 2019. In total, the distribution data comprise 771 georeferenced points identified at the species level (Fig. 1A, Suppl. material 1: figs S1–S6, table S1). Species were identified based on shell characteristics (Vermeulen 1994; Liew et al. 2014a). Specimens that could not be identified due to being juvenile, damaged, or lacking complete location information were excluded. In addition to compiling the presence dataset of *Plectostoma* species as described above, we also compiled the absence dataset based on the limestone areas with intensive land snail inventory studies that confirmed the absence of the genus from the same data sources above (Fig. 1A).

Classification of bioregions and spatial units

One important aspect of biogeographical analysis is delineating spatial units and determining unit cell sizes. For *Plectostoma* species, many of which are endemic to limestone hills, the smallest unit is a limestone hill or outcrop. However, in many cases, the limestone hills that exist today were once part of more extensive limestone surfaces that, over tens of millions of years, have become dissected and isolated from each other by the process of karstification. In the early stages (Fengcong karst) of karstification, continuity of the limestone surface is maintained (Waltham 2008), potentially providing dispersal pathways for limestone-obligate species such as *Plectostoma*. However, as karstification progresses, continuity of the limestone surface is lost as deepening of valleys and deposition of alluvium along streams isolates remnant karst towers (Fenglin karst) and creates a barrier for limestone obligates to disperse between them. Therefore, using spatial units that reflect biologically meaningful connectivity, rather than treating every hill as an isolated ‘island’, should provide a more accurate framework for biogeographic analysis. We refer to these spatial units, defined by clusters of limestone hills with similar species composition, as “bioregion areas” (i.e., biogeographical region areas).

Each bioregion area also consists of grid cells (hereafter referred to as bioregion cells), with a size large enough to account for potential sampling biases (e.g. unsampled limestone hills), while being small enough to allow accurate estimation of the biogeographical determinants, species richness, and endemism. In addition, bioregion areas

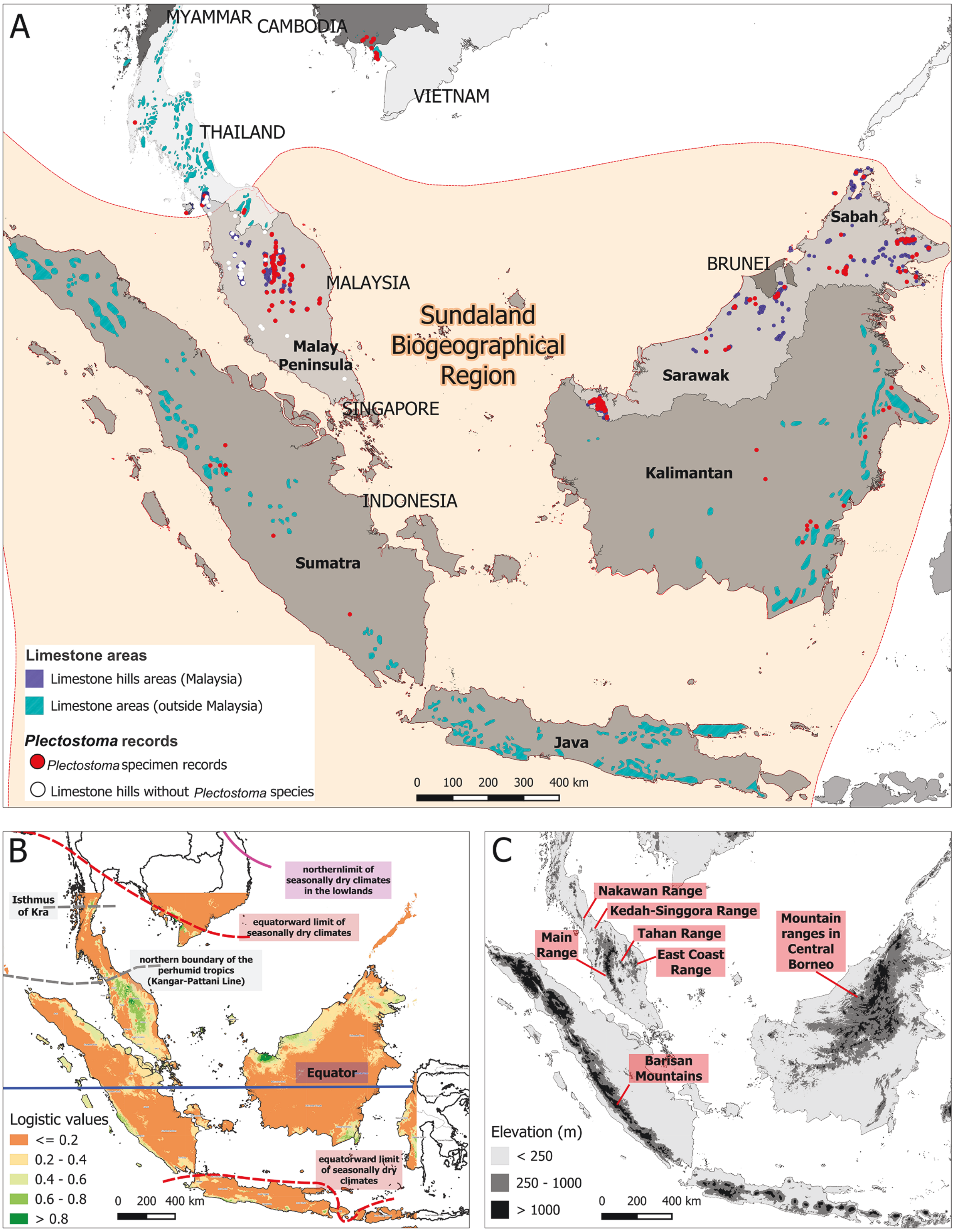

Figure 1. Map of Southeast Asia showing the distribution of limestone hills, occurrences of *Plectostoma* species in the Sundaland biogeographical region, the climate suitability model for the genus *Plectostoma*, boundaries of major forest types, and topographical features. **A.** Limestone areas in Malaysia were based on Liew et al. (2021), while limestone areas in other regions were digitised from Laumanns and Price (2010a, 2010b). Point occurrences of *Plectostoma* species were compiled from published sources (Vermeulen 1994; Liew et al. 2014a), specimen collections (BORMOL, JJ, YSC, RMNH/ZMA, MZB, MZU, ME), and both unpublished and published land snail inventories from limestone hills in the Malay Peninsula collected between 2018 and 2019, as well as previous studies (Clements et al. 2008; Foon et al. 2017; Phung et al. 2018); **B.** Climate suitability model for the genus *Plectostoma* based on MaxEnt analysis; higher values indicate more suitable climates. The logistic values represent the predicted probability of occurrence, with 0 being unsuitable and 1 being optimal. The model was overlaid with the boundaries of major forest types adapted from Morley (2018); **C.** Topographical features of Sundaland with the annotations of key mountain ranges mentioned in this study.

and bioregion cells should be relevant to conservation implications. For instance, they are meaningful for the determination of "Area of occupancy" (AOO) in conservation assessment by the IUCN standard for the assessment at the species (2 km grid size) and ecosystem (10 km grid size) levels (IUCN 2024a, 2024b).

We used Infomap Bioregions v2.7.1 to identify bioregions of *Plectostoma* and generate a species richness heatmap based on species composition across the taxon's entire distribution range (Edler et al. 2017). Infomap Bioregions identifies units based on an information-theoretic clustering algorithm known as Infomap. This approach clusters bipartite networks of species and grid cells, identifying the underlying structure in distributions more effectively than traditional similarity-index methods. The process utilises an adaptive spatial resolution to bin species records into discrete geographical grid cells. This is particularly suited for limestone-obligate taxa like *Plectostoma*, where habitats are naturally fragmented and traditional interpolation methods may fail. The resolution of the bioregion cells was approximately 15.625 km (Grid resolution setting = Max and Min cell size of 1/8°, Max and Min cell capacities of 1–70 records). The process of network mapping and clustering to generate bioregions was as follows: Patch sparse cells = True; Number of trials = 10; Number of cluster cost = 1; Weight on abundance = FALSE. The analyses were conducted using the web application "mapequation" (https://www.mapequation.org/bioregions/).

The output was a vector polygon file with multiple grid cells, and each grid cell was represented as a square feature in a polygon vector file of approximately 15.625 km in length and height (i.e., bioregion cell) (Fig. 2). Areas in the landscape where *Plectostoma* was present were mapped as bioregion cells, with each cell containing attributes such as the number of specimen records, species richness, and the bioregion designation with a numeric identifier. Limestone areas with intensive land snail inventory studies that confirmed the absence of the genus were generated in the same way to represent the bioregion areas where the genus was absent. In addition to bioregion cells, the bioregion area was created by dissolving multiple bioregion cells with the same bioregion designation into a single polygon.

Plectostoma species richness and endemism classification

The species richness for each bioregion cell was obtained directly from the output of Infomap Bioregions v2.7.1 as described above. For the bioregion area, species richness was calculated based on the number of *Plectostoma* species present. Species endemism composition was determined by tabulating the total number of species into four distribution range categories for each bioregion area and bioregion cell.

We first obtained the distribution range of each species by calculating the pairwise distance between records of the same species using the "Distance Matrix" in QGIS. The longest distance among records of the same species in the linear distance matrix was used as the distribution range (i.e., the maximum range). The *Plectostoma* species were then categorised into four geographic range categories, based on the extent of occurrence (EOO) criteria of IUCN (ver. 16; IUCN 2024a), as follows:

(1) short-range endemic species: EOO < 100 km^2 for IUCN B1 for Critically Endangered (CR), i.e., species with maximum distribution ranges < 10 km;
(2) mid-range endemic species: EOO < 5,000 km^2 for IUCN B1 for Endangered (E), i.e., species with maximum distribution ranges < 70 km;
(3) wide-range endemic species: EOO < 20,000 km^2 for IUCN B1 for Vulnerable (VU), i.e., species with maximum distribution ranges < 140 km;
(4) widespread species: species with maximum distribution ranges > 140 km.

There are 23 species with a single record or occurring on a single limestone outcrop, and these were treated as short-range endemic species.

Biogeographical determinants

Climate suitability variables

To gain insight into the ecological niche of the genus *Plectostoma*, we estimated climate suitability and identified key climatic variables associated with the distribution of the genus. We used the bioclimatic dataset version 1.4 (http://www.worldclim.org/current; Fick and Hijmans 2017). All current bioclimatic layers were clipped to the extent of SE Asia, focusing on the genus distribution extent (93°E, 10°S–120°E, 12°N). To evaluate collinearity among the 19 climatic variables, we sampled bioclimatic data from 500 random locations and performed pairwise Pearson's correlation (Suppl. material 2: fig. S1, table S1). After removing highly correlated variables ($r > 0.8$), nine climatic variables were selected for species distribution modelling, namely; BIO1 Annual Mean Temperature, BIO2 Mean Diurnal Range, BIO3 Isothermality, BIO7 Temperature Annual Range, BIO12 Annual Precipitation, BIO15 Precipitation Seasonality, BIO16 Precipitation of Wettest Quarter, BIO18 Precipitation of Warmest Quarter, and BIO19 Precipitation of Coldest Quarter.

We used MaxEnt software (ver. 3.4.1) to generate a logistic probability map (i.e. climate suitability map of cell size ~ 1 km^2) of species presence, with logistic values ranging from 0 (unsuitable) to 1 (optimal climates) (Phillips et al. 2006; Phillips and Dudík 2008). The model was run with the following settings: the maximum number of background points = 10,000; replicates = 100; and replicate run type = Bootstrap. Duplicated presence records were removed and all other parameters were kept at

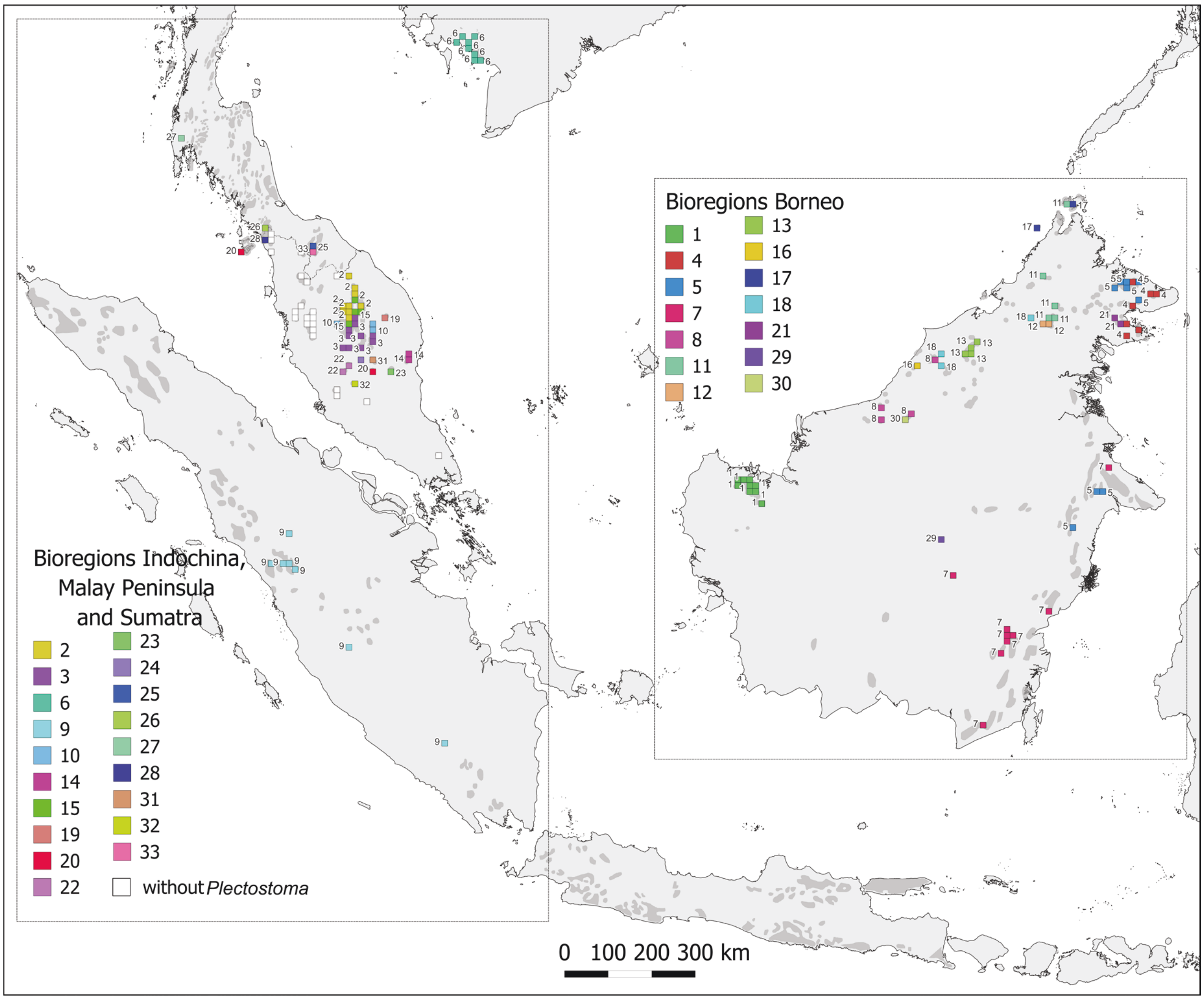

Figure 2. Spatial distribution of 33 bioregion areas classified based on *Plectostoma* species occurrences in Southeast Asia using Infomap Bioregions v2.7.1, with a grid resolution of approximately 15.625 km. Each bioregion cell is assigned a unique number identifier. These identifiers are assigned numerically by the Infomap algorithm during the clustering process.

default values. The average of the logistic probability of species occurrence for each suitability map grid cell was calculated from the 100 bootstrap replicates.

The climate suitability for each bioregion area and each bioregion cell was summarised into two climatic variables by calculating the mean and standard deviation of the logistic values in the climate suitability raster layer using “Zonal statistics”. The mean value represents the average climate suitability score for each bioregion cell (hereafter referred to as “climate suitability”), while the standard deviation represents the variability of the climate (hereafter referred to as “climate variability”).

Geological background

We adopted the litho-tectonic blocks and mega-units of Sundaland from published geological literature to illustrate the different origins of Sundaland’s constituents in the Late Cretaceous. As the Malay Peninsula and Borneo have different geological histories, the geological background of the Malay Peninsula was obtained from Metcalfe (2013) while that of Borneo was obtained from Ramasamy et al. (2021).

Based on the availability of detailed digital data for individual limestone karst hills, our bioregion analysis focuses on four regions: Centre of the Malay Peninsula (CMP) (Fig. 3), and in Borneo, namely; West Sarawak (WS) (Fig. 4), North Sarawak (NS) (Fig. 5), and Interior and East Sabah (IES) (Fig. 6). Depositional ages of the carbonates range from Lower Palaeozoic to Mesozoic (CMP), Triassic–Cretaceous (WS), Eocene–Miocene (NS), and Oligocene (IES). Their depositional environments include both shallow-sea platform carbonates (CMP and Mulu in NS) and reef complexes (WS). Thermogeochemical studies in Peninsular Malaysia indicate that geological exhumation on a regional scale started in the Upper Cretaceous at 85 Ma and continued, at intervals, into the Oligocene (Cottam et al. 2013; Sautter 2019). Exposure and karstification of limestones in the CMP likely started in the early Cenozoic and continued thereafter.

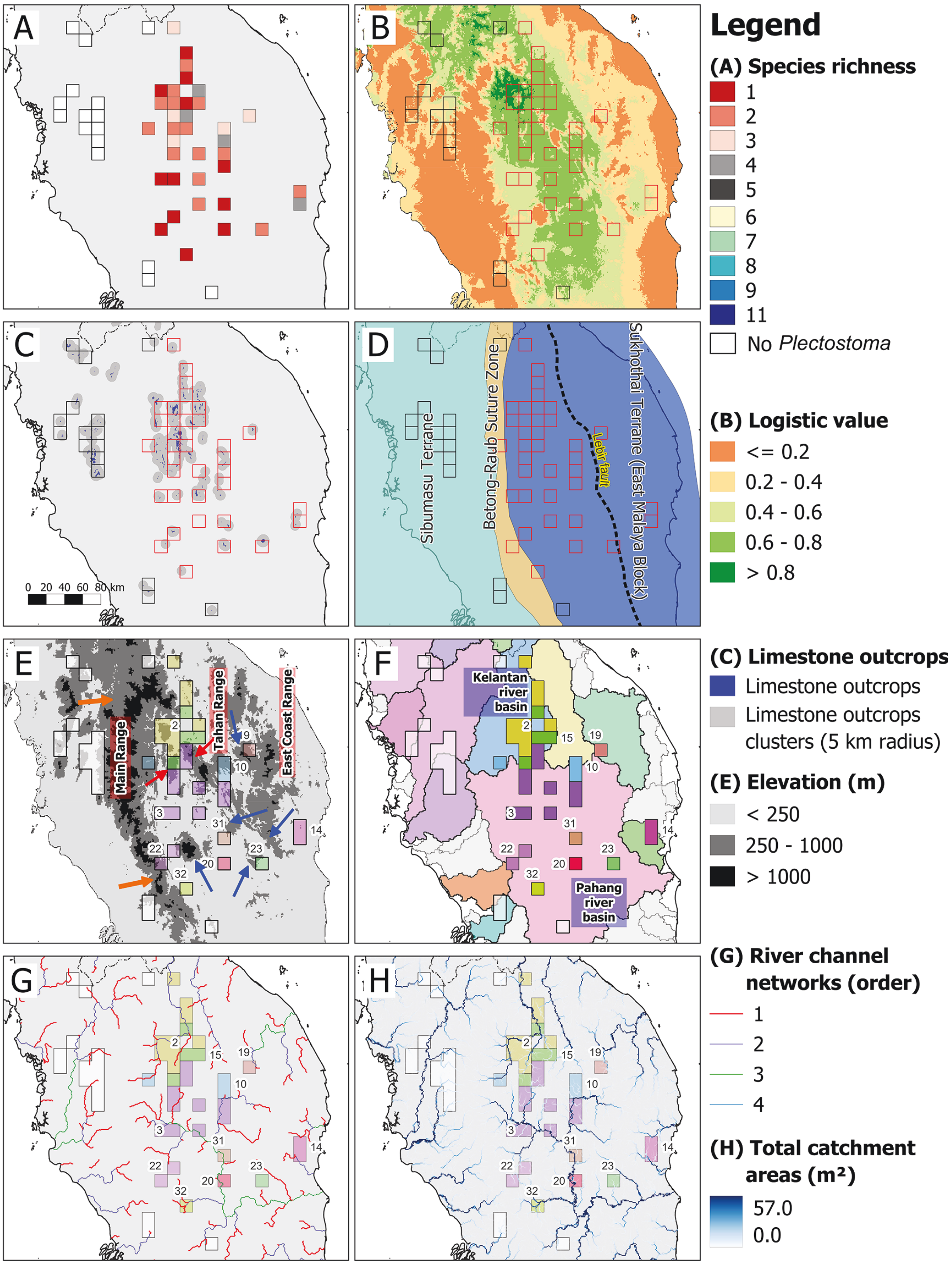

Figure 3. Spatial patterns of *Plectostoma* species richness, habitat characteristics, and biogeographical variables in the Centre of the Malay Peninsula that includes 11 Bioregion Areas (BA): BA2, BA3, BA15, BA19, BA10, BA22, BA32, BA20, BA31, BA23, and BA14. Each panel displays maps with different overlays for these areas. **A.** Species richness in each bioregion cell; **B.** Climate suitability map from MaxEnt analysis overlaid with bioregion cells containing *Plectostoma* species (red outline squares) and without *Plectostoma* species (black outline squares). The logistic values represent the predicted probability of occurrence, with 0 being unsuitable and 1 being optimal; **C.** Distribution of limestone clusters and limestone outcrops, with sites lacking overlaid bioregion cells indicating unsampled locations with no *Plectostoma* data; **D.** Geological background of the Centre of the Malay Peninsula, adapted from Metcalfe (2013); **E.** Topography of the areas, with arrows indicating the major upland (elevation > 250 m) that separate the bioregion areas within Gua Musang-Kuala Krai limestone cluster (red), between Gua Musang-Kuala Krai limestone cluster and adjacent smaller limestone clusters (blue), and between east and west coasts of the Malay Peninsula (orange); **F.** River basins containing bioregion areas, differentiated by colour; distinct colours indicate separate river basins, while those without bioregion areas are not shown; **G.** River networks map, illustrating how bioregion areas may connect via different branching and flow directions (i.e., Strahler order); **H.** River catchment areas map showing the relative size of drainage areas across bioregions, with larger values indicating major river channels.

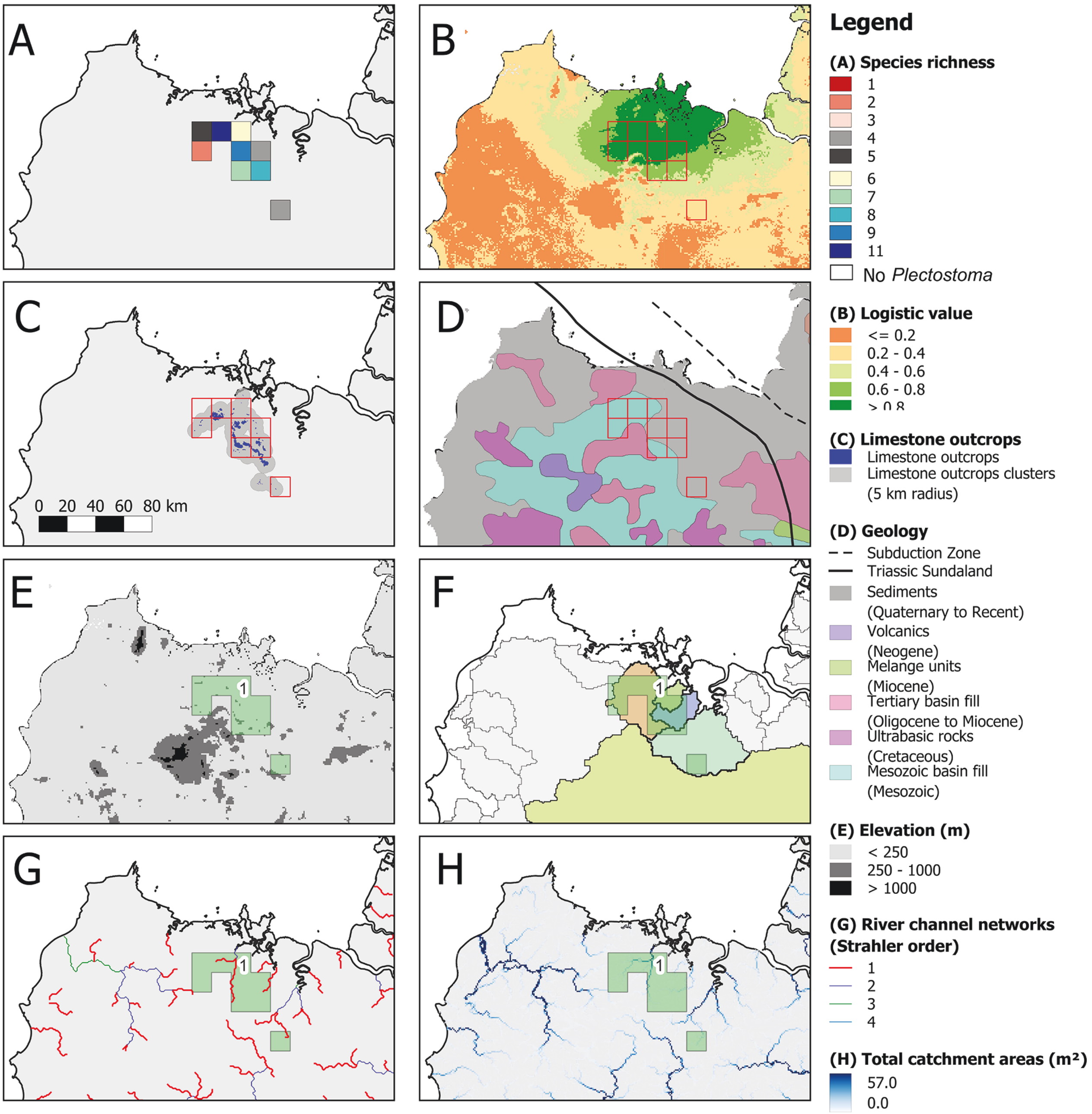

Figure 4. Spatial patterns of *Plectostoma* species richness, habitat characteristics, and biogeographical variables in the West of Sarawak that includes one Bioregion Area (BA): BA1. Each panel displays maps with different overlays for these areas. **A.** Species richness in each bioregion cell; **B.** Climate suitability map from MaxEnt analysis overlaid with bioregion cells containing *Plectostoma* species (red outline squares). The logistic values represent the predicted probability of occurrence, with 0 being unsuitable and 1 being optimal; **C.** Distribution of limestone clusters and limestone outcrops, with sites lacking overlaid bioregion cells indicating unsampled location with no *Plectostoma* data. (D) Geological background of the West of Sarawak, adapted from Ramasamy et al. (2021); **E.** Topography of the areas; **F.** River basins containing bioregion areas, differentiated by colour; distinct colours indicate separate river basins, while those without bioregion areas are not shown; **G.** River networks map, illustrating how bioregion areas may connect via different branching and flow directions (i.e., Strahler order); **H.** River catchment areas map showing the relative size of drainage areas across bioregions, with larger values indicating major river channels.

Hydrological and topographical features

We obtained geomorphological features for our study region, including drainage basins, river channels, river networks, and total catchment areas, based on SRTM 1 Arc-Second Global (Digital Object Identifier (DOI) number: /10.5066/F7PR7TFT). The "Basic Terrain Analysis" module of SAGA GIS ver. 9.3.1 was used to generate the following outputs: (1) "Drainage Basin" – a polygon shapefile representing water catchments; (2) "Channel Network" – a line shapefile representing drainage networks, with the hierarchical position of the drainages or rivers in the

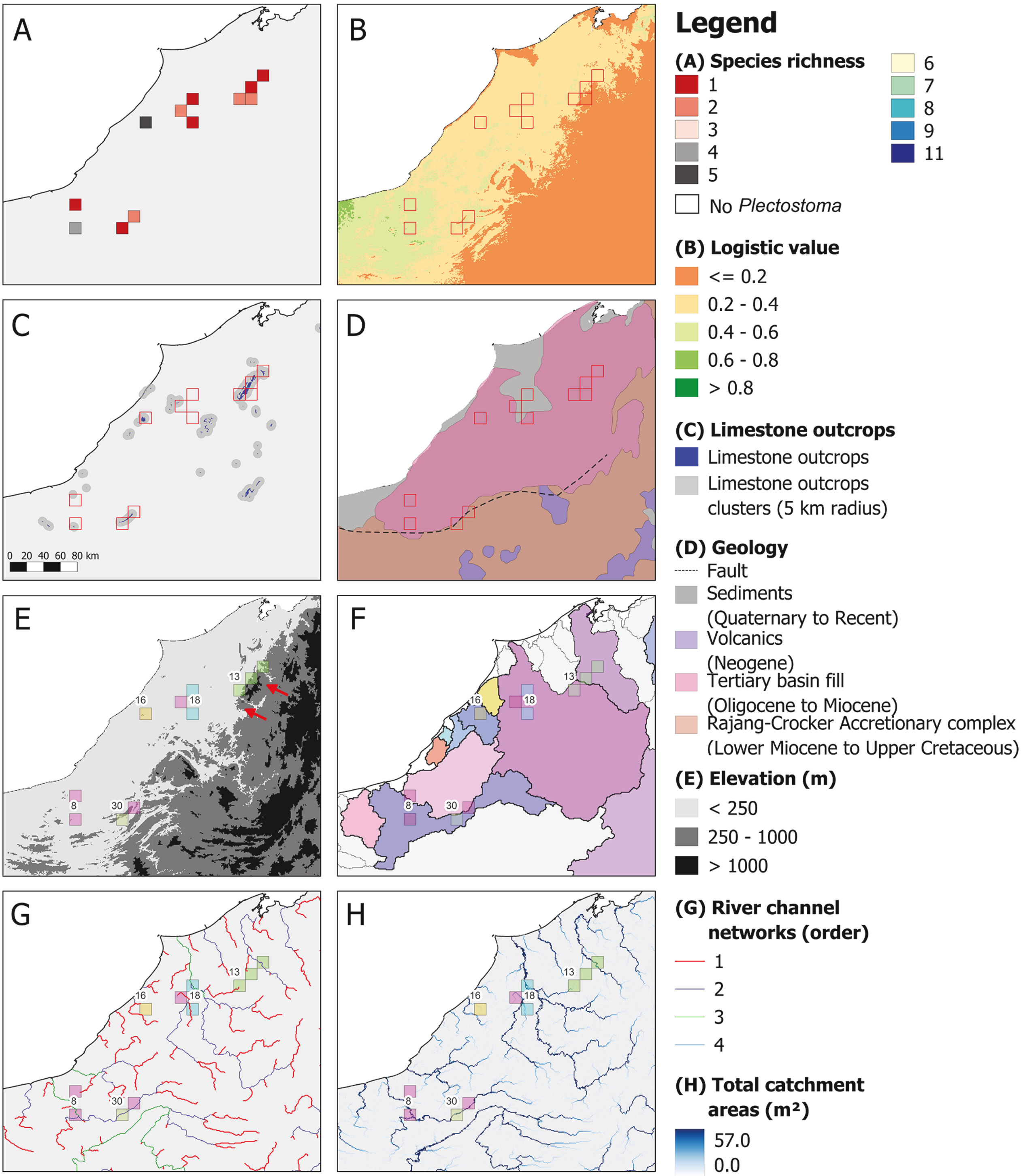

Figure 5. Spatial patterns of *Plectostoma* species richness, habitat characteristics, and biogeographical variables in the North of Sarawak that includes five Bioregion Areas (BA): BA8, BA30, BA16, BA18, and BA13. Each panel displays maps with different overlays for these areas. **A.** Species richness in each bioregion cell; **B.** Climate suitability map from MaxEnt analysis overlaid with bioregion cells containing *Plectostoma* species (red outline squares). The logistic values represent the predicted probability of occurrence, with 0 being unsuitable and 1 being optimal; **C.** Distribution of limestone clusters and limestone outcrops, with sites lacking overlaid bioregion cells indicating unsampled location with no *Plectostoma* data; **D.** Geological background of the North of Sarawak, adapted from Ramasamy et al. (2021); **E.** Topography of the areas, with arrows indicating the major upland (elevation > 250 m); **F.** River basins containing bioregion areas, differentiated by colour; distinct colours indicate separate river basins, while those without bioregion areas are not shown; **G.** River networks map, illustrating how bioregion areas may connect via different branching and flow directions (i.e., Strahler order); **H.** River catchment areas map showing the relative size of drainage areas across bioregions, with larger values indicating major river channels.

network (i.e. Strahler order); (3) "Total Catchment Area" – a raster file showing how water flows across the landscape (Conrad et al. 2015). Cells with larger values indicate locations that receive drainage from a greater land area, corresponding to major channels. This layer was used as a proxy for relative river size and drainage magnitude. Topographic features, such as mountain ranges and valley depth, were extracted from the SRTM.

Island biogeography variables

The island biogeography analysis was conducted only for the bioregion areas in Malaysia, where detailed information about the limestone hill distribution and sizes are available. The analyses were performed separately at two scales: bioregion areas and bioregion cells. Data layers were generated for variables commonly regarded as determinants of limestone karst island biogeography, namely; the number of limestone hills (hereafter referred to as "hill numbers"), the availability of limestone areas (hereafter referred to as "limestone areas"), and the degree of isolation (hereafter referred to as "hills' isolation"). All analyses were performed in QGIS ver. 3.28 (QGIS.org 2022).

The limestone hills point vector file was created from the centroid of each limestone hill polygons vector file by using the "Centroid" function. The total number of points for each bioregion cell and area were obtained using the "Count Points in Polygon" function. A raster layer of limestone hills was created by converting the limestone hill polygons vector file (UTM/WGS 84 projection) to a raster with 50 m resolution (~ 0.0025 km^2), assigning a raster value of "1". The total area of limestone hills in each bioregion cell and area were then obtained using "Zonal statistics" to sum raster values for each bioregion cell, which were multiplied by the limestone raster cell size (0.0025 km^2).

To calculate the degree of isolation of the limestone hills in an area, we first determined the pairwise distances between each of the limestone hills and its 50 nearest adjacent hills using the limestone hills point vector file (UTM/WGS 84 projection). The "Statistics by categories" function was then used to calculate the mean of the 50 distance values for each hill, summarising the pairwise distance analysis results. Subsequently, the "Join Attributes by Location (Summary)" function was used to calculate the mean of the average distance values (in kilometres) of all the hills within each bioregion cell and area.

Data analyses

Qualitative overlay analysis of topographic and geological factors on bioregion areas

First, we qualitatively explored the role of topography and geological background in shaping bioregion areas' size, location, and boundaries, as well as in determining the species richness, endemism, and island biogeography. Using GIS overlay techniques, we visually examined the spatial relationships among these data layers to identify potential patterns and associations. This qualitative analysis focused on regions with high concentrations of bioregions, varied bioregion sizes, and substantial *Plectostoma* species richness. These regions are: (1) Centre of the Malay Peninsula (CMP) – encompassing 11 bioregion areas with 23 *Plectostoma* species; (2) West Sarawak (WS) – a single bioregion area hosting 16 species; (3) North Sarawak (NS) – comprising five bioregion areas with 17 species; and (4) Interior and East Sabah (IES) – including five bioregion areas and 16 species.

Effects of biogeographical variables on species richness

We used Generalised Linear Mixed Models (GLMMs) to address the following research questions: (1) What is the effect of island biogeography variables and climate suitability on overall species richness? (2) How do these effects vary when accounting for spatial autocorrelation and random variations between regions (Malay Peninsula vs Borneo) or among bioregion areas?

The first set of GLMM analyses were performed at the bioregion area scale to evaluate the effects of island biogeography variables: "hill numbers", "limestone areas", and "hills' isolation", along with ecological variables: "climate suitability" and "climate variability" on the species richness. All five variables were included as fixed effects, while the region (Malay Peninsula and Borneo) was included as a random effect variable to account for spatial autocorrelation and different geological histories.

A total of 24 out of the 33 bioregions in the Malaysian part of the Malay Peninsula and Borneo (Sarawak and Sabah) were included in this analysis (Table 1). Seven other bioregion areas were excluded from the analysis because they were located outside Malaysia and lacked detailed limestone outcrop data. These included two from the Indonesian part of Borneo (BA7 and BA29), three from the Thai part of the Malay Peninsula (BA25, BA27, and BA33), and one each from Sumatra (BA9) and Vietnam (BA6). Additionally, one bioregion area from offshore islands (BA17) was excluded to minimise potential confounding factors associated with offshore islands, as the focus was on the island biogeography of limestone outcrops. Finally, BA24 was removed due to uncertain location data.

A second set of GLMM analyses were performed at the bioregion cell scale for 77 bioregion cells from the 24 bioregion areas, using the same fixed effect variables as in the first set of GLMMs (Suppl. material 3: table S1). Bioregion area identity was included as a random effect variable to account for spatial autocorrelation.

For both GLMMs, the hills' area and the hills' isolation were standardised to a mean of 0 and a standard deviation of 1 to assess the relative strength of parameter estimates (Jongman et al. 1987; Ramette 2007). Multicollinearity among variables was assessed using the variance inflation factor (VIF), implemented in the 'check collinearity' function of the R package 'performance' (James et al. 2013). None of the habitat covariates were excluded, as collinearity among variables was low: VIF ≤ 4.0 for the bioregion area scale analysis and VIF ≤ 1.9 for the bioregion cell scale analysis.

We constructed four thematic candidate models for both GLMMs, incorporating the random effect variable: Model 0 – null model with only the random effect variable; Model 1 – island biogeography variables as fixed effects and the random effect variable; Model 2 – climate suitability variables as fixed effects and the random effect variable, and Model 3 – all island biogeography and climate suitability variables as fixed effects and the random effect variable. Following the initial evaluation of each of the thematic candidate models, we constructed a final integrated model (Model 4). This model was developed by combining the specifically significant predictors identified from both the island biogeography and climate suitability thematic models. This theory-driven integration allowed us to move beyond comparing isolated thematic hypotheses and instead identify the most parsimonious combination of drivers.

The GLMMs were performed with a Poisson family and a log link function using the 'glmer' function in the R package 'lme4' (Bates et al. 2015). We used the corrected Akaike's Information Criterion (AIC_c) to identify the best-supported models (i.e., models with the lowest AIC_c and a ΔAIC_c value < 2 from the highest-ranked model; Burnham and Anderson 2002). Information criteria (AIC_c, ΔAIC_c, model likelihoods, and model weights [wi]) were summarised and compared to evaluate the relative quality of different models, using the 'AICtable' function in the R package 'wiqid' (Meredith 2015).

After selecting the best models, we computed marginal R-squared (R^2m) and conditional R-squared (R^2c) values to assess how well these models explained the variability in the data, using the 'r.squaredGLMM' function in the R package 'MuMIn' (Barton 2020). All analyses were performed using R ver. 4.4.1 (R Core Team 2024).

CCA analysis of biogeographical drivers of species endemism composition

In addition to the GLMM analyses, we performed a Canonical Correspondence Analysis (CCA) to examine the relationships between species endemism composition and both island biogeography and climate variables. This analysis addressed the following questions: (1) How does species endemism composition relate to gradients represented by island biogeography and climate suitability variables? (2) Which environmental factors are associated with the distribution of different endemism categories (short-range, mid-range, wide-range endemics, and widespread species)?

The primary matrix in the CCA comprised the number of species in four endemism categories: (1) short-range endemic species, (2) mid-range endemic species, (3) wide-range endemic species, and (4) widespread species. The secondary matrix consisted of the same three island biogeography variables and two climate suitability variables used in the GLMM analyses.

As with the GLMM analyses, we conducted CCA separately at two spatial scales: bioregion areas and bioregion cells. For each spatial scale, the CCA ordination was performed using the 'cca' function in the R package 'vegan' (Oksanen et al. 2025). The significance of the CCA models, both overall and for individual marginal predictors, was assessed using permutation tests (the 'anova' function in 'vegan') with 1,000 permutations.

Results

Bioregion delineation of Malaysian limestone clusters: elevation, distance, and drainage patterns

For bioregion delineation, a total of 116 bioregion grid cells (bioregion cells) were generated by Infomap Bioregions analysis, belonging to 33 designated bioregion areas (BA) (Fig. 2, Table 1). The Malay Peninsula and Borneo have 14 unique bioregion areas, while the remaining five bioregion areas are unique to Southern Thailand (BA25, BA27, BA33), Ha Tien in Vietnam and the adjoining border of Cambodia (BA6), and Sumatra (BA9). The largest is BA3 in Malay Peninsula with 10 bioregion cells (Fig. 2B); followed by BA1, BA2, BA5, and BA7, each with nine bioregion cells, all in Borneo, except BA2 in Malay Peninsula; BA6 in Vietnam with eight bioregion cells; BA4 in Borneo and BA9 in Sumatra, each with seven bioregion cells. Each of the remaining 25 bioregion areas consists of five or fewer bioregion cells (Table 1). Thirteen bioregion areas have only one cell – seven in the Malay Peninsula, three in Borneo and three in Southern Thailand.

When compared to the 34 previously delineated limestone clusters on the Malay Peninsula mainland, defined as groups of limestone outcrops located less than 10 km apart and at least 10 km away from other clusters (table 5.9 and fig. 5.8 in Liew et al. 2020), it is now apparent that the same cluster can include multiple bioregion areas. Conversely, limestone karsts located too distantly to be classified as part of a cluster can be part of the same bioregion. For example, on the Permo–Triassic platform limestones in the Centre of Malay Peninsula, the Lipis-Gua Musang-Kuala Krai limestone cluster hosts three different bioregion areas: (1) in the north, predominantly within the Kelantan river basin, BA2 and BA15 trending north-south, with the latter central to the former, along major drainages; (2) further south, predominantly in the upper Pahang River basin, an extensive area occupied by BA3 (Fig. 3F–H). BA 10 is located peripheral to the Lipis-Gua Musang-Kuala Krai limestone cluster with a single cell in the west, near the Raub-Bentong suture zone, separated by a distance of 80 km from BA10 on the eastern side of the Tahan Range (Figs 2B, 3E).

Table 1. Summary of *Plectostoma* bioregions across Sundaland, detailing bioregion size, species richness, endemism, and habitat characteristics in terms of limestone outcrops and climate suitability. Each row represents a bioregion within a specific geographic area, showing bioregion size (in number of grid cells), total number of *Plectostoma* species, and a breakdown of endemism levels (short-range, mid-range, wide-range, and widespread species). The number of limestone outcrops, mean distance between outcrops, total limestone area, and mean climate suitability score are not available for regions without detailed information.

Country	Region	Limestone clusters (Liew et al, 2021)	Bioregion Areas	Bioregion Size (number of grid cells – bioregion cells)	Total number of species	Number of short-range endemic species	Number of mid-range endemic species	Number of wide-range endemic species	Number of widespread species	Number of limestone outcrops	Mean ± SD distances between limestone outcrops (km)	Total areas of limestone outcrops (km^2)	Mean ± SD climate suitability score (ENM logistic value)
Malaysia - West Malaysia	Malay Peninsula												
		Setir, Jentera-Betis, north Lipis-Gua Musang-Kuala Krai	BA2	9	6	0	3	2	1	175	9.03 ± 5.67	55.20	0.70 ± 0.12
		Kuala Tahan, Merting, Kenong Rimba, Bama, Sungai Koyan, south Lipis-Gua Musang-Kuala Krai	BA3	10	6	0	2	2	2	99	10.83 ± 10.50	19.21	0.64 ± 0.13
		Taman Negara,a small cluster of limestone hills in the western part of south Lipis-Gua Musang-Kuala Krai	BA10	3	5	1	1	2	1	13	29.72 ± 4.15	1.82	0.59 ± 0.15
		Kuantan	BA14	2	5	5	0	0	0	4	92.47 ± 1.11	1.33	0.37 ± 0.05
		centre Lipis-Gua Musang-Kuala Krai	BA15	4	2	0	1	1	0	73	7.56 ± 3.81	23.36	0.72 ± 0.08
		Kenyir	BA19	1	3	3	0	0	0	3	54.19 ± 0.29	1.56	0.29 ± 0.11
		Temerloh, Langkawi	BA20	2	2	0	0	0	2	5	62.18 ± 0.52	3.00	0.66 ± 0.02
		Balong	BA22	2	1	0	1	0	0	5	53.14 ± 3.13	1.73	0.37 ± 0.13
		Mengapur	BA23	1	2	1	0	0	1	3	77.03 ± 0.58	7.11	0.47 ± 0.07
		Perlis	BA26	1	2	1	0	0	0	2	14.80 ± 0.55	24.65	0.57 ± 0.10
		Perlis	BA28	1	1	1	0	0	0	32	8.15 ± 1.31	19.43	0.16 ± 0.14
		Kota Gelanggi	BA31	1	1	1	0	0	0	5	52.35 ± 1.06	1.93	0.65 ± 0.04
		Cintamanis	BA32	1	1	1	0	0	0	1	71.60 ± 0.00	0.10	0.50 ± 0.08
			BA24*	1	1	1	0	0	0	-	-	-	-
Malaysia - Sarawak	Borneo main island												
		Bau-Padawan-Serian	BA1	9	17	7	9	0	1	90	12.26 ± 3.24	99.32	0.75 ± 0.18
		Bukit Sarang, Sungai Kakus, Bukit Sidang, Beluru	BA8	4	7	4	1	0	2	15	62.07 ± 36.19	6.27	0.42 ± 0.08
		Mulu	BA13	4	3	1	2	0	0	33	29.61 ± 5.33	72.45	0.28 ± 0.07
		Niah	BA16	1	5	5	0	0	0	6	45.55 ± 0.67	15.04	0.33 ± 0.04
		Sungai Baram	BA18	3	1	0	0	0	1	1	38.27 ± 18.36	0.24	0.33 ± 0.07

Country	Region	Limestone clusters (Liew et al, 2021)	Bioregion Areas	Bioregion Size (number of grid cells – bioregion cells)	Total number of species	Number of short-range endemic species	Number of mid-range endemic species	Number of wide-range endemic species	Number of widespread species	Number of limestone outcrops	Mean ± SD distances between limestone outcrops (km)	Total areas of limestone outcrops (km²)	Mean ± SD climate suitability score (ENM logistic value)
		Sungai Kakus	BA30	1	1	1	0	0	0	9	91.27 ± 1.24	4.80	0.35 ± 0.06
Malaysia - Sabah	Borneo main islands												
		Lower Kinabatangan, Tabin, Ulu Segama, Madai Baturong, Batu Tengar, Kampung Check Point	BA4	7	6	2	0	3	1	33	37.59 ± 17.08	18.90	0.39 ± 0.08
		Lower Kinabatangan, Sabahmas	BA5	9	4	1	1	1	1	28	22.54 ± 6.58	24.28	0.28 ± 0.05
		Sapulut, Bukit Melikop, Trusmadi	BA11	5	2	1	0	0	1	9	50.40 ± 10.18	4.84	0.39 ± 0.14
		Batu Temurung	BA12	2	7	3	1	0	3	16	50.31 ± 2.50	2.98	0.38 ± 0.08
		Madai Baturong	BA21	2	1	0	1	0	0	2	42.61 ± 1.91	0.98	0.48 ± 0.08
	Borneo offshore small islands	Mantanani	BA17**	2	3	1	0	1	1	3	-	-	-
Thailand – South Thailand	Malay Peninsula												
			BA25	1	1	1	0	0	0	-	-	-	-
			BA27	1	1	1	0	0	0	-	-	-	-
			BA33	1	1	1	0	0	0	-	-	-	-
Indonesia - Kalimantan	Borneo main island												
			BA7	9	2	0	0	0	2	-	-	-	-
			BA29	1	1	1	0	0	0	-	-	-	-
Indonesia -Sumatra	Sumatra												
			BA9	7	1	0	0	0	1	-	-	-	-
Vietnam - South Vietnam	Indochina												
			BA6	8	3	2	1	0	0	-	-	-	-

* Bioregion area 24 were created based on the species record is available based on museum collection but no limestone hills were available in the area. Probably the location on the specimen label is not accurate. ** Bioregion 17 encompasses the limestone hills of the two-small island, and hence the estimation of distance between hills and ENM cannot be performed.

The limestone clusters in the Pahang river basin south of BA3 form five separate bioregion areas (BA20, BA22, BA23, BA31, BA32) (Fig. 3F–H). BA22 consists of two adjoining cells in the same drainage sub-basin. In contrast, the other four bioregion areas each consist of a single cell isolated by at least 20 km, with the exception of BA20 and BA31, which are located in different drainage sub-basins. Bioregions BA14 and BA19 are uniquely located, on Carboniferous and Permian limestones, respectively, to the east of the Lebir Fault on the Eastern Belt of the Eastern Malaya Block of Metcalfe (2013) (Fig. 3D).

Bioregion areas without mountain ranges (> 250 m elevation) separating limestone clusters often form a single bioregion area if the clusters are within adjacent river networks and catchment areas, even when they are in different river basins. This is evident in West of Sarawak (Fig. 4C, E–H: bioregion 1) and East of Sabah (Fig. 6C, E–H: bioregion areas 4 and 5). However, limestone clusters located within valley landscapes with elevation higher than 250 m tend to be more isolated, forming separate bioregion areas, such as BA11 and BA12 (Fig. 6C, E–H). When limestone clusters are further apart and there is a lack of connection to adjacent river networks and catchment, they form distinct bioregion areas, as seen in the north of Sarawak, such as BA8, BA30, BA16, BA18, and BA13 (Fig. 5C, E–H).

Broad-scale climate suitability based on climatic variables does not appear to play a major role in delineating bioregion areas, as there is no clear “ecotone” or transitional boundary corresponding to bioregion area boundaries (Figs 3B, 4B, 5B, 6B). For example, in the Malay Peninsula, areas west of the Main Range where the genus is absent are predicted by the MaxEnt model to have low climate suitability (most with logistic values < 0.4), while the occupied areas east of the Main Range are predicted to have higher suitability (most with logistic values > 0.4) (Fig. 3B). However, in Borneo, *Plectostoma* thrives even in areas with low climate suitability that similar with the areas at the west of the Malay Peninsula’s Main Range, where the genus is absent (Figs 5B, 6B).

In the CMP, almost all the Permo–Triassic platform limestone hills within the Central Belt of the East Malaya Block (east of the Raub–Bentong Suture) host *Plectostoma*. Even more striking, when compared to this abundance, is the complete absence of *Plectostoma* from all the limestone hills to the west of the Raub–Bentong Suture and south of the Kangar–Pattani Line (Fig. 1B).

Species richness, distribution and endemism of *Plectostoma* species

Despite having the less number of bioregion areas, species richness in Borneo is higher than in the Malay Peninsula (52 species vs 28 species). The remaining species are in Southern Thailand (three species, one in each of the three bioregion areas), one species in Sumatra, and three species in South Vietnam (Table 1). There are no *Plectostoma* species on the west coast of the Malay Peninsula from southern Perlis until Selangor on the west side of the Main Range, and in the southern part of the Malay Peninsula beyond the Main Range (Figs 1A, C, 2B, 3A).

The tabulation of species richness for each bioregion area reveals that areas with high *Plectostoma* species richness often coincide with larger bioregion areas (i.e. more bioregion cells) and contain extensive, continuous areas of suitable limestone habitat (Table 1, Figs 3B, 4B). Only 4 of the 13 single-cell bioregion areas contain more than one *Plectostoma* species, namely, BA16 in the Niah limestone cluster with five species, BA14 near Kuantan with five species, BA19 in the Kenyir limestone cluster with three species, and BA23 and BA26, each with two species (Table 1).

The highest species richness was recorded in BA1, located in the Bau-Padawan-Serian limestone cluster, with 17 species (Table 1, Fig. 4C). Other species-rich bioregion areas include: BA8 in the limestone cluster at the North of Sarawak, with seven species (Fig. 5C), BA12 in the limestone cluster of Interior of Sabah, also with seven species (Fig. 6C), BA2 in the northern Lipis-Gua Musang-Kuala Krai limestone cluster within Kelantan river basin, with six species (Fig. 3C), BA3 in the southern Lipis-Gua Musang-Kuala Krai limestone cluster and adjacent smaller limestone clusters in the north of Pahang river basin, with six species (Fig. 3C), and BA4 in East of Sabah, with six species (Fig. 6C). Interestingly, high species richness can also occur in areas with relatively lower climate suitability – in North of Sarawak and Sabah (e.g., BA5 with four species) (Figs 5B, 6B).

Plectostoma species exhibit significant variabilities in distribution ranges across Sundaland (Suppl. material 1: figs S1–S6). A total of 73 out of 84 *Plectostoma* species are restricted to a single bioregion area. More than half of the species (n = 47) are short-range endemics, with distribution ranges limited to a few limestone outcrops less than 10 km apart or confined to a single hill (Suppl. material 4: table S1). Ten species have distribution ranges spanning multiple bioregion areas: *P*. *wallacei busauense* (E. A. Smith, 1893) in Sarawak; *P*. *obliquedentatum* (Vermeulen, 1994), *P*. *cyrtopleuron* (Vermeulen, 1994), *P*. *brevituba* (Vermeulen, 1994) and *P*. *concinnum* (Fulton, 1901) in Sabah; and *P*. *salpidomon* (van Benthem Jutting, 1952), *P*. *davisoni* T.-S. Liew, Vermeulen, Marzuki & Schilthuizen, 2014 , *P*. *christae* (Maassen, 2001), *P*. *crassipupa* (van Benthem Jutting, 1952), and *P*. *relauensis* T.-S. Liew, Vermeulen, Marzuki & Schilthuizen, 2014 in the Lipis-Gua Musang-Kuala Krai limestone cluster of Malay Peninsula.

In the west of Sundaland, the sole species in Sumatra is a widespread species (ranges > 140 km). One of the three species in Southern Vietnam, occurring in Ha Tien and the adjoining Cambodian limestone outcrops, is a wide-range endemic species (Fig. 1). Six out of 28 species in the Malay Peninsula are wide-range endemic or widespread, found in the Gua Musang-Kuala Krai

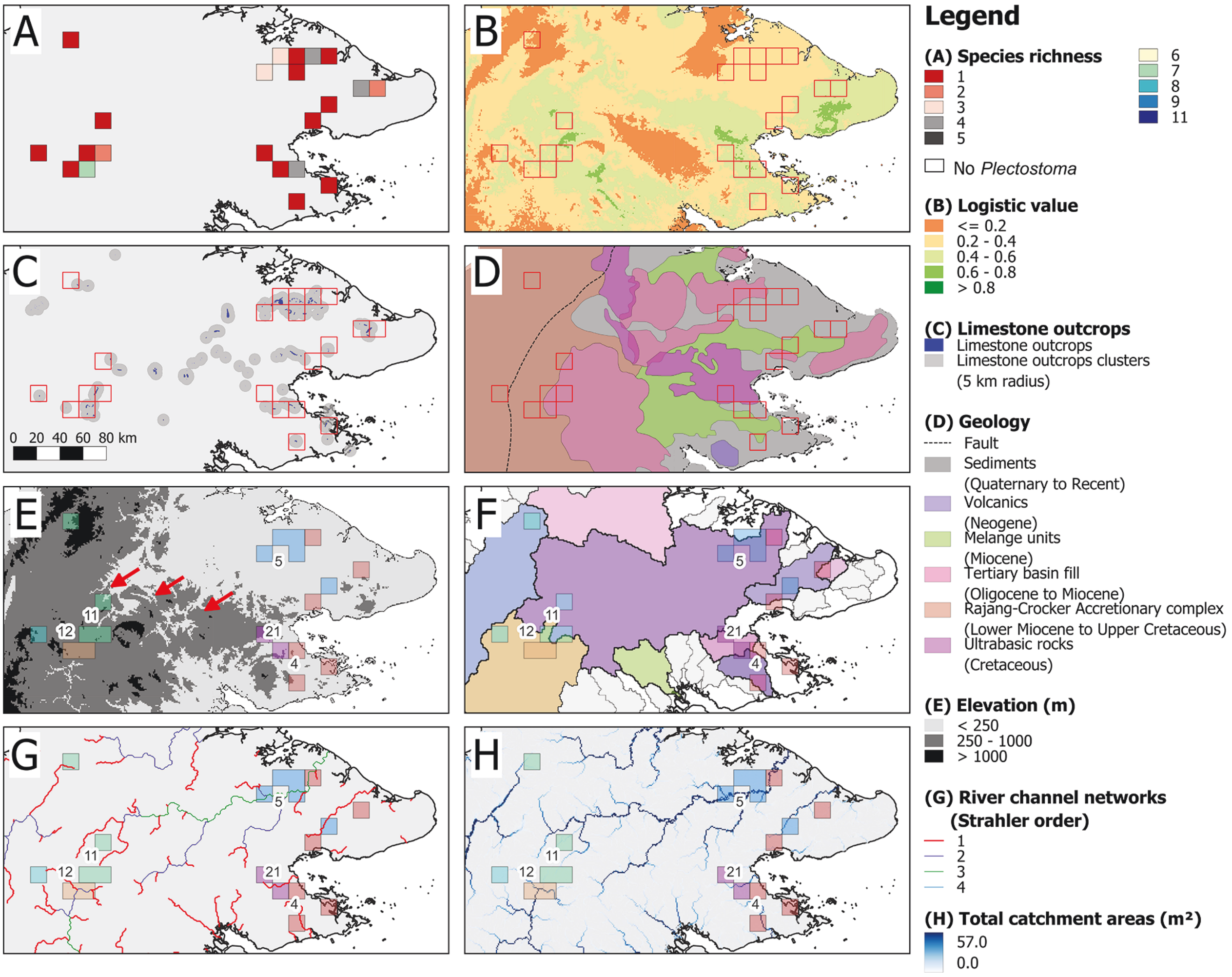

Figure 6. Spatial patterns of *Plectostoma* species richness, habitat characteristics, and biogeographical variables in the Interior and East of Sabah, covering five Bioregion Areas (BAs): BA12, BA11, BA21, BA5, and BA4. Each panel displays maps with different overlays for these areas. **A.** Species richness in each bioregion cell; **B.** Climate suitability map from MaxEnt analysis overlaid with bioregion cells containing *Plectostoma* species (red outline squares). The logistic values represent the predicted probability of occurrence, with 0 being unsuitable and 1 being optimal; **C.** Distribution of limestone clusters and limestone outcrops, with sites lacking overlaid bioregion cells indicating unsampled location with no *Plectostoma* data; **D.** Geological background of the Interior and East of Sabah, adapted from Ramasamy et al. (2021); **E.** Topography of the areas, with arrows indicating the major upland (elevation > 250 m) that separate the bioregion areas between Interior and East of Sabah; **F.** River basins containing bioregion areas, differentiated by colour; distinct colours indicate separate river basins, while those without bioregion areas are not shown; **G.** River networks map, illustrating how bioregion areas may connect via different branching and flow directions (i.e., Strahler order); **H.** River catchment areas map showing the relative size of drainage areas across bioregions, with larger values indicating major river channels.

limestone cluster within the Kelantan River basin and Pahang River basin, and smaller limestone clusters to the south of the Gua Musang-Kuala Krai limestone cluster (i.e. BA2, BA3, and BA15) (Table 1, Suppl. material 1: fig. S1). Each of these three bioregions hosts at least one widespread endemic species (Table 1), but only the eastern limestone cluster of BA10 hosts a short-range endemic. In contrast, each of the isolated limestone clusters further south of Pahang hosts a short-range endemic species (BA23, BA31, and BA32). The sole occurrence of a widespread species in these isolated limestone clusters is *P. davisoni* in BA23. Furthermore, BA19 and BA14, at the east of the Lebir fault, have three and five short-range endemics, respectively, while widespread species are absent in both bioregions.

In the east of Sundaland, 10 of the 52 *Plectostoma* species are widespread or wide-range endemic species predominantly occurring in the east, south, and north of Borneo (BA4, BA5, and BA7) (Fig. 2, Suppl. material 1: fig. S4). Half of the short-range endemic species are concentrated in the West of Borneo, particularly in the Bau-Padawan-Serian limestone cluster (BA1), which hosts seven short-range endemic species (Supplemenrary material 1: figs S3, S5; Suppl. material 4: table S1). This is followed by the Niah limestone cluster (BA16), which contains five short-range endemic species (Suppl. material 1: fig. S5C; Suppl. material 4: table S1).

Climate suitability analysis

The climate suitability analysis for *Plectostoma* was conducted using a MaxEnt model with 100 bootstrap replicates, achieving an average AUC of 0.906 (±0.007), indicating high predictive accuracy (Suppl. material 2: fig. S3). The model identified several key environmental predictors influencing *Plectostoma* distribution, with BIO19 (Precipitation of Coldest Quarter) contributing the highest importance (29.3%), followed by BIO3 (Isothermality, 14.7%) and BIO15 (Precipitation Seasonality, 12.8%) (Suppl. material 2: table S2). Other contributing factors included Annual Mean Temperature (BIO1, 11.8%) and Precipitation of Warmest Quarter (BIO18, 8.3%) (Suppl. material 2: table S2).

Spatially, the predicted climate suitability maps revealed that high-suitability areas coincided with the regions of large continuous limestone formations, particularly in the central and eastern parts of the Malay Peninsula, West Borneo, and parts of Sabah (Figs 1B, 3B, 4B, 5B, 6B). The response curve analysis suggested that *Plectostoma* species prefer stable temperature regimes and moderate precipitation variability (Suppl. material 2: fig. S6).

Effects of biogeographical variables on species richness

For bioregion areas, the two thematic models, Model 2 and Model 1, have AIC_c values of 116.68 and 116.69, respectively. The small ΔAIC_c value (0.03) between these models, along with similar model weights (0.28) and model likelihood (0.68 and 0.66, respectively), indicates that both models are almost equally plausible (Table 2). Model 2 has a higher conditional R-squared (0.54), suggesting that when both fixed and random effects are considered, it explains more variance in the data compared to Model 1. However, Model 1 has a higher marginal R-squared (0.39), indicating that its fixed effects alone explain more variance than those in Model 2. However, the best-fitting model was the integrated Model 4 (AIC_c = 115.87), which combined the significant predictors from the two thematic models. This model outperformed the climate-only Model 2 ΔAIC_c = 0.79) and the island-biogeography-only Model 1 (ΔAIC_c = 0.82).

For bioregion cells, the best-fitting model is Model 1, with an AIC_c value of 272.05. The ΔAIC_c between this and the second-best model is large (2.47) (Table 2). Model 1 also has a much higher model weight (0.66) and model likelihood (1.00) compared to the second-best model. The conditional R-squared for Model 1 is 0.33, while the marginal R-squared is relatively low (0.08). The large difference between the marginal and conditional R-squared values indicates that the random effects (i.e., bioregion identity) contribute significantly to the model. This suggests that spatial autocorrelation or unmeasured variables at the bioregion area level play an important role in explaining the variation in the response variable.

For bioregion areas, in Model 2, both climate suitability ($p = 0.0105$) and climate variability ($p = 0.0294$) are statistically significant predictors of species richness. In contrast, Model 1, total limestone area ($p = 0.0278$) is a significant predictor, while hill numbers and hills' isolation are not statistically significant ($p > 0.05$) (Table 3). This implies that climate suitability and variability (from Model 2) and total limestone area (from Model 1) are core

Table 2. Summary of generalised linear mixed models (GLMM) evaluating the effects of various biogeographical predictors on species richness across bioregion areas and bioregion cells. To identify the most parsimonious determinants, we initially compared thematic suites (Models 0–3) before developing an integrated model (Model 4) that combines significant predictors from both suites. Model comparisons are shown with degrees of freedom (df), corrected Akaike Information Criterion (AIC_c), AIC_c differences (Δ Delta), model likelihood (ModelLik), model weight (ModelWt), marginal R-squared (R^2m) representing variance explained by fixed effects, and conditional R-squared (R^2c) capturing variance explained by both fixed and random effects.

Model	df	AIC_c	Δ (Delta)	ModelLik	ModelWt	R^2m	R^2c
GLMM Bioregion areas							
M4 (Integrated). Species richness ~ climate suitability + climate variability + limestone areas + (1 | Regions)	5	115.87	0.00	1.00	0.42	0.35	0.42
M2 (Climate). Species richness ~ climate suitability + climate variability + (1 | Regions)	4	116.66	0.79	0.68	0.28	0.32	0.54
M1 (Island Biogeography). Species richness ~ hill numbers + limestone areas + hills' isolation + (1 | Regions)	5	116.69	0.82	0.66	0.28	0.39	0.42
M3. Species richness ~ hill numbers + limestone areas + hills' isolation + climate suitability + climate variability + (1 | Regions)	7	121.65	5.77	0.06	0.02	0.36	0.45
M0. Species richness ~ (1 | Regions)	2	131.51	15.64	0.00	0.00	0.00	0.17
GLMM Bioregion cells							
M1 (Island Biogeography). Species richness ~ hill numbers + limestone areas + hills' isolation + (1 | Bioregion areas)	5	272.05	0.00	1.00	0.66	0.08	0.33
M3. Species richness ~ hill numbers + limestone areas + hills' isolation + climate suitability + climate variability + (1 | Bioregion areas)	7	274.52	2.47	0.29	0.19	0.12	0.31
M0. Species richness ~ (1 | Bioregion areas)	2	275.86	3.81	0.15	0.10	0.00	0.27
M2 (Climate). Species richness ~ climate suitability + climate variability + (1 | Bioregion areas)	4	277.49	5.44	0.07	0.04	0.05	0.27

Table 3. Coefficient estimates, standard errors, z-values, and p-values for significant models (from Table 2) in the GLMM analysis of species richness across bioregion areas and cells. This includes the Integrated Model (Model 4), which evaluates the relative contribution of significant climatic and biogeographical drivers of Model 1 and Model 2 to address the non-exclusivity of these predictors.

	Estimate coefficients	Std. error coefficients	z value	Pr(>|z|)
		GLMM Bioregion areas		
Bioregion area M4 (Integrated).				
(Intercept)	1.218	0.169	7.268	<0.0000***
climate suitability	0.147	0.140	1.048	0.2948
climate variability	0.134	0.122	1.097	0.2726
limestone areas	**0.251**	**0.128**	**1.966**	**0.0493***
Bioregion area M2 (Climate).				
(Intercept)	1.238	0.271	4.566	<0.0000***
climate suitability	**0.312**	**0.122**	**2.560**	**0.0105***
climate variability	**0.240**	**0.110**	**2.178**	**0.0294***
Bioregion area M1 (Island Biogeography).				
(Intercept)	1.216	0.142	8.583	<0.0000***
hill numbers	0.195	0.154	1.266	0.2055
limestone areas	**0.337**	**0.153**	**2.201**	**0.0278***
hills' isolation	0.131	0.156	0.840	0.4008
		GLMM Bioregion cells		
Bioregion cell M1.				
(Intercept)	0.694	0.133	5.220	<0.0000***
hill numbers	0.157	0.103	1.530	0.1260
limestone areas	0.136	0.086	1.577	0.1150
hills' isolation	0.037	0.120	0.307	0.7590

determinants of species richness. In the integrated Model 4, total limestone area was the only statistically significant predictor (p = 0.0493), while climate suitability and variability were not significant within this combined context. These findings suggest that total limestone area is a robust determinant of species richness across models, but the influence of climate variables may overlap with other factors when analysed together.

For bioregion cells, in Model 1, none of the predictors—hill numbers, limestone areas, or hills' isolation—show statistically significant relationships with species richness (p > 0.05, Table 3). This suggests that, at the scale of bioregion cells, these variables do not independently explain variation in species richness. The significance of the intercept (p < 0.0001) and the high contribution of random effects (as evidenced by the large difference between marginal and conditional R-squared values) indicate that unmeasured factors, such as spatial autocorrelation or other ecological characteristics, play a more dominant role in influencing species richness within these cells.

Biogeographical drivers of species endemism composition

The CCA for bioregion areas explained 44.1% of the total variance (CCA axis 1 = 28.3% and CCA axis 2 = 15.8%) (Fig. 7). Permutation tests for this overall CCA model were statistically significant (p = 0.01) (Suppl. material 5: tables S1–S3). Further tests of individual marginal predictors revealed that the total number of limestone hills and total limestone area were statistically significant drivers of endemism patterns (p = 0.002 and p = 0.004, respectively). This suggests that larger and more numerous limestone hills in the bioregion areas support *Plectostoma* species with varying levels of endemism (i.e., different distribution ranges). Conversely, hill isolation, mean climate suitability, and climate suitability variability were not statistically significant individually.

The CCA for bioregion cells only explained 25.8% of the variance (CCA axis 1 = 15.6% and CCA axis 2 = 10.2%), indicating that this model captured only a weaker gradient in species endemism composition along climatic and island biogeography variables than CCA for bioregion areas (Suppl. material 5: fig. S2, tables S4–S6). The overall CCA model for bioregion cells was statistically significant (p = 0.001). At this scale, individual marginal predictors tests identified hill isolation, total limestone area, and mean climate suitability as statistically significant drivers of endemism patterns (p = 0.001, p = 0.003, and p = 0.017, respectively).

Discussion

Distribution of the genus *Plectostoma* in Southeast Asia

The genus *Plectostoma* thrives in the perhumid rainforests of the Malay Peninsula, Borneo, and Sumatra. Only a few species are found in the seasonally dry forests located between the Kangar–Pattani line and the Kra Isthmus (Fig. 1B). Despite intensive land snail research, *Plectostoma* has not been recorded in limestone outcrops in Java

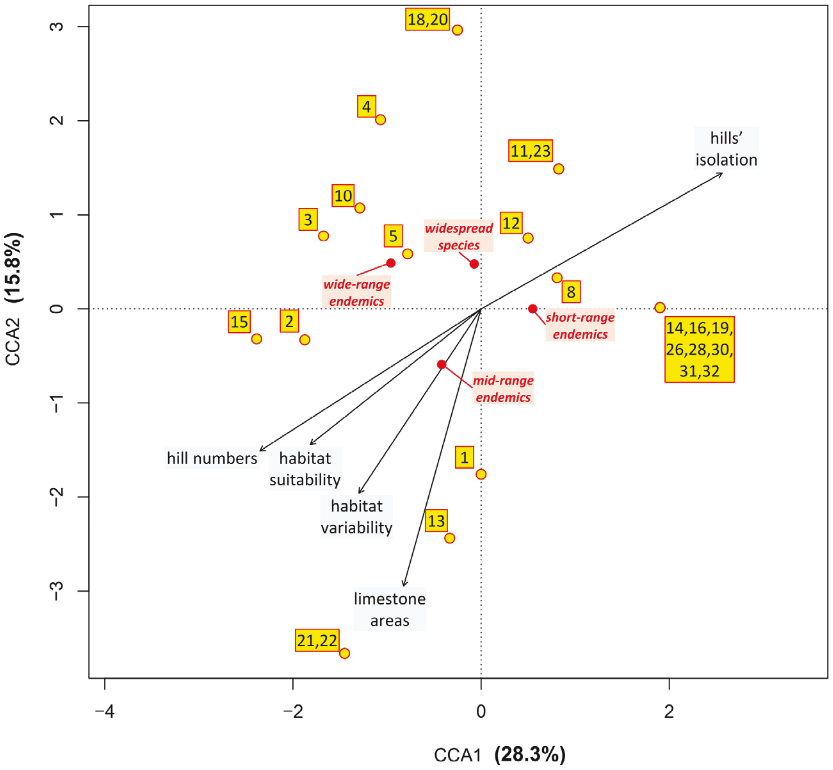

Figure 7. Canonical Correspondence Analysis (CCA) ordination plot illustrating the relationship between species endemism composition and variables related to island biogeography and climate suitability. The plot visualises species distribution patterns across four endemism categories: short-range endemics, mid-range endemics, wide-range endemics, and widespread species. Environmental gradients, represented by arrows, include limestone hills' isolation, limestone hill numbers, climate suitability, climate variability, and limestone area. These factors are projected in relation to the CCA axes, where CCA1 explains 28.3% and CCA2 explains 15.8% of the variation. Red points represent four endemism categories, while yellow-highlighted numbers correspond to bioregion designations for the points that may overlap in the plot.

and Indochina beyond (or north of) the Thai portion of the Malay Peninsula (Nurinsiyah and Hausdorf 2017; Vermeulen et al. 2019a, 2019b; Sutcharit et al. 2020; Dumrongrojwattana and Wongkamhaeng 2024).

The genus's distribution limits generally correspond to the Sundaland biogeographical region boundaries, with the exception of the northern border and its absence from Java. While the northern border of the Sundaland biogeographical region is situated around the Kangar–Pattani Line on the Malay Peninsula mainland, *Plectostoma* can be found at the Vietnam-Cambodia border and on the Thai part of the Malay Peninsula, no further than the Isthmus of Kra. These areas are characterised by semi-evergreen and deciduous forests with seasonally dry climates (Ashton 2014; Morley 2018) (Fig. 1A, B). The genus is absent in Java, which is mainly covered by moist deciduous forests shaped by prolonged dry seasons (Ashton 2014; Louys and Roberts 2020).

The association of *Plectostoma* distribution limits with vegetation types, primarily controlled by the length of the dry season, suggest that climatic factors may determine the genus's distribution limit. This is supported by our climate suitability analysis, which identified several key environmental predictors influencing *Plectostoma* distribution: Precipitation of Coldest Quarter (BIO19) was the most significant contributor (29.3%), followed by Isothermality (BIO3, 14.7%) and Precipitation Seasonality (BIO15, 12.8%). Although the Malay Peninsula, Borneo, and Sumatra are all broadly characterised as closed canopy tropical rainforests, we found substantial climatic variability. The climate suitability analysis highlights that many *Plectostoma* distribution hotspots are areas with moderate precipitation during the coldest quarter and low rainfall seasonality. Highly suitable regions (logistic value above 0.4) include the eastern part of the central Malay Peninsula, especially the Gua Musang-Kuala Krai limestone regions (Fig. 3B), Bau-Padawan-Serian in western Sarawak (Fig. 4B), parts of Sabah in Borneo (Fig. 6B), and the Vietnam-Cambodia border limestone (Fig. 2B).

However, *Plectostoma* also thrives in some regions predicted to have lower climate suitability (logistic value between 0.2 and 0.4 in Fig. 2B), such as in North Sarawak and East of Sabah, whereas other areas with low predicted suitability (logistic value < 0.4), most notably the entire western side of the Malay Peninsula, south of the Kangar-Pattani Line (Fig. 2), are completely devoid of the genus. This total absence is particularly significant because, as our bioregion delineation analysis shows, topography and drainage patterns are often more decisive than distance or climate alone (more in the next section). Furthermore, many limestone areas in Thailand, Sumatra, and Kalimantan within the range of *Plectostoma* are unoccupied, which is likely due to the unsuitable climatic conditions (logistic value < 0.2) (Fig. 1B). These discrepancies strongly suggest that while climate is a contributing factor, other factors also play a role in shaping the genus's absolute range limits.

A possible ecological explanation for micro-snails like *Plectostoma* to thrive in areas that the MaxEnt model considers to have less suitable climatic conditions is that habitability may be determined more by small-scale niche variables. As obligate limestone dwellers, *Plectostoma* species are confined to limestone outcrops with dense vegetation, which provides humid, cooler habitats essential for their survival (Berry 1961, 1962, 1963; Schilthuizen et al. 2003a, 2003b, 2005; Liew et al. 2014a). Furthermore, this discrepancy likely reflects the inherent limitations of coarse-resolution interpolated climate data, such as WorldClim, which may not accurately represent the raw climatic conditions in vast, undersampled regions of Sundaland. Interpolated grids often fail to predict microclimates in topographically complex landscapes, where local temperature and humidity can differ significantly from regional averages (Faye et al. 2014). Hence, the many microhabitats available on limestone outcrops in regions of low modelled climate suitability may still support the occurrence of the species, though species richness can be low, as observed in southern Thailand's portion of the Malay Peninsula, Sumatra, and the Kalimantan part of Borneo (Fig. 1A, B).

Following from the above, it also seems likely that the complete absence of the genus from the karst hills on the west side of the Malay Peninsula cannot result solely from a less suitable climate, as suggested by MaxEnt, or a complete absence of suitable habitat niches. It is our view that the most likely explanation for their absence results from the geological events after the collision of the Sibumasu and Indochina Terranes closed the Palaeo-Tethys along the Raub–Bentong suture. The limestones on the west belong to the Sibumasu Terrane while those east of the Raub–Bentong suture are part of the East Malaya Block (Fig. 3D) (Metcalfe, 2013, 2017). These limestones are separated by the mountains of the Main Range that form a central spine to the Malay Peninsula. This spine is a product of regional uplift and emplacement of the Main Range granite batholith in the Late Triassic. Exhumation of the granite started in the late Cretaceous (Cottam 2013; Sautter et al. 2019), and the mountains have probably been a topographic high since at least the Paleocene (Hall 2013).

Thus, the Main Range could have been both a formidable topographic barrier and, in the absence of limestone, a lithological-geochemical barrier to the dispersal of *Plectostoma* from east to west for as long as the genus has existed (Figs 1C, 3E–H). The regional tectonic evolution since the Paleocene (c. 65 Ma), the era when *Plectostoma* diverged (Köhler 2024), has favoured trans-regional drainage systems that bypass the west side of the Malay Peninsula entirely. While intensive paleo-drainage networks such as the proto-Sarawak river (~ 60 Ma) and Sunda River (c. 30–17 Ma) established long-distance sediment and dispersal corridors between the East side of the Malay Peninsula and the active formations of Borneo, no such major drainage systems were created to connect the eastern and western sides of the Main Range (Breitfeld et al. 2020; Zhu et al. 2025).

Hence, the Main Range serves as a primary drainage divide, separating the river basins of the Malay Peninsula into two distinct systems that flow in opposite directions. Because drainage systems may act as the primary corridors for the passive dispersal of these snails, this hydrological segregation, combined with upland terrain exceeding 250 m, effectively have prevented long-distance dispersal to the west for tens of millions of years.

The Main Range may also have separated the Siam Basin from the Malacca Strait Basin, further restricting dispersal, as shown in studies of other taxa (e.g., de Bruyn et al. 2013). However, the effect of the Main Range barrier diminishes toward its northern end near the Kangar–Pattani line. The presence of *Plectostoma* in Perlis (BA25, BA26, BA28, and BA33 in Fig. 2B), nestled between the Kedah-Singgora Range and Nakawan Range, suggests a historical connection to the Siam Basin (Fig. 1C). These nestled limestone hills in Perlis belong to the Setul limestone formation, which extends into southern Thailand (Bunopas 1983). The specific mechanisms of how such drainage patterns and topographical features dictate the boundaries of *Plectostoma* bioregions are discussed in further detail in the following section.

Drainage patterns and topography determine *Plectostoma* bioregion delineation

Our bioregion delineation reveals that 33 bioregions, resulting from different sets of *Plectostoma* species, are spatially grouped within the genus's distribution range. The delineation and distribution of the identified bioregions largely coincide with topography and drainage patterns, in addition to the geographical distances among the limestone clusters. Limestone clusters in low-lying plain landscapes (< 250 m in elevation) are more likely to form distinct bioregion areas when these clusters are isolated by a distance of 20 km and not connected by drainage (e.g., BA 14 in Fig. 3), or when they are located adjacent to a first-order river channel as headwater streams that do not have any other streams flowing into them (e.g., BA22, BA23, BA31, and BA32 in the South of Pahang River basin: Fig. 3; all BAs in North of Sarawak: Fig. 5). Larger limestone clusters that are adjacent to each other tend to form larger bioregion areas (Fig. 4E; BA4 and BA5 in Fig. 6E). These larger areas could be divided into several distinct bioregion areas where the boundaries coincide with upland terrain (> 250 m in elevation) (BA2, BA3, BA10, and BA15 in Fig. 3E; BA11 and BA 12 in Fig. 6E). These factors collectively shape the distribution and size of the bioregion areas, although they are not mutually exclusive.

Isolation by distance undeniably influences dispersal, a critical biogeographical process for land snails in fragmented habitats like tropical limestone hills (Clements et al. 2008). Our study shows that over 80% of *Plectostoma* species are confined to a single bioregion area, with most of these areas separated by distances of approximately 20 km. Additionally, more than half of these species are classified as short-range endemics, having distribution ranges smaller than 10 km. This suggests that limestone clusters or outcrops 10–20 km apart will likely harbour unique species and form distinct bioregion areas. While isolation by distance among limestone clusters is an important factor, our study emphasises that drainage patterns and topography are additional critical drivers in defining bioregion areas. Bioregion delineation is not solely dictated by limestone cluster isolation, as previously assumed by Liew et al. (2021), based on geographical distance alone (Table 1). For instance, rivers and drainage systems serve as natural corridors for passive dispersal while simultaneously limiting species exchange depending on the surrounding topography. Migration between hills within the same limestone cluster is more likely than between isolated limestone outcrops (Tweedie 1961; Hoekstra and Schilthuizen 2011; Hendriks et al. 2019), probably via floodwaters (Tweedie 1961). These factors reinforce boundaries between adjacent bioregion areas by acting as barriers to species exchange, shaping species distribution and composition both within and across limestone clusters.

While hydrological and topographical barriers predominate, other passive dispersal mechanisms, though stochastic, cannot be entirely ruled out. Over shorter distances, the transport of minute shells via strong wind events (Roszkowska and Książkiewicz 2022) or attachment to and survival through the digestive tracts of mobile animals, such as birds, may facilitate infrequent species exchange across seemingly impassable terrain (Gittenberger 2012; Kramarenko 2014; Simonová et al. 2016).

Importantly, topography and drainage patterns are themselves products of a region's geological and geomorphic history. That these features are critical in delineating bioregions further underscores the foundational role of geological and geomorphic processes, including the karstification of limestone landscapes (Waltham 2008). Although Tweedie (1961) acknowledged this relationship, more recent interpretations have often emphasised episodic events such as passive dispersal by rivers in flood, potentially overlooking the importance of landscape evolution over geological timescales (Hendriks et al. 2019).

It is plausible that *Plectostoma* species may have dispersed across larger areas during the early (Fengcong) stage of karstification when lithological connectivity between limestone karst hills was maintained. The occurrence of wide-range endemics, both along and across drainages, supports this possibility (Suppl. material 1: fig. 1). Dispersal across formerly continuous limestone karst landscapes would have contributed to similar species assemblages on what are now isolated limestone outcrops, thereby influencing current bioregion boundaries.

This pattern is exemplified in the river basins of the Central Malay Peninsula (CMP), where several widespread *Plectostoma* species occur in bioregion areas situated both along and across the subsequent drainage system (Fig. 3F). For instance, bioregions BA2, BA3, BA10, and BA15 span different drainage sub-basins and host at least one of the five wide-range endemic species (Suppl. material 1: fig. 1; Suppl. material 4: table S1). This pattern is repeated in Borneo, where in the low-lying plains of West Sarawak (Fig. 4C–H), the single bioregion BA1 acts as a large, interconnected habitat, and in East Sabah (Fig. 6), where BA4 and BA5 form similarly broad units.

This suggests that these species were already widely distributed before the incision of the present drainage system. However, within the CMP, there is the possibility that their range was further extended, along the regional North–South geological and topographic trend, by passive fluvial dispersion as incision of the subsequent drainages exposed new outcrops of limestone for colonisation. Notably, there is little evidence to support the hypothesis of short-range endemism, which might be expected to develop on isolated limestone karsts. This suggests that the present bioregion structure was initially shaped by autonomous dispersal, the active movement of individuals using their own locomotive capabilities, across a once-continuous limestone surface.

Further to the south of CMP, the isolated limestone karsts in BA14, BA20, BA22, BA23, BA31, and BA32 are characterised by highly localised short-range endemic species, with the exception of the occurrence of *P. davisoni* in BA23 and BA31. Only the limestones in BA20, BA23, and BA31 are of the same age and lithologically similar to the Merapoh Limestone, deposited on a shallow marine platform (Mohamed et al. 2016; Metcalfe and Crowley 2020). They might, therefore, have been part of, and at some stage of their exhumation, shared continuity with the platform limestones further north. This is hinted at by the presence of *P. davisoni* in BA23 and BA31. However, regardless of the possibility of past connectivity of BA20, BA23, and BA31, the limestone karsts in this region are now isolated in individual drainage sub-basins and, where there might once have been passive transport along a river, the karsts in BA20, BA32, and BA22 have now reached the Fenglin stage of karsification whereby they are separated from their former drainage by wide deposits of alluvium. A similar pattern is also clearly visible in North Sarawak (Fig. 5C–H), where clusters like Niah (BA16) are hydrologically isolated and have fostered their own sets of endemic species, and in the interior of Sabah, where uplands separate the highland bioregions like BA11 and BA12 from their coastal counterparts (Fig. 6C–H).

To summarise the role of landscape evolution, we observe in the dispersion of *Plectostoma*, the early stages of karstification (e.g., Fengcong karst) maintain limestone continuity, enabling the dispersal of limestone-obligate taxa such as *Plectostoma* across broader areas, despite their low vagility. As karstification progresses to the Fenglin stage, limestone hills become isolated towers rising from an alluvial floodplain, reducing connectivity and limiting dispersal. In the final stages, deep erosion, base level drop, and landscape evolution may isolate limestone karsts beyond the reach of passive dispersal via surface water. Only this final stage of karsification aligns closely with the oceanic island model of endemism, as the biogeographical dynamics shift from connected systems to highly isolated units.

The determinants of species richness and endemism in bioregion areas

The interplay of distance isolation, drainage patterns, topography, and geological timing that underpin the delineation of bioregion areas should also determine the species richness and endemism within and across bioregion areas. By examining species richness and endemism across these different bioregions that each consists of clusters of limestone hills as an island archipelago, we gain insight into the evolutionary and ecological processes driving biodiversity patterns (Slatter 1990). Land snails have long served as effective models for studying such patterns in isolated habitats, including oceanic islands, highland refugia, and edaphically isolated karsts (Gittenberger 2007).

Island biogeography studies on land snails often treat each island as an independent unit, focusing on total richness or specific taxa at broader taxonomic levels (e.g., Heller 1976; Nilsson et al. 1988; Gibson and Köhler 2012; Cameron et al. 2013; Schilthuizen et al. 2013; Triantis et al. 2016). However, such approaches can obscure lineage-specific patterns. By focusing on a single, species-rich genus, our study minimises the confounding effects of taxonomic variability and offers clearer insights into how island-like fragmentation influences richness and endemism. While the resulting bioregion areas are specifically tailored to the distribution and dispersal limits of *Plectostoma*, they provide a baseline for comparing how other limestone-obligate groups with similar or different vagility respond to the same landscape features.

Our results show that bioregion areas with larger and more numerous limestone hills support both wide-ranging and short-range endemic *Plectostoma* species, driving higher overall species richness. This finding aligns with predictions from island biogeography theory, which links greater habitat area with increased biodiversity (MacArthur and Wilson 2001; Gibson and Köhler 2012; Parent 2012). Our integrated GLMM (Model 4) identified total limestone area as the most consistent and statistically significant predictor of species richness. While climate suitability and variability were significant in thematic models, their individual significance was masked in the integrated framework. This suggests that while climate defines the broad habitable envelope, the specific species count within a bioregion is primarily constrained by the physical extent of the limestone substrate.

While vagility is often cited as a key factor explaining endemicity patterns, low vagility promoting speciation and high vagility supporting colonisation, *Plectostoma* species are uniformly low-vagility. However, over geological timescales, even extremely slow dispersers can move across large distances if suitable substrate continuity is maintained. The active dispersal distance of *Plectostoma* remains unknown, but data from similarly sized land snails suggest movement rates in the range of 0.93–2.14 m/year (Kramarenko 2014). As a conservative theoretical illustration, even assuming an extremely low active dispersal rate of just 0.1 m/year, a species could theoretically traverse 100 km over the course of 1 million years. Given that karstification processes span 10–20 million years (Waltham, 2008), early-stage limestone connectivity could have allowed *Plectostoma* to disperse widely before habitat fragmentation-imposed dispersal barriers.

Thus, patterns of narrow-range endemism in *Plectostoma* may not reflect low vagility per se, but rather the timing and degree of limestone karst disconnection. As suggested by Hendriks et al. (2019) and Hausdorf et al. (2024), long-distance dispersal, including rare passive transport events (e.g., via rivers), likely contributes to the complex, disjunct distribution patterns we observe today. Over time, localised speciation in isolated clusters could lead to an “archipelago effect”, where many small, fragmented habitats host more species collectively than a single contiguous one (Aguilée et al. 2021; Horsák et al. 2024). Speciation in *Plectostoma* is likely to be non-ecological—that is, not accompanied by significant niche differentiation. As such, when two closely related species come to share the same outcrop, competitive exclusion may eventually occur. However, because *Plectostoma* snails have extremely low-vagility, this process is likely to be slow, allowing species to accumulate within limestone karst systems faster than competition can remove them.

Conclusion

Our study provides significant insights into the biogeography of *Plectostoma* snails in Sundaland, a region renowned not only as a global biodiversity hotspot but also as pivotal in the development of biogeographical science. The spatial patterns of *Plectostoma* species richness and endemism in Sundaland’s bioregion areas cannot be solely explained by island biogeography and climate variables. Other factors, such as topography and drainage patterns, which result from the geological history of the limestone deposits and the subsequent geomorphological evolution of the limestone karst landscape, play crucial roles in shaping the distribution of bioregion areas and their biodiversity patterns. Future research incorporating multi-taxon approaches and phylogenetic and phylogeographic analyses of *Plectostoma* will provide deeper insights into the evolutionary processes that have driven endemism in limestone habitats. Such studies can enhance our understanding of how historical and ecological factors have shaped biodiversity across Sundaland’s limestone ecosystems.

Acknowledgements

We gratefully acknowledge the following curators and institutions for granting access to museum collections: Petherine Jimbau (BOR), Jonathan Ablett and Fred Naggs (BMNH), and Jeroen Goud, Rob Moolenbeek, and Bram van der Bijl (Naturalis). We thank Robert Whittaker, Sérgio Ávila, Bernhard Hausdorf, Dinazarde Raheem, and an anonymous reviewer for their constructive comments, which significantly improved the manuscript.

Fieldwork conducted between 2010 and 2024 across various limestone ecosystems in Malaysia was made possible through permits issued by federal and state authorities: **Sarawak**: Sarawak Forestry Cooperation (SFC.810-461(2023)-213) for M.Z. Khalik (2023–2024); State Planning Unit Sarawak ((47)UPN/S/G1/I/10.1 vol.27), Forest Department Sarawak (NPW.907.4.4(V)-19), Park Permit No. 07/2010, and Export Permit No. 09003 for T.-S. Liew (2010–2014); Sarawak Forest Department (NPW.907.4.4(-Jld.14)-31) and Park Permit WL14/2017 for M.E. Marzuki (2017–2019). **Sabah**: Wildlife Department of Sabah (JHL.600-6/1 JLD.6 and JHL.6000.6/1/2 JLD.8) for T.-S. Liew (2009–2012). **Peninsular Malaysia**: Economic Planning Unit (UPE: 40/200/19/2524) for T.-S. Liew (2010–2014); Department of Wildlife and National Parks (B-00013-15-18); Forestry Department (JH/100 Jld. 20 (12) & JH/100 Jld. 21(44)), with additional permits from state and district offices including: Johor: PHJ.PP/192/676/48 JLD.5 (53), PMJS 494/2019, PHD.JS.OP.192/686/2/1 JLd. 50(35); Kedah: JH/100 Jld. 19(7), KT 89/2019, PHDKT (F) 2/2019; Kelantan: PHN.KN.130/1/9 J5 (55), PMDB.68-19; PHJ.KBT: 7/8/2/J.5 (66), DT(PM)-17-19; PHJKT.5.1.55.21/(43); Negeri Sembilan: JH/100 Jld. 20 (12), 025/2019, PHD.NSU.600-1/1/3-Klt.2(16); Pahang: PHN.PHG.(PEM)118/146 BHG.9 (29), PHD.TEM.016/2018, PHD.TEM.100.21/0/9/1 JLD.10(10), PHD.TEM.12.2019, PHD.TEM.100.21/0/9/1 JLD.10 (42), PHDL.61/2018 (Bil (21) dlm. PHDL.800-1/1/9 Jld 2), PHDL.52/2019 (Bil (48) dlm. PHDL.800-1/1/9 Jld 2), PHDL.25/2019 (Bil (26) dlm. PHDL.800-1/1/9 Jld 2), (98) dlm. PHDK.80/1/23 Jld.9; Perak: PPN.PK.600/03/01 Jld.12 (62), PMH/247/2018, PHD.HPK.28/16 Jld. 26(64); Perlis: JH/100 Jld. 21 (44); Selangor: PHN.SEL.07/5 Jld.14 Bil. (2), US/1/2018, PHDUS.6005/2/16(6); Terengganu: PHNT.100/58/2Bhg.9-(37) for J.-K. Foon (some jointly with T.-S. Liew) (2018–2019).

For research conducted in Indonesia, we thank BRIN for granting the Research Permit 757/SIP/IV/FR/10/2024 and Animal Experiment Research Ref No.: 216/KE.02/SK/09/2024 to T.-S. Liew (2024–2025) and the Natural Resources Conservation Agency (BKSDA) of South Sumatra for providing permits for specimen transport to A.S. Nurinsiyah.

Funding

This study was supported by funding from the Research Council for Earth and Life Sciences (ALW-NWO), project 819.01.012 to M. Schilthuizen (2010–2014). Subsequent sampling and data collection were funded by the UMS-UNIMAS Collaboration Research Grant (GL/F07/UMS/02/2017 and GKP0011) (2017–2019), and the Ministry of Natural Resources and Environment, Malaysia, through the National Conservation Trust Fund for the project Conservation of Limestone Ecosystems in Malaysia (GLK0014-2018) (2018–2019) awarded to T.-S. Liew. The specimen collection in South Sumatra was funded by the Budget Implementation List (DIPA) of the Deputy for Life Sciences, Indonesian Institute of Sciences (LIPI), awarded to A.S. Nurinsiyah. Data analysis and manuscript preparation were carried out by T.-S. Liew under the BRIN Visiting Researcher Program 2024 (Batch 2).

Author contributions

Thor-Seng Liew: Conceptualisation, Writing - original draft, Writing - review & editing, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualisation; Menno Schilthuizen: Conceptualisation, Writing - review & editing, Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision; Junn Kitt Foon: Writing - original draft, Data curation, Investigation; W. K. Fletcher: Conceptualisation, Writing - original draft, Writing - review & editing, Investigation; Nurinsiyah Ayu Savitri, Mohammad Effendi Marzuki, and Jaap Vermeulen: Writing - review & editing, Data curation, Investigation; Nur Atirah Bian, Yansen Chen, and Mohd Zacaery Khalik: Writing - review & editing, Data curation.

Use of AI

The authors declare that generative AI has been used for final proofreading to correct the language errors. We have reviewed and edited the content after using this tool.

Data accessibility statement

All supporting data have been provided via Frontiers of Biogeography online supplementary documentation. This includes the 771 georeferenced records for the genus *Plectostoma* and the environmental variables analysed for the bioregion cells. All other data that support the findings of this study are available in the main text.

References

Advokaat EL, van Hinsbergen DJ (2023) Finding Argoland: reconstructing a microcontinental archipelago from the SE Asian accretionary orogen. Gondwana Research 128: 161–263. https://doi.org/10.1016/j.gr.2023.10.005

Aguilée R, Pellerin F, Soubeyrand M, Choin J, Thébaud C (2021) Biogeographic drivers of community assembly on oceanic islands:

The importance of archipelago structure and history. Journal of Biogeography 48: 2616–2628. https://doi.org/10.1111/jbi.14228

Ashton PS (2014) On the Forests of Tropical Asia. Lest the Memory Fade. Kew Publishing, Royal Botanic Gardens Kew, and Arnold Arboretum, Harvard University, 670 pp.

Atkins HJ, Bramley GL, Johnson MA, Kartonegoro A, Nishii K, Kokubugata G, Michael M, Hughes M (2020) A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography. Frontiers of Biogeography 12: e44814. https://doi.org/10.21425/F5FBG44184

Azevedo L, Zappi DC, de Oliveira DMG, Meyer L, Lughadha EN, Clegg R, Meireles LD, de Melo PHA, Pennington RT, Neves DM (2024) On the rocks: Biogeography and floristic identity of rocky ecosystems in eastern South America. Journal of Systematics and Evolution 62: 305–320. https://doi.org/10.1111/jse.13052

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67: 1–48. https://doi.org/10.18637/jss.v067.i01

Barton K (2020) MuMIn: Multi-Model Inference. R Package Version 1.43.17

Berry AJ (1961) The habitats of some minute cyclophorids, hydrocenids and vertiginids on a Malayan limestone hill. The Bulletin of the National Museum 30: 101–105. https://doi.org/10.25662/61jp-jq4

Berry AJ (1962) The growth of *Opisthostoma* (*Plectostoma*) *retrovertens* Tomlin, a minute cyclophorid from a Malayan limestone hill. Journal of Molluscan Studies 35: 46–49. https://doi.org/10.1093/oxfordjournals.mollus.a064891

Berry AJ (1963) Growth and variation of the shell in certain Malayan limestone hill snails. Journal of Molluscan Studies 35: 203–206. https://doi.org/10.1093/oxfordjournals.mollus.a064919

Breitfeld HT, Hennig-Breitfeld J, BouDagher-Fadel MK, Hall R, Galin T (2020) Oligocene-Miocene drainage evolution of NW Borneo: Stratigraphy, sedimentology and provenance of Tatau-Nyalau province sediments. Journal of Asian Earth Sciences 195: 104331. https://doi.org/10.1016/j.jseaes.2020.104331

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information Theoretic Approach. Springer, New York. https://doi.org/10.1007/b97636

Bunopas S (1983) Paleozoic Succession in Thailand. In: Nutalaya P (Ed.) Proceedings of the workshop on stratigraphic correlation of Thailand and Malaysia Vol. 1, Haad Yai, Thailand, September 8-10, 1983. Geological Societies of Thailand and Malaysia, 29–76.

Cameron RA, Triantis KA, Parent CE, Guilhaumon F, Alonso MR, Ibánez M, de Frias Martins AM, Ladle RJ, Whittaker RJ (2013) Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models. Journal of Biogeography 40: 117–130. https://doi.org/10.1111/j.1365-2699.2012.02781.x

Clegg R, Azevedo L, Martinez-Ugarteche MT, Neves D, Kidner C, Hind DN, Antonelli A, Rowland L, Pennington RT (2025) Plant biogeography of rock outcrops in South American tropical lowlands. Frontiers of Biogeography 18: e145659. https://doi.org/10.21425/fob.18.145659

Clements R, Sodhi NS, Schilthuizen M, Ng PK (2006) Limestone karsts of Southeast Asia: imperiled arks of biodiversity. Bioscience 56: 733–742. https://doi.org/10.1641/0006-3568(2006)56[733:LKOSAI]2.0.CO;2

Clements R, Ng PK, Lu XX, Ambu S, Schilthuizen M, Bradshaw CJ (2008) Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. Biological Conservation 141: 2751–2764. https://doi.org/10.1016/j.biocon.2008.08.011

Conrad O, Bechtel B, Bock M, Dietrich H, Fischer E, Gerlitz L, Wehberg J, Wichmann V, Böhner J (2015) System for automated geoscientific analyses (SAGA) v. 2.1.4. Geoscientific Model Development 8: 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015

Cottam MA, Hall R, Ghani AA (2013) Late Cretaceous and Cenozoic tectonics of the Malay Peninsula constrained by thermochronology. Journal of Asian Earth Sciences 76: 241–257. https://doi.org/10.1016/j.jseaes.2013.04.029

De Bruyn M, Rüber L, Nylinder S, Stelbrink B, Lovejoy NR, Lavoué S, Tan HH, Nugroho E, Wowor D, Ng PKL, Siti Azizah MN, Von Rintelen T, Hall R, Carvalho GR (2013) Paleo-drainage basin connectivity predicts evolutionary relationships across three Southeast Asian biodiversity hotspots. Systematic Biology 62: 398–410. https://doi.org/10.1093/sysbio/syt007

De Bruyn M, Stelbrink B, Morley RJ, Hall R, Carvalho GR, Cannon CH, Van den Bergh G, Meijaard E, Metcalfe I, Boitani L, Maiorano L, Shoup R, & Von Rintelen T (2014) Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. Systematic Biology 63: 879–901. https://doi.org/10.1093/sysbio/syu047

Derkarabetian S, Baker CM, Giribet G (2021) Complex patterns of Gondwanan biogeography revealed in a dispersal limited arachnid. Journal of Biogeography 48: 1336–1352. https://doi.org/10.1111/jbi.14080

Dumrongrojwattana P, Wongkamhaeng K (2024) Chapter 17. Two decades of microsnails (Gastropoda: prosobranchia: Pulmonata) study in Thailand and ongoing research. In: Claude J, Kitana N (Eds) On the Edge of the Sixth Mass Extinction in Biodiversity Hotspots: Facts, Needs, Solutions and Opportunities in Thailand and Adjacent CountriesCentre of Learning Network for the Region, Chulalongkorn University, Bangkok, 313–336.

Edler D, Guedes T, Zizka A, Rosvall M, Antonelli A (2017) Infomap Bioregions: Interactive mapping of biogeographical regions from species distributions. Systematic Biology 66: 197–204. https://doi.org/10.1093/sysbio/syw087

Faye E, Herrera M, Bellomo L, Silvain JF, Dangles O (2014) Strong discrepancies between local temperature mapping and interpolated climatic grids in tropical mountainous agricultural landscapes. PLoS ONE 9: e105541. https://doi.org/10.1371/journal.pone.0105541

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1 km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37: 4302–4315. https://doi.org/10.1002/joc.5086

Foon JK, Clements GR, Liew TS (2017) Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. ZooKeys 682: 1–94. https://doi.org/10.3897/zookeys.682.12999

Garg KM, Chattopadhyay B, Cros E, Tomassi S, Benedick S, Edwards DP, Rheindt FE (2022) Island biogeography revisited: museomics reveals affinities of shelf island birds determined by bathymetry and paleo-rivers, not by distance to mainland. Molecular Biology and Evolution 39: msab340. https://doi.org/10.1093/molbev/msab340

Gibson L, Köhler F (2012) Determinants of species richness and similarity of species composition of land snail communities on Kimberley islands. Records of the Western Australian Museum 81: 1461–1906. https://doi.org/10.18195/issn.0313-122x.81.2012.041-066

Gittenberger E (2007) Islands from a Snail's Perspective. In: Renema W (Ed) Biogeography, Time, and Place: Distributions, Barriers, and Islands, Springer, Dordrecht, Netherlands, 347–363. https://doi.org/10.1007/978-1-4020-6374-9_11

Gittenberger E (2012) Long distance dispersal of molluscs:'Their distribution at first perplexed me much'. Journal of Biogeography 39: 10–11. https://doi.org/10.1111/j.1365-2699.2011.02638.x

Hall R (2013) The palaeogeography of Sundaland and Wallacea since the late Jurassic. Journal of Limnology 72: 1–17. https://doi.org/10.4081/jlimnol.2013.s2.e1

Hausdorf B, Xu J, Bamberger S (2024) Repeated colonization of the Northern Limestone Alps from the Southern Limestone Alps by the rock-dwelling snail species *Cochlostoma henricae*. Zoological Scripta 53: 580–593. https://doi.org/10.1111/zsc.12659

Heller J (1976) The biogeography of Enid landsnails on the Aegean Islands. Journal of Biogeography 3: 281–292. https://doi.org/10.2307/3038018

Hendriks KP, Alciatore G, Schilthuizen M, Etienne RS (2019) Phylogeography of Bornean land snails suggests long-distance dispersal as a cause of endemism. Journal of Biogeography 46: 932–944. https://doi.org/10.1111/jbi.13546

Hoekstra P, Schilthuizen M (2011) Phylogenetic relationships between isolated populations of the limestone dwelling microsnail *Gyliotrachela hungerfordiana* (Gastropoda: Vertiginidae). Journal of Zoological Systematics and Evolutionary Research 49: 266–272. https://doi.org/10.1111/j.1439-0469.2011.00623.x

Horsák M, Ortiz D, Nekola JC, Van Bocxlaer B (2024) Intercontinental dispersal and niche fidelity drive 50 million years of global diversification in *Vertigo* land snails. Global Ecology and Biogeography 33(5): e13820. https://doi.org/10.1111/geb.13820

Hosoishi S, Maruyama M, Yamane S, Jaitrong W, Hashim R, Syaukani S, Sokh H, Itioka T, Meleng P, Pham TH (2023) Multilocus phylogeny and historical biogeography of the *Crematogaster inflata*-group (Hymenoptera: Formicidae) in South-East Asia. Zoological Journal of the Linnean Society 198: 901–922. https://doi.org/10.1093/zoolinnean/zlad005

IUCN (2024a) The IUCN Red List of Threatened Species. Version 2024-2. https://www.iucnredlist.org [Visited on 10/11/2024]

IUCN (2024b) Guidelines for the application of IUCN Red List of Ecosystems Version 2.0. Gland, Switzerland: IUCN.

James G, Witten D, Hastie T, Tibshirani R (2013) An Introduction to Statistical Learning: with Applications in R. Springer, New York. https://doi.org/10.1007/978-1-4614-7138-7_2

Jongman RH, ter Braak CJF, van Tongeren OFR (1987) Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, 127 pp.

Köhler F (2024) Peeking back in time: Novel insights into the evolutionary relationships of diplommatinids (Caenogastropoda, Cyclophoroidea) from around Australia. Zoologica Scripta 53: 78–86. https://doi.org/10.1111/zsc.12629

Kramarenko S (2014) Active and passive dispersal of terrestrial mollusks: a review. Ruthenica 24: 1–14.

Laumanns M, Price L (2010a) Atlas of the Great Caves and the Karst of Southeast Asia. Part 1: Introduction – Malaysia. Berliner Höhlenkundliche Berichte Vol. 40. Selbstverlag des Speläoclub, Berlin.

Laumanns M, Price L (2010b) Atlas of the Great Caves and the Karst of Southeast Asia. Part 2: Myanmar – Vietnam. Berliner Höhlenkundliche Berichte Vol. 41. Selbstverlag des Speläoclub, Berlin.

Liew TS, Vermeulen JJ, bin Marzuki ME, Schilthuizen M (2014a) A cybertaxonomic revision of the micro-landsnail genus *Plectostoma* Adam (Mollusca, Caenogastropoda, Diplommatinidae), from Peninsular Malaysia, Sumatra and Indochina. ZooKeys 393: 1–107. https://doi.org/10.3897/zookeys.393.6717

Liew TS, bin Marzuki ME, Schilthuizen M, Chen Y, Vermeulen JJ, Mohd-Azlan J (2020) Molecular phylogenetics and evolutionary history of the endemic land snail genus *Everettia* in northern Borneo. PeerJ 8: e9416. https://doi.org/10.7717/peerj.9416

Liew TS, Foon JK, Clements GR (2021) Conservation of Limestone Ecosystems of Malaysia, Part I, Acknowledgements, Methodology, Overview of limestone outcrops in Malaysia, References, Detailed information on limestone outcrops of the states: Johor, Negeri Sembilan, Terengganu, Selangor, Perlis. Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia, 495 pp. https://doi.org/10.6084/m9.figshare.14907846

Louys J, Roberts P (2020) Environmental drivers of megafauna and hominin extinction in Southeast Asia. Nature 586: 402–406. https://doi.org/10.1038/s41586-020-2810-y

MacArthur RH, Wilson EO (2001) The Theory of Island Biogeography. Princeton university Press, Princeton, 203 pp.

Meredith M (2015) wiqid: Quick and Dirty Estimates for Wildlife Populations. R package, version 0.1.0. https://doi.org/10.32614/cran.package.wiqid

Metcalfe I (2013) Tectonic evolution of the Malay Peninsula. Journal of Asian Earth Sciences 76: 195–213. https://doi.org/10.1016/j.jseaes.2012.12.011

Metcalfe I (2017) Tectonic evolution of Sundaland. Bulletin of the Geological Society of Malaysia 63: 27–60. https://doi.org/10.7186/bgsm63201702

Metcalfe I, Crowley JL (2020) Upper Permian and Lower Triassic conodonts, high-precision U-Pb zircon ages and the Permian-Triassic boundary in the Malay Peninsula. Journal of Asian Earth Sciences 199: 104403. https://doi.org/10.1016/j.jseaes.2020.104403

Mohamed KR, Joeharry NAM, Leman MS, Ali CA (2016) The Gua Musang Group: A newly proposed stratigraphic unit for the Permo-Triassic sequence of Northern Central Belt, Peninsular Malaysia. Bulletin of the Geological Society of Malaysia 62: 131–142. https://doi.org/10.7186/bgsm62201614

MolluscaBase eds. (2024) MolluscaBase. https://www.molluscabase.org [Visited on 28/01/2024]

Morley RJ (2018) Assembly and division of the South and South-East Asian flora in relation to tectonics and climate change. Journal of Tropical Ecology 34: 209–234. https://doi.org/10.1017/S0266467418000202

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501

Nilsson SG, Bengtsson J, As S (1988) Habitat diversity or area per se? Species richness of woody plants, carabid beetles and land snails on islands. The Journal of Animal Ecology 57: 685–704. https://doi.org/10.2307/4933

Nurinsiyah AS, Hausdorf B (2017) Revision of the Diplommatinidae (Gastropoda: Cyclophoroidea) from Java. Zootaxa 4312: 201–245. https://doi.org/10.11646/zootaxa.4312.2.1

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Borman T, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2025) vegan: Community Ecology Package. R package version 2.7-0. https://doi.org/10.32614/cran.package.vegan

Parent CE (2012) Biogeographical and ecological determinants of land snail diversification on islands. American Malacological Bulletin 30: 207–215. https://doi.org/10.4003/006.030.0118

Phung, C. C., Yong, Y. Z., Said, M. A. M., & Liew, T. S. (2018) Land snail fauna in Gunung Kuang Limestone Hill, Perak, Malaysia and its conservation implications (Mollusca, Gastropoda). ZooKeys 769: 1–11. https://doi.org/10.3897/zookeys.769.25571

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and comprehensive evaluation. Ecography 31: 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

QGIS.org (2022) QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Version 4.4.1. https://doi.org/10.32614/r.manuals

Ramasamy N, Franz LK, Jong J, Muthuvairavasamy R, Muhammad AA, Dayong V, Shanmugarajah L, Vusak N, Sivanasvaran K, Kinanthi D (2021) Geochemistry of the Palaeocene Eocene Upper Kelalan Formation, NW Borneo: Implications on palaeoweathering, tectonic setting, and provenance. Geological Journal 56: 2500–2527. https://doi.org/10.1002/gj.3950

Ramette A (2007) Multivariate analyses in microbial ecology. FEMS Microbiology Ecology 62: 142–160. https://doi.org/10.1111/j.1574-6941.2007.00375.x

Roszkowska M, Książkiewicz Z (2022) Blown with the wind—The role of wind in passive dispersion of two land snails: *Vertigo moulinsiana* and vertigo antivertigo. Canadian Journal of Zoology 101: 75–80. https://doi.org/10.1139/cjz-2022-0071

Sautter B, Pubellier M, Schlögl SK, Matenco L, Andriessen P, Mathew M (2019) Exhumation of west Sundaland: A record of the path of India? Earth-Science Reviews 198: 102933. https://doi.org/10.1016/j.earscirev.2019.102933

Schilthuizen M (2003) Sexual selection on land snail shell ornamentation: a hypothesis that may explain shell diversity. BMC Evolutionary Biology 3: 1–6. https://doi.org/10.1186/1471-2148-3-13

Schilthuizen M, Rosli R, Ali AMM, Salverda M, van Oosten H, Bernard H, Ancrenaz M, Lackman-Ancrenaz I (2003a) The ecology and demography of *Opisthostoma* (*Plectostoma*) *concinnum* (Gastropoda: Diplommatinidae) on limestone outcrops along the Kinabatangan river. In: Mohamed M, Takano A, Goossens B, Indran R (Eds) Lower Kinabatangan Scientific Expedition 2002. Universiti Malaysia Sabah, Kota Kinabalu, 55–71.

Schilthuizen M, Chai HN, Kimsin TE, Vermeulen JJ (2003b) Abundance and diversity of land-snails (Mollusca: Gastropoda) on limestone hills in Borneo. Raffles Bulletin of Zoology 51: 35–42. https://doi.org/10.5281/zenodo.13229358

Schilthuizen M, Liew TS, Elahan BB, Lackman-Ancrenaz I (2005) Effects of karst forest degradation on pulmonate and prosobranch land snail communities in Sabah, Malaysian Borneo. Conservation Biolog 19: 949–954. https://doi.org/10.1111/j.1523-1739.2005.00209.x

Schilthuizen M, Liew TS, Liew TH, Berlin P, King JP, Lakim M (2013) Species diversity patterns in insular land snail communities of Borneo. Journal of the Geological Society 170: 539–545. https://doi.org/10.1144/jgs2012-014

Schwendinger PJ (2020) A revision of the trapdoor spider genus *Liphistius* (Mesothelae: Liphistiidae) in peninsular Malaysia; part 1. Revue Suisse de Zoologie 124: 391–445. https://doi.org/10.5281/zenodo.893555

Sheldon FH, Lim HC, Moyle RG (2015) Return to the Malay Archipelago: the biogeography of Sundaic rainforest birds. Journal of Ornithology 156: 91–113. https://doi.org/10.1007/s10336-015-1188-3

Simonová J, Simon OP, Kapic Š, Nehasil L, Horsák M (2016) Medium-sized forest snails survive passage through birds' digestive tract and adhere strongly to birds' legs: More evidence for passive dispersal mechanisms. Journal of Molluscan Studies 82: 422–426. https://doi.org/10.1093/mollus/eyw005

Slatter RJ (1990) Limestone communities and island biogeography. Journal of Biological Education 24: 87–92. https://doi.org/10.1080/00219266.1990.9655116

Sutcharit C, Thach P, Chhuoy S, Ngor PB, Jeratthitikul E, Siriwut W, Srisonchai R, Ng TH, Pholyotha A, Jirapatrasilp P, Panha S (2020) Annotated checklist of the land snail fauna from southern Cambodia (Mollusca, Gastropoda). ZooKeys 948: 1–46. https://doi.org/10.3897/zookeys.948.51671

Triantis KA, Rigal F, Parent CE, Cameron RA, Lenzner B, Parmakelis A, Yeung NW, Alonso MR, Ibáñez M, de Frias Martins AM, Teixeira DNF, Griffiths OL, Yanes Y, Hayes KA, Preece RC, Cowie RH (2016) Discordance between morphological and taxonomic diversity: land snails of oceanic archipelagos. Journal of Biogeography 43: 2050–2061. https://doi.org/10.1111/jbi.12757

Tweedie M (1961) On certain Mollusca of the Malayan limestone hills. Bulletin of the Raffles Museum 26: 49–65. https://doi.org/10.25662/960t-rq0c

Vermeulen JJ (1994) Notes on the non-marine molluscs of the island of Borneo 6. The genus *Opisthostoma* (Gastropoda Prosobranchia: Diplommatinidae), part 2. Basteria 58: 75–191.

Vermeulen JJ, Luu HT, Theary K, Anker K (2019a) New species of land snails (Mollusca: Gastropoda: Caenogastropoda and Pulmonata) of the Mekong Delta limestone hills (Cambodia, Vietnam). Folia Malacologica 2: 7–41. https://doi.org/10.12657/folmal.027.001

Vermeulen JJ, Luu HT, Theary K, Anker K (2019b) Land snail fauna of the Mekong Delta Limestone Hills (Cambodia, Vietnam): *Notharinia* Vermeulen, Phung et Truong, 2007, and a note on *Plectostoma* A. Adams, 1865 (Mollusca: Gastropoda: Caenogastropoda: Diplommatinidae). Folia Malacologica 27: 168–177. https://doi.org/10.12657/folmal.027.015

Waltham T (2008) Fengcong, fenglin, cone karst and tower karst. Cave and Karst Science 35: 77–88.

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology and Systematics 36: 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Zhu Z, Yan Y, Zhao Q, Dilek Y, Carter A, Hassan MHA, Yan W, Sun P, Zhou Y (2025) Provenance of Cretaceous-Miocene sediments in Borneo: Implications for paleogeographic patterns and tectonic evolution. Earth-Science Reviews: 105165. https://doi.org/10.1016/j.earscirev.2025.105165

Supplementary materials

Supplementary material 1

Details on the geographic distribution of *Plectostoma* species used in this study (.docx)
Link: https://doi.org/10.21425/fob.19.155940.suppl1

Supplementary material 2

MaxEnt Analysis - Variable Selection and Model Results (.docx)
Link: https://doi.org/10.21425/fob.19.155940.suppl2

Supplementary material 3

Bioregion cells summary, including species richness, environmental variables, and biogeographical classifications (.docx)
Link: https://doi.org/10.21425/fob.19.155940.suppl3

Supplementary material 4

***Plectostoma* species' IUCN conservation status and endemicity levels (.docx)**
Link: https://doi.org/10.21425/fob.19.155940.suppl4

Supplementary material 5

Canonical Correspondence Analysis (CCA) results (.docx)
Link: https://doi.org/10.21425/fob.19.155940.suppl5