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RESEARCH ARTICLE

Diversification and Colonisation in the Indo-Australian Archipelago: Genomic Insights From Colubrid Snakes

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ABSTRACT

Aim: The Indo-Australian Archipelago (IAA) is one of the most geologically complex and species-rich regions on Earth. However, our knowledge of the geological processes and dispersal mechanisms that generate archipelago-wide distributions across the IAA is limited to a few vertebrate groups and often solely attributed to Plio-Pleistocene sea-level fluctuations. In this study, we use phylogenomics-based analyses to investigate two speciose and closely related genera of snakes, *Lycodon* and *Stegonotus* (Serpentes: Colubridae), which are widely distributed across the IAA to identify which biogeographic and environmental processes have shaped snake diversity in this region.

Location: South Asia and the Indo-Australian Archipelago (Indochina, Sundaland, Philippines, Wallacea, Australasia).

Taxon: Snakes (Colubridae: *Lycodon, Stegonotus*).

Methods: We inferred a phylogeny using a genomic dataset consisting of ultraconserved elements, anchored hybrid enrichment loci, and protein-coding genes (~5400 nuclear loci) from 38 species (154 samples) of *Lycodon* and *Stegonotus*. We used ancestral range estimation analysis to identify dispersal patterns across the IAA. Additionally, we implemented ensemble species distribution models to identify potential hotspots of *Lycodon* and *Stegonotus* species richness and determined the environmental influence on geographic distributions and species diversity.

Results: We find that these snakes comprise six deeply divergent lineages (genera) that initially originated in Mainland Southeast Asia during the Oligocene. Diversification of these lineages is influenced not by Plio-Pleistocene sea-level fluctuations but by multiple historical processes, including in situ diversification, island hopping, long-distance rafting, possible microcontinental block drifting, Cenozoic land bridge migrations and founder events. The species distribution models do not consistently estimate lower or higher species richness in any particular region within the IAA, but precipitation overall is considered an important factor in estimated species richness.

Main Conclusion: Although Plio-Pleistocene sea-level fluctuations are notorious species pump diversification paradigms in the IAA, multiple and more ancient geological processes and environmental factors contributed to current diversity levels and distributions. Our approach expands future investigations of alternative hypotheses of biodiversity sources in the IAA and greatly expands the diversity of causal mechanisms for discussions of terrestrial Southeast Asian biodiversity beyond dispersal versus vicariance hypotheses.

1 | Introduction

Islands have long been recognised for their unique community composition and serve as a platform for many long-standing evolutionary theories (Darwin 1871, 1859; MacArthur and Wilson 1967; Wallace 1860, 1863). Since MacArthur and Wilson's (1963) development of the Equilibrium Theory of Island Biogeography, islands and archipelagos around the world have become models for studying the speciation and diversification processes that generate faunal and floral assemblages and patterns of species richness (Warren et al. 2015). Their isolation, smaller sizes relative to the mainland and abundance worldwide are key factors in generating species, many of which are endemic and/or autochthonous, having evolved in situ, where they are found today. Many archipelagos have become model systems for studying colonisation, diversification and extinction (West Indies; Brown, et al. 2013; Ricklefs and Bermingham 2008), repeated evolutionary scenarios (Grant and Grant 2007; Muñoz et al. 2023), species–area relationships and the effects of habitat heterogeneity on species richness (Aegean Archipelago; Sfenthourakis and Triantis 2017; Triantis et al. 2003, 2005) and adaptive radiations (Canary, Galápagos and Hawaiian Islands; Gillespie 2004; Jorgensen and Olesen 2001; Schluter 1988). Understanding these biogeographic patterns has become more feasible with the rise of genomic datasets that provide greater resolution and support of evolutionary relationships. There has been significant progress in identifying the historical processes that generate species diversity and distributions in archipelagos. However, the historical biogeography of the largest archipelago on the planet, the Indo-Australian Archipelago, remains comparatively underexplored.

The Indo-Australian Archipelago (IAA; Figure 1), also known as the Malay Archipelago, is one of the largest and most complex biogeographic realms on the planet (Lohman et al. 2011). The continental part of this archipelago is represented by the Thai-Malay Peninsula (Peninsular Malaysia and Thailand) on the western edge of this region. The insular portions of the IAA consist of more than 20,000 islands, including the oceanic islands of Wallacea (e.g., Sulawesi, Maluku, Nusa Tenggara) and the Philippines, and the continental islands of Sundaland (Singapore, Borneo, Sumatra, Java, Bali) and New Guinea. Additionally, while not considered part of the archipelago, Indochina's connection to the Thai-Malay Peninsula on the western edge, and Australia's historical land bridge connection with and proximity to New Guinea (jointly referred to as Sahul) on the eastern edge, bring a mosaic of faunal element to the IAA.

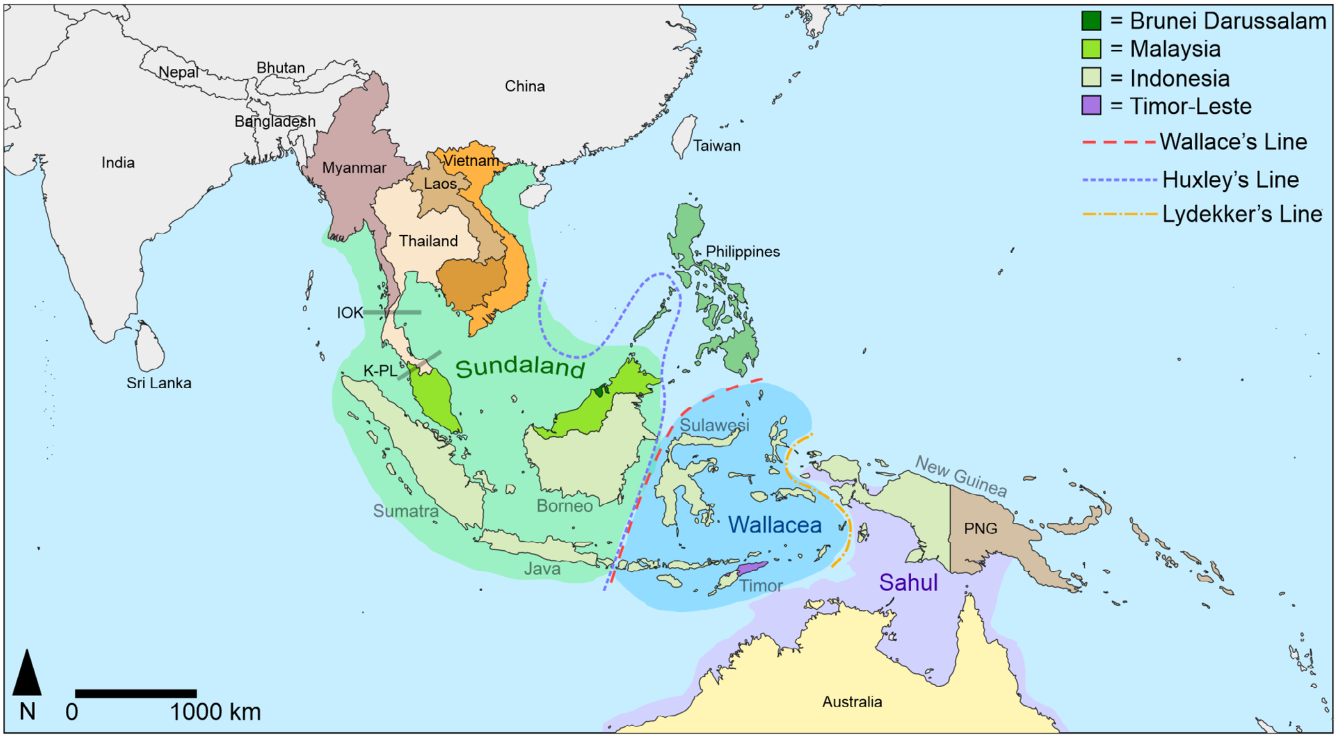

FIGURE 1 | Map of South Asia, East Asia, the Indo-Australian Archipelago (IAA) and Australia. Countries belonging to the IAA are colour-filled; subregions of the IAA are coloured by polygon (Sundaland, Wallacea and Sahul). Wallace's, Huxley's and Lydekker's Lines show the respective hypothesised faunal demarcations. Islands of Borneo, Sumatra, Java, Sulawesi, Timor and New Guinea are labelled outside the island boundary and coloured in by political division (country). Brunei Darussalam, Malaysia, Indonesia and Timor-Leste are shown through a colour key for ease of viewing. Abbreviations as indicated—IOK, Isthmus of Kra; K-PL, Kangar-Pattani Line; PNG, Papua New Guinea.

Ancient, recent and current plate tectonics have created unique opportunities for flora and fauna to colonise and diversify across the IAA (Baldwin et al. 2012; Hall 1998, 2009, 2011; Hall et al. 2012; Hamilton 1979; Spakman and Hall 2010; Van Ufford and Cloos 2005; Yumul et al. 2003, 2008). In addition to the spatial arrangement and varying origins of islands in this region, several aquatic and terrestrial biogeographic divides are known to demarcate various organismal groups. Although not universal across all taxa (Simpson 1977), Wallace's Line (including its modification, Huxley's Line) has become the most well-known faunal boundary in biogeography, describing the faunal turnovers between the Asian Sunda (Mainland Southeast Asia + Greater Sunda Islands) and Australian Sahul (Australia + New Guinea) shelves (Dickerson 1928; Huxley 1868; Lydekker 1896; Wallace 1860, 1863) (Figure 1). Marine barriers such as the ancient, deep-sea trenches at the Makassar Strait (Hall 2009), and enormous, terrestrial, mountainous divides such as the Central Cordillera in New Guinea have been correlated with increased species diversity (Roycroft et al. 2022; Tallowin et al. 2018). Perhaps, the most well-known geological phenomena are the Plio-Pleistocene sea-level fluctuations that have been shown to cyclically connect and separate landmasses (and drainage basins; Cheng and Faidi 2025; de Bruyn et al. 2013) on the Sunda and Sahul shelves and in the Philippines, as well as their respective flora and fauna, ultimately leading to species-pump paradigms for the IAA (de Bruyn et al. 2014; Hall 2009; Lohman et al. 2011; Oliver et al. 2020; Sholihah et al. 2021; Wüster et al. 2005). A wide range of terrestrial groups have diversified within distinct subregions of the IAA (Esselstyn et al. 2021; Kennedy et al. 2022; Sholihah et al. 2021; Weinell and Brown 2018), resulting in high levels of endemism (Myers et al. 2000). The heterogeneity of landscapes, diversity of fauna and mosaic of geological histories serve as an opportunity to identify which dispersal and colonisation processes have generated the current distribution patterns across and within the IAA.

Investigations of lineage diversification in the IAA often focus on specific regions, such as Sundaland, Wallacea, Sahul and the Philippines. For example, Sundaland and the Philippines are often characterised by Plio-Pleistocene sea-level fluctuations (Cheng and Faidi 2025; Voris 2000) and species pump effects (Brown, et al. 2013; de Bruyn et al. 2014; Esselstyn and Brown 2009; Li and Li 2018). The Philippines, on its own, is regarded as a biogeographically distinct unit within Southeast Asia, known for its complex geological histories with various colonisation routes, high levels of endemism, and in situ diversification scenarios (Brown, et al. 2013). Wallacea, having been mostly absent of any land bridge connections during sea-level minima, has been colonised through overwater dispersal events and stepping-stone scenarios (Mcguire et al. 2023; Reilly et al. 2021; Rowe et al. 2019). Finally, tectonic collisions and orogenesis in New Guinea and environmental changes in Australia are linked with many extant megadiverse groups (Brennan et al. 2024; Hill et al. 2023; Kennedy et al. 2022). The IAA's dynamic and complex geological history has led to the discovery of broad, archipelago-wide patterns of dispersal in invertebrates and plants (Grudinski et al. 2014; Hausdorf 2018; Joyce et al. 2021; Toussaint et al. 2020; Toussaint and Balke 2016). Yet, although several geological processes shape faunal distributions in the IAA, the Plio-Pleistocene sea-level fluctuations from ~2.5 million years ago (mya) to ~11.7 thousand years ago (kya) are still the prevailing paradigm for regional biogeographic hypotheses, while alternative hypotheses are neglected from consideration. Additionally, despite being one of the most diverse terrestrial vertebrate groups across the IAA, with a wide variety of life histories, squamates have rarely been investigated for region-wide patterns (but see Barley et al. 2015; Grismer et al. 2022).

Snakes in the colubrid genera *Lycodon* (wolf snakes) and *Stegonotus* (ground snakes) are two presumed to be closely-related and widespread genera in Asia and the IAA, containing 81 and 26 species (Figueroa et al. 2016; Pyron et al. 2013; Uetz et al. 2025), respectively. In the last decade, 15 species (~20% of the known genus diversity) of *Lycodon* and 8 species (~30%) of *Stegonotus* have been described. *Lycodon* are characterised by their slender bodies, variable colour patterns and fang-like anterior maxillary and mandibular teeth. *Lycodon* comprises one of the most widespread vertebrate genera in the world, ranging from Mauritius through South Asia, all of Southeast Asia and East Asia, with Japan as the easternmost extent. *Stegonotus*, a genus of medium-sized, primarily terrestrial snakes, are known from Sundaland (Borneo), Wallacea, the Philippines, New Guinea and the nearby Bismarck and Louisiade Archipelagos, and northern Australia. The evolutionary relationship between *Lycodon* and *Stegonotus* is unclear, with published phylogenies limited in sampling (Figueroa et al. 2016; Pyron et al. 2013). For *Lycodon*, the lack of densely sampled phylogenies has led to confusing generic taxonomy, with the genera *Lycodon*, *Lepturophis*, *Dryocalamus* and *Dinodon* inconsistently used to refer to various *Lycodon* species (Guo et al. 2013; Uetz et al. 2025; Wallach et al. 2014; Zaher et al. 2019). Indeed, molecular systematic efforts have increased our understanding of diversification within *Lycodon* and *Stegonotus* (Ruane et al. 2017; Siler et al. 2013). However, studies relying on mitochondrial datasets are prone to mito-nuclear discordance, even among closely related species (Dufresnes et al. 2024; Talavera et al. 2025). Until now, *Lycodon* and *Stegonotus* have yet to be studied using genomic datasets with sampling across multiple divergent lineages. Even in regard to other vertebrate groups, studies with genomic data and dense taxonomic sampling for testing broader biogeographic hypotheses are lacking for the IAA. Thus, while these species can aid our understanding of species dispersal patterns and the evolution of IAA vertebrates with moderate-dispersal capabilities, this goal is impeded by unresolved systematics of *Lycodon* and *Stegonotus*.

In this study, we take a phylogenomic approach to investigate the evolutionary history and historical biogeography of the IAA using a moderate-dispersal capacity vertebrate system: snakes in the genera *Lycodon* and *Stegonotus*. We generate a novel genomic dataset to identify dispersal patterns across the archipelago and adjacent regions, while resolving the systematics of long-debated species in taxonomic flux (Boulenger 1984a; Guo et al. 2013; Wall 1909; Wallach et al. 2014). In addition, as new species of both genera are continuously being described (e.g., Kaiser et al. 2021; Nguyen et al. 2024; Nguyen, Poyarkov, et al. 2025; Nguyen, Lee, et al. 2025; Nguyen and Vogel 2025; O'Shea and Richards 2021; Ruane et al. 2017), we use environmental data to create ensemble species distribution models and identify potential environmental correlates with species diversity in these snakes. We aim to answer three questions: (i) are Plio-Pleistocene sea-level fluctuations the dominant mechanism of generating snake diversity in the IAA (divergence dates ≤2.5 mya)? (ii) is the distribution of snakes in the IAA better explained by geological or environmental factors, or a mix of both? and (iii) what are the evolutionary relationships within and between *Lycodon* and *Stegonotus*?

2 | Materials and Methods

2.1 | Taxonomic Sampling and Data Generation

We obtained fresh liver and muscle tissue from 84 *Stegonotus* (14 species) and 70 *Lycodon* (24 species) for this study, for a total of 154 individuals (Table S1). Although our sampling only consists of ~29% of *Lycodon* and ~58% of *Stegonotus* known species diversity, we provide the most comprehensive dataset in taxon sampling and molecular data to date and include species across the entire range of both genera for biogeographic investigation. Tissues were obtained from field collection efforts or from the following natural history collections/field series: Australian Museum, Sydney (AMS), Bernice P. Bishop Museum (BPBM), Burke Museum of Natural History and Culture (UWBM), California Academy of Sciences (CAS), Field Museum of Natural History (FMNH), University of Kansas Biodiversity Institute and Natural History Museum (KU), Louisiana State University Museum of Natural Science (LSUMZ), Museum of Comparative Zoology (MCZ), Museum of Vertebrate Zoology (MVZ), Museum Zoologicum Bogoriense (MZB), Papua New Guinea National Museum and Art Gallery (PNGNM), South Australian Museum (SAMA) and the field series of Benjamin J. Evans (BJE) and Rafe M. Brown (R.M.B.). All museum codes follow Sabaj (2023). Although the biogeographic focus of our sampling is on the Indo-Australian Archipelago, we include several widespread species that extend outside this region. Specifically, we include *Lycodon zawi*, *L. jara* and *L. aulicus* in South Asia (including Mauritius, off the east coast of Africa) (Ganesh and Vogel 2018).

We extracted total genomic DNA from fresh tissues using Qiagen DNeasy blood and tissue kit protocols. We used a Qubit 3 fluorometer (high sensitivity; Thermo Fisher Scientific: Invitrogen) for quantification. Samples were sent to Daicel Arbor Biosciences for DNA sequencing. The samples used in this study were sequenced using different probe sets, as they were part of multiple projects distinct from this study. Samples were either optimised for target capture using the UCE Tetrapods 5Kv1 probe set (Faircloth et al. 2012), targeting ~5000 ultraconseved elements (UCEs) or the Squamate Conserved Loci (SqCL) v2 probe set (Singhal et al. 2017). The SqCL probes target 5462 nuclear loci consisting of UCEs, AHEs and NPCGs commonly used in Squamate phylogenetic studies (e.g., BDNF, CMOS, RAG2). Due to potential taxonomic uncertainty, we also performed *post hoc* data mining of mitochondrial DNA from the UCE bycatch of a formalin-preserved specimen of *Stegonotus modestus* (not initially included due to missing data), the type species of the genus *Stegonotus*. All details for library preparation and genomic sequencing can be found in Appendix S1.

2.2 | Bioinformatics and Phylogenomic Analysis

2.2.1 | Nuclear and Mitochondrial Data Processing

Raw genomic reads were processed using the *Phyluce* v1.7.3 pipeline (Faircloth 2016). We trimmed adapter and barcode sequences using illumiprocessor with default settings (Del Fabbro et al. 2013; Faircloth 2011; Lohse et al. 2012). We then assembled the trimmed reads using SPAdes v3.14.1 (Bankevich et al. 2012) under default parameters. Reads that mapped to multiple UCEs (potential paralogous regions) were removed using *phyluce_assembly_match_contigs_to_probes*. Homologous sites of UCEs were aligned and then edge-trimmed, and data matrices were created for each locus that contained at least 75% of the taxa in the dataset (75% completeness matrix). Raw reads were submitted to NCBI's Sequence Read Archive (BioProject ID: PRJNA1337899). Outgroups for this study can be found under SRA Project Number PRJNA790029.

We initially extracted and sequenced DNA from the *S. modestus* individual (formalin-preserved) as per the protocols of Bernstein and Ruane (2022). However, due to a lack of coverage for the UCE dataset, we did not include it in the planned phylogenetic analyses of this study. Instead, we used the mapping method in Geneious R11 to extract mitochondrial *cytochrome-b* (~1117 bp) from the raw sequencing reads of *S. modestus* and a subset of our *Stegonotus* individuals using fresh tissues for phylogenetic analysis to better clarify the resulting generic-level taxonomy.

2.2.2 | Phylogenetic Reconstruction

For all downstream analyses, we reconstructed a maximum likelihood phylogeny of the group. We also included two samples of *Tropidonophis dendrophiops* from Roberts, Kraus, et al. (2024) to use as outgroups, and extracted UCEs from the whole genome of *Psammodynastes pulverulentus* (Roberts, Bernstein, et al. 2024) for use with respect to a divergence date calibration (see *Divergence Date and Ancestral Range Estimation*) and outgroup choice (Das et al. 2024). We concatenated all UCEs of the 75% completeness matrix and used IQ-TREE v2.2.0 for phylogenetic reconstruction to identify taxonomic groupings for subsequent species tree analysis. We used a GTR + G model of molecular substitution and assessed branch support with 1000 ultrafast bootstrap (UFB) iterations (Hoang et al. 2018). We considered relationships that had UFB ≥95 as strongly supported. To take gene tree-species tree discordance into account, we also generated a nuclear coalescent tree (species tree) with ASTRAL-III (Zhang et al. 2018). For this analysis, we generated individual UCE trees (hereafter called ‘gene trees’) for each locus in the 75% completeness matrix. Gene trees were reconstructed using IQ-TREE with the same parameters used for the concatenated nuclear tree, with the exception that we used ModelFinder (Kalyaanamoorthy et al. 2017) to determine the best substitution model for each gene tree. These trees were used as input for ASTRAL-III, which was run using default parameters and with a mapping file to collapse tips with multiple individuals of the same species. Relationships in the species tree were considered supported if Bayesian Posterior Probabilities were ≥0.95. Additionally, after obtaining our results, we observed that the sister taxon to all other ingroup taxa had a short branch length (see *Results*); to increase our confidence in determining if this topology was real phylogenetic signal, we calculated gene concordance factors (gCF) using IQ-TREE v2.2.0 (Minh et al. 2020). Using the same phylogenetic workflow, we also reconstructed a maximum likelihood phylogeny of *Stegonotus* using a fragment of the mitochondrial gene *cytochrome-b* to confirm the phylogenetic position of the type species *S. modestus* and its affiliation with other lineages in Australia and New Guinea.

2.2.3 | Divergence Date and Ancestral Range Estimation

The geological history of the IAA is a mosaic of plate collisions, island arc accretions and cyclic sea-level fluctuations that have impacted the distribution of species at different points in history. We estimated divergence times of *Lycodon* + *Stegonotus* to identify when and how dispersal events between subregions of the IAA took place, and test if Plio-Pleistocene sea fluctuations are correlated with species diversity (i.e., divergence events take place ≤2.5 mya to 11.7 kya). We estimated divergence times of our species trees using treePL v1.0 (S. A. Smith and O'Meara 2012). We obtained optimal parameters for treePL and ran the analysis until convergence using the *prime* and *thorough* commands, respectively. We performed this process five times to ensure consistency of parameters. We used random subsample and replicate cross-validation (RSRCV) to choose the best smoothing parameter for taking rate variation across the tree into account. The RSRCV approach randomly samples multiple terminal nodes with replacement and calculates the rates and dates of the tree with the terminal nodes removed. Then, the average error is sampled over the nodes (Smith and O'Meara 2012). We ran treePL with the optimal smooth parameter chosen by RSRCV (=1000; lowest error).

To calibrate our divergence time estimation analysis, we used fossil data outside of our ingroup, as well as secondary calibrations, due to the absence of known fossils from within *Lycodon* or *Stegonotus*. For our primary calibration, we used the stem-Colubroidea calibration from Smith (2013) to set a minimum date of 35.2 million years old (my) at the node where *Psammodynastes* splits from all other taxa; we also set the maximum date to 46.76 my, using the upper end of the 95% highest posterior density (HPD) of this divergence as in Burbrink et al. (2020). For secondary calibrations, we also used the 95% HPD of the Colubridae–Natricidae split (*Tropidonophis*-Ingroup in our tree; 39.9–43.0 my) from Burbrink et al. (2020), and a strict calibration of 17.8 my at the most recent common ancestor (MRCA) of *Lycodon davisonii* and *Stegonotus batjanensis*, which comes from Zaher et al. (2019), the only study that has a divergence date for any of our ingroup taxa.

We used the dated species tree to estimate ancestral ranges and obtain quantitative support of dispersal routes through South Asia and the IAA. We reconstructed ancestral ranges using *BioGeoBEARS* (Matzke 2013a) with our time-calibrated species tree as the input tree. Demarcation of ancestral ranges are prone to subjectiveness. Thus, biogeographic ranges were chosen based on regions of endemism, geological history (e.g., Pleistocene land bridges; Hall 2009; Voris 2000) and biogeographic barriers. Mainland Southeast Asia (Indochina) is considered a distinct biodiversity hotspot (de Bruyn et al. 2014) and is surrounded by several geological features that separate it from East Asia and South Asia, such as the Red River, Black River, Shan Plateau and Yunnan-Guizhou Plateau, that most likely impact dispersal of low-elevation inhabiting, low-dispersal capable vertebrates like snakes. Our state of Sundaland includes the Greater Sunda Islands due to historic land bridge connectivity and faunal similarities (Voris 2000; de Bruyn et al. 2014) and the Thai-Malay Peninsula which is demarcated from Indochina at the Isthmus of Kra (Figure 1), a known faunal and floral turnover point (de Bruyn et al. 2014; Hughes et al. 2003). We keep the islands of the Philippines and Wallacea as their own ancestral ranges due to their distinct geological histories as oceanic islands, and endemic faunal assemblages (Philippines; Brown et al. 2013) or a lack of land connectivity to any mainland source (Philippines and Wallacea; Voris 2000). Although New Guinea and Australia have been connected through a Plio-Pleistocene land bridge, we keep them as separate range states due to their differences in habitat, flora and fauna (Byrne et al. 2008; Cámara-Leret et al. 2020).

This resulted in the selection of nine range states: South Asia, Indochina, East Asia, Sundaland (Thai-Malay Peninsula and the Greater Sunda Islands), Philippines, Wallacea, New Guinea, Australia and Africa (Mauritius). Our inclusion of Mauritius is represented by only one species in our sampling, *L. aulicus*. As we have representative species from all parts of *Lycodon* and *Stegonotus* distributions, we are confident that our taxonomic sampling is sufficient for ancestral range estimation and that we will not miss any major range/state transitions, as shown in other studies with partial species-level sampling (Fric et al. 2022; Peterson et al. 2022; Schools et al. 2022). Our analysis tested six models that differ in cladogenetic range evolution processes (Matzke 2013a, 2014): Dispersal-Extinction-Cladogenesis (DEC; Ree and Smith 2008); DIVALIKE, a likelihood version of the parsimony model Dispersal-Vicariance (DIVA; Ronquist 1997); BAYAREALIKE, a likelihood version of the BAYAREA model (Landis et al. 2013). The DEC model assumes that daughter lineages inherit the ancestral area state if the MRCA is limited to a small range (a single area), or, if the MRCA is widely distributed, the daughter lineage inherits a range that is within the MRCA's ancestral area (Ree and Smith 2008). For the DIVA model, speciation is dependent on vicariance events and does not assume any relationships between areas (Ronquist 1997). Finally, the BAYAREA model assumes no range evolution during cladogenetic events, so daughter lineages inherit the ancestral range of the MRCA (Landis et al. 2013; Matzke 2013b). We also ran our analysis of these models with the '+J' jump dispersal parameter to allow for founder-event speciation: DEC+J, DIVALIKE+J, BAYAREALIKE+J (Matzke 2013b, 2014), which is likely given the high number of single-island endemics in these groups of snakes. While there has been concern over the use of the DEC and DEC+J models leading to inaccurate biogeographic inference (Ree and Sanmartín 2018), simulations in Matzke (2014) show that *BioGeoBEARS* inference is not strongly biassed if extinction is random (an assumption we have made), and that *d* and *j* parameters are identifiable (Klaus and Matzke 2020; N. J. Matzke 2014). The statistical validity of the *BioGeoBEARS* framework has been supported when compared to ClaSSE models (Matzke, 2021), and thus we are confident in our pipeline of ancestral range estimation. We statistically compared the fit of all models under different dispersal scenarios using the

Akaike Information Criterion corrected for small sample sizes (AICc; Akaike 1974; Burnham and Anderson 2002, 2004), considering models with the lowest AICc scores (and highest weight) to have the best fit to our data. Likelihood ratio tests were performed to assess if models with and without the +J parameter differ significantly in likelihood.

2.3 | Ensemble Species Distribution Models

The species richness of *Lycodon* and *Stegonotus* is higher at the mainland and continental island margins of their ranges compared to the middle of the distribution on the oceanic islands of Wallacea. Only ~3% of *Lycodon* and ~30% of *Stegonotus* species are found in Wallacea. Given the environmental heterogeneity across the IAA, we used ensemble species distribution models (ESDMs) to test if Wallacea is environmentally unsuitable for these taxa, as well as to identify regions of high species richness for subsequent field efforts. Alternatively, higher species richness may be due to increased land area in Sundaland and Australasia, as expected by island biogeography theory (MacArthur and Wilson 1963, 1967). Ensemble models can account for the variability across different modelling algorithms and provide a measure of central tendency at the consensus areas of habitat suitability for one or multiple species, making them ideal for estimating habitat suitability at the community level (Araujo and New 2007).

We generated spatial datasets using occurrence records from the samples in our genomic dataset. We also downloaded occurrences from the Global Biodiversity Information Facility (GBIF; see Table S2 for download GBIF DOIs for each taxon) using the R package *rgbif* v3.8.1 (www.gbif.org; R Core Team 2023). We included the current and older (synonymised) taxonomy in our GBIF search terms to maximise our occurrence. To ensure models were statistically reliable, we only retained species datasets that contained more than 10 records for our ESDMs. For species that have extremely limited ranges or represent a region that was not climatically encapsulated from other taxa, we used a minimum threshold of five records; only five species had less than ten records (see below). We manually removed erroneous occurrences (e.g., in the ocean) and used a combination of field guides, taxonomic studies and published phylogenies (David and Vogel 1996; Fukuyama et al. 2025; Ganesh and Vogel 2018; Kaiser et al. 2018; Leviton et al. 2018; Nguyen, Poyarkov, et al. 2025; Nguyen, Lee, et al. 2025; O'Shea and Richards 2021; Ruane et al. 2017; de Lang 2013; Stuebing et al. 2014; Uetz et al. 2025; Yang and Yeung 2024) to remove duplicate data, occurrence records that had questionable taxonomic identification, or data that were identified as introduced/invasive populations. This resulted in a total of 4916 observations.

To better understand the results of our niche models in an evolutionary context (and to remain conservative as to which species are discussed), we limited our modelling approach to taxa that are in our UCE phylogeny. Our phylogeny (see *Results*) highlights the need to revise the genus-level taxonomy of the *Lycodon* + *Stegonotus* clade, and thus for the remainder of the manuscript we refer to the taxa in our tree using generic classification that historically has been used for species of *Lycodon* (*Lycodon sensu stricto* [*s.s.*], *Lepturophis*, *Dinodon* and *Dryocalamus*, collectively referred to from now on as *Lycodon sensu lato* [*s.l.*]) and *Stegonotus* (*Stegonotus s.s.* and *Lielaphis*, collectively referred to as *Stegonotus s.l.*). Due to this revision, we stacked species from five genera into five genus-level models (26 species total, occurrence dataset sizes less than 10 given parenthetically): *Dinodon*—*Dinodon fasciatus* comb. nov., *Dinodon flavozonatus*, *Dinodon gongshan* comb. nov. (9), *Dinodon ruhstrati* comb. nov., *Dinodon sealei* comb. nov. (9), *Dinodon septentrionalis*, *Dinodon subcinctus* comb. nov.; *Dryocalamus*—*Dryocalamus davisonii*, *Dryocalamus subannulatus*, *Dryocalamus tristrigatus*; *Lycodon s.s.*—*Lycodon aulicus*, *Lycodon capucinus*, *Lycodon effraenis*, *Lycodon jara*, *Lycodon laoensis*, *Lycodon zawi*; *Stegonotus s.s.*—*Stegonotus alcalai* comb. nov. (5), *Stegonotus batjanensis*, *Stegonotus muelleri*, *Stegonotus philippinensis* comb. nov.; *Lielaphis*—*Lielaphis australis* comb. nov., *Lielaphis diehli* comb. nov., *Lielaphis guentheri* comb. nov. (9), *Lielaphis iridis* comb. nov. (9), *Lielaphis melanolabiatus* comb. nov., *Lielaphis reticulatus* comb. nov. We used the 19 bioclimatic variables from WorldClim (Fick and Hijmans 2017) at a 2.5 min resolution (~5 km) to summarise regional temperature and precipitation variables; we removed bioclimatic variables 18 (precipitation of the warmest quarter) and 19 (precipitation of the coldest quarter) due to variable discontinuity (Booth 2022). This resulted in the use of the following variables: bio1: annual mean temperature, bio2: mean diurnal range, bio3: isothermality, bio4: temperature seasonality, bio5: max temperature of warmest month, bio6: min temperature of coldest month, bio7: temperature annual range, bio8: mean temperature of wettest quarter, bio9: mean temperature of driest quarter, bio10: mean temperature of warmest quarter, bio11: mean temperature of coldest quarter, bio12: annual precipitation, bio13: precipitation of wettest month, bio14: precipitation of driest month, bio15: precipitation seasonality, bio16: precipitation of wettest quarter, bio17: precipitation of driest quarter. All ESDMs were constructed in the R package *SSDM* v 0.2.11 (Schmitt et al. 2017) using the default parameters of three different modelling algorithms: maximum entropy (Maxent), generalised linear models (GLM) and support vector machine (SVM), with an ensemble threshold of 0. We summed the ensemble habitat suitability models for each species using the pSSDM method in the *SSDM* R package to produce a single species richness map, each, for *Dinodon*, *Dryocalamus*, *Lycodon s.s.*, *Stegonotus s.s.* and *Lielaphis*. The ensemble models for each species in each genus were then constructed into stacked species distribution models (SSDM) to identify community-level patterns of species richness. Additionally, as we could not run a stacked model for the genus *Lepturophis*, as it is only represented by one species in our study (*Lepturophis albofuscus*), we only ran an ensemble model for this species using the above approach with the Maxent, GLM and SVM algorithms. The performance of individual Maxent models was evaluated using the area under the receiving operating characteristic curve (AUC). This statistic is threshold-independent and ranges from 0 to 1, in which a value of 1 represents perfect model performance and 0.5 represents models that perform no better than random (Peterson et al. 2011). For our models, we considered AUC values of 0.7 or greater to represent good model performance (Peterson et al. 2011). We also used Cohen's kappa (κ), a simpler (fewer parameters) statistic that corrects the overall accuracy of model predictions by the accuracy expected to occur by chance, and is tolerant of zeros in the confusion matrix (Manel et al. 2001). Cohen's kappa is a standardised value that ranges from −1 to +1, where values of zero and below indicate model performance no better than random chance, and values above 1 indicate perfect agreement in models

(Cohen 1960). We also report model sensitivity and specificity, which are defined as the rate at which the model can correctly identify positive (occurrences; true positives) and negative (absences; true negatives) values.

3 | Results

3.1 | Phylogenomics of Colubrids in the IAA

Sequencing resulting in a total of 2666 shared UCEs across 157 samples (38 species across all in group genera), which, when concatenated, resulted in a DNA alignment of 3,268,586 base pairs in length. The topology of the concatenated phylogeny, if using the previous taxonomy of only *Lycodon s.l.* and *Stegonotus s.l.*, recovers these genera as non-monophyletic; most nodes are strongly supported, except one clade from mainland Southeast and East Asia (Figure S1). Due to this non-monophyly, observed in all trees (Figure S1), we refer to these six groups by redefining *Lycodon s.l.* and *Stegonotus s.l.*, and resurrect the following genera: *Lepturophis*, *Dinodon*, *Dryocalamus* and *Lielaphis* (Figure 2). These six genera are deeply divergent, with *Lepturophis* having diverged from all other lineages ~25.6 mya, and all other genera divergent from ~17 mya (*Dryocalamus*, *Lielaphis* and *Stegonotus s.s.*) to ~24 mya (*Dinodon* and *Lycodon s.s.*). These clades are comprised

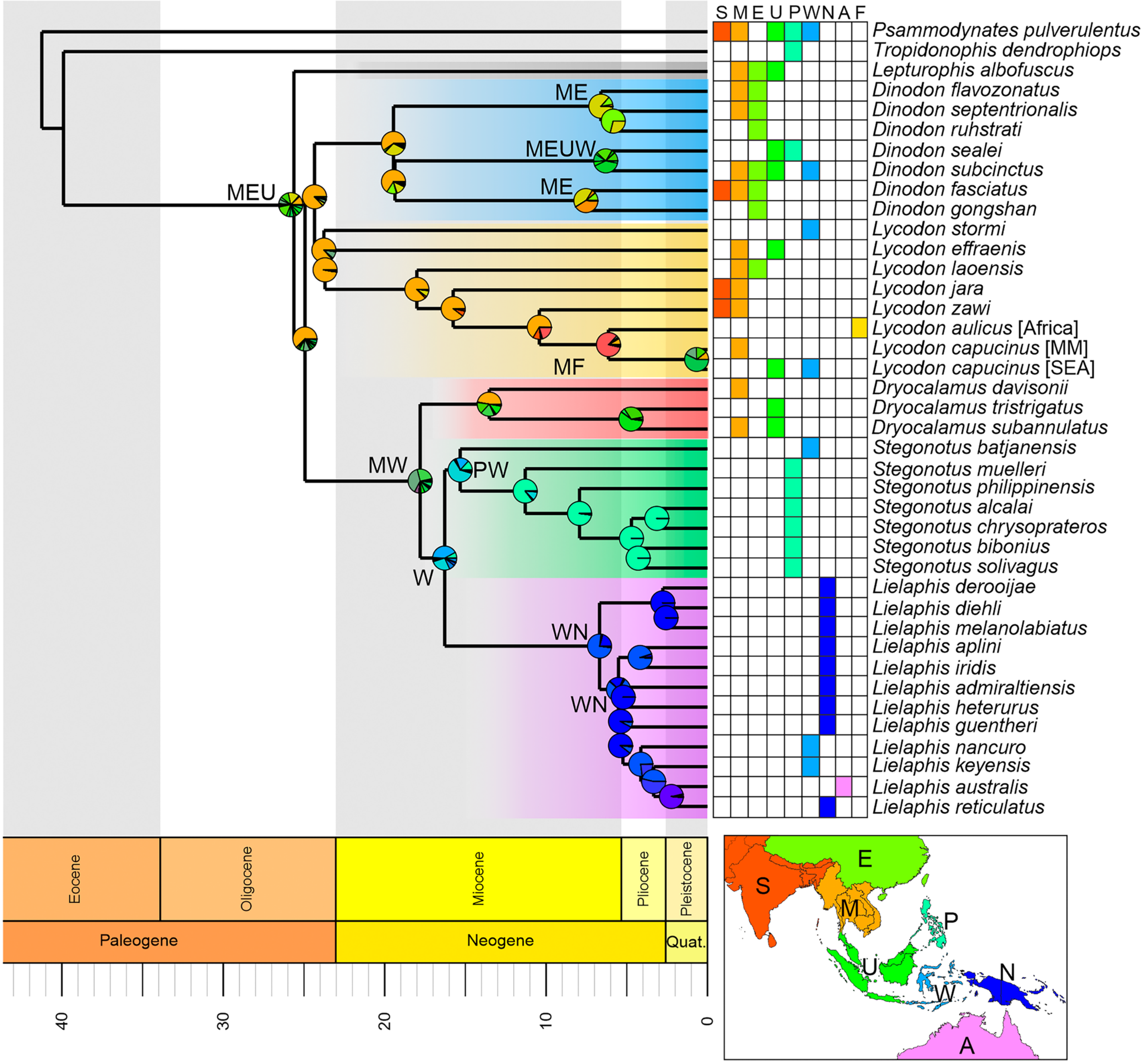

FIGURE 2 | Time-calibrated species tree of all genera in this study. Pie charts at nodes represent ancestral range estimation likelihood charts; colours correspond to the ancestral areas in the inset map—A, Australia; E, East Asia; F, Africa [Mauritius] (not shown in map); M, Mainland Southeast Asia (Indochina); N, New Guinea; P, Philippines; S, South Asia; U, Sundaland; W, Wallacea. Ancestral ranges comprising more than one of these states are given at the respective nodes. Coloured grid to the left of species names represents their known extant range. Two populations of *L. capucinus* were used, MM (Myanmar) and SEA (all Southeast Asian localities).

of taxa that have regional distributions, with *Lepturophis* in Sundaland, *Dinodon* primarily in Indochina and East Asia, *Lycodon* ranging from South Asia and eastward to Sundaland and Wallacea, *Stegonotus s.s.* primarily restricted to the Philippines (except for the Wallacean endemic *S. batjanensis*), and *Lielaphis* consisting of species in Wallacea, New Guinea and Australia. *Lepturophis* is the sister taxon to all other species, which are then split into two clades: one in which *Dinodon* is the sister genus to *Lycodon*, and another with *Dryocalamus* as the most closely related genus to the sister genera *Stegonotus s.s.* and *Lielaphis*. Because *Lepturophis* is monotypic and represented by a single, short branch diverging from the other genera, we checked the gene concordance factor to identify if this topology is broadly consistent across gene trees. We found that this topology is the majority topology and is present in over 90% of loci (gCF = 93.1), giving us confidence in this relationship as real phylogenetic signal.

Most species were monophyletic, except for *Dinodon subcinctus* and *Stegonotus muelleri*, rendered paraphyletic by *D. sealei* and *S. dumerilii*, respectively. The species (ASTRAL) tree, analysed from 2666 gene trees, yielded a similar phylogeny, except for two relationships: the placement of the *D. sealei*, *D. fasciatus* and *D. flavozonatus* groups (poorly supported in both concatenated and species trees), and the placement of *Lielaphis guentheri* (strongly supported in the species tree) (Figure S1). Despite these topological differences, they do not change the biogeographic interpretation of our results. Thus, we focus the rest of our results and discussion on the species tree.

3.2 | Divergence Dating and Ancestral Range Estimation

Divergence date analysis places the origin of *Lepturophis*, *Dinodon*, *Dryocalamus*, *Lycodon*, *Stegonotus s.s.* and *Lielaphis* in the Oligocene, ~25.6 mya, with the common ancestor of all genera except *Lepturophis* subsequently diverging at ~24.9 mya (Figure 2; Figure S1). The intergeneric splits and crown groups of *Dinodon* (~19.5 mya), *Stegonotus* (~15.3 mya), *Dryocalamus* (~13.5 mya) and *Lielaphis* (~6.7 mya) all date back to the Miocene, with *Lycodon* being an older lineage (Oligocene; ~23.8 mya). Only one interspecific node in the tree had a date of ≤ 2.5 mya, which rejects the hypothesis that sea-level fluctuations drove diversification patterns of these snakes in the IAA.

Our ancestral range analysis identified the DEC model as the best fit for our data (log likelihood = −107.2; AICc = 218.7; Table S3). We found no significant difference between the log likelihoods of the DEC and DEC+J models (likelihood ratio test; $p = 1.00$), which showed near-identical results in ancestral range states (Figure S2). The geographic origins of all ingroup genera are in Mainland Southeast Asia + Indochina + Sundaland (Figure 2). Throughout the Oligocene and Miocene, several lineages diversified within these regions, with *Dinodon* and *Lycodon s.s.* dispersing into South Asia, East Asia and the Thai-Malay Peninsula and Greater Sunda Islands. Only one species in these two genera, *Dinodon sealei*, is distributed in present-day Philippines (Palawan; Figure 2). Although *Lycodon* is represented by species as far west as Mauritius (*L. aulicus*), the origin of this group, based on our sampling, is in Mainland Southeast Asia (Indochina). At ~17.8 mya, the common ancestor of *Dryocalamus* continued to speciate within Mainland Southeast Asia and Sundaland and the ancestral lineages of *Stegonotus s.s.* and *Lielaphis* dispersed into Wallacea, followed by migration into the Philippines and Australasia, respectively, in the mid- to late Miocene (Figure 2). Throughout the Miocene, Pliocene and Pleistocene, *Stegonotus s.s.* speciated in a south-to-north direction through the Philippine islands, evidenced by *S. batjanensis* from Batjan (=Bacan) Island (Moluccan Islands in Wallacea, south of the Philippines) as sister to all other congenerics. Within *Lielaphis*, our results indicate that speciation took place once a common ancestor reached New Guinea in the late Miocene (Figure 2). Several founder speciation events occurred, with *Lielaphis nancuro* comb. nov. (Timor-Leste) and *Lielaphis keyensis* comb. nov. (Kei Islands) back-dispersing into Wallacea, and *L. australis* inhabiting Australia's northern coast as the continent's only *Lielaphis* species. Overall, our divergence dating and ancestral range estimations highlight that present-day diversity in these groups is likely due to a variety of dispersal patterns and geological processes (see *Discussion*) that predate the Plio-Pleistocene sea-level fluctuations (Figure 3).

3.3 | Species Distribution Models and Patterns of Species Richness

While our divergence dating and ancestral range analyses provide insight into periods of divergence and potential geological drivers, these analyses do not test for associations between environmental factors and patterns of species richness (e.g., lower species diversity in Wallacea). To test for this and identify possible areas of estimated elevated richness for future surveys, we generated SSDMs for *Dinodon*, *Dryocalamus*, *Lycodon s.s.*, *Stegonotus s.s.* and *Lielaphis* using occurrence records that we compiled ourselves, as well as from published occurrence records. Predictive performance for the ensemble models based on AUC was high for all algorithms (SVM, GLM, and Maxent AUC > 0.933; Table S4). Model sensitivity (true positive rate) was also high for all algorithms across genera (sensitivity ≥ 0.867), while model specificity (true negative rate) was high for SVM and GLM algorithms (specificity ≥ 0.873), but low for Maxent (0.446–0.539) (Table S4). The mean Cohen's kappa (standard deviation given parenthetically; Table S4) for each genus was: *Dinodon* $\kappa = 0.992$ (0.017); *Dryocalamus* $\kappa = 1.107$ (0.052); *Lielaphis* $\kappa = 0.980$ (0.003); *Lycodon* $\kappa = 0.995$ (0.011); *Stegonotus s.s.* $\kappa = 1.121$ (0.050); *Lepturophis s.s.* $\kappa = 0.413$.

Although we project our niche models to the entire extent of the IAA and South Asia, we limit our results and discussion of each genus to their known biogeographic range. Along with our estimates of species richness, we also provide the genus-level distributions based on our sampling and occurrence record datasets. Across genera, we did not observe Wallacea having lower levels of species richness in compared to other subregions of the IAA (e.g., Indochina, Sundaland, Australasia; Figure 4). *Lycodon s.s.* has a wide distribution that ranges from Mauritius, to South Asia, with *L. capucinus* as one of the most wide-ranging snakes throughout Southeast Asia, including the Philippines and

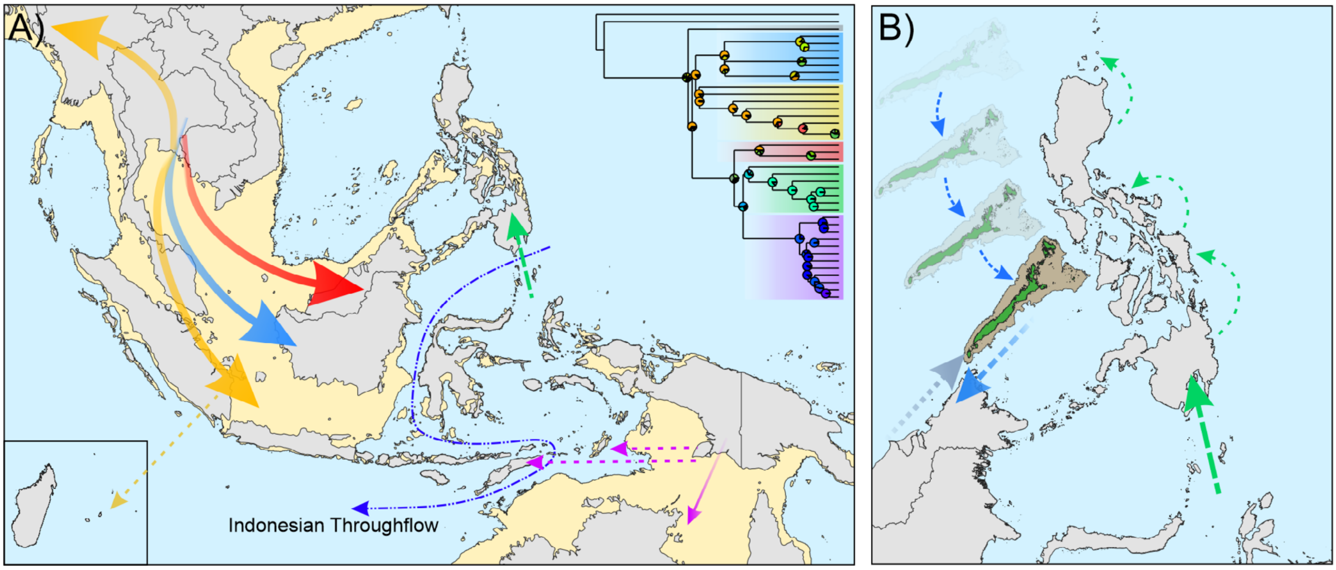

FIGURE 3 | Modes of dispersal in the Indo-Australian Archipelago. (A) Dispersal mechanisms based on phylogenomic species tree (inset). Arrows are coloured by clade (blue: *Dinodon*; yellow: *Lycodon s.s.*; red: *Dryocalamus*; green: *Stegonotus s.s.*; purple: *Lielaphis*). Solid arrows represent land-bridge facilitated migrations; dashed arrows indicate overwater dispersal (Mauritius inset). The dark blue dotted-dashed line shows the primary current of the Indonesian Throughflow. (B) Dispersal of *Stegonotus* and *Dinodon* in the Philippines. Migration of *Stegonotus* through the southern colonisation route was followed by island-hopping. *Dinodon sealei* arrived through the rafting of the Palawan microcontinental block (solid colour = current geographic position) or through dispersal from Borneo into Palawan (grey dashed arrow).

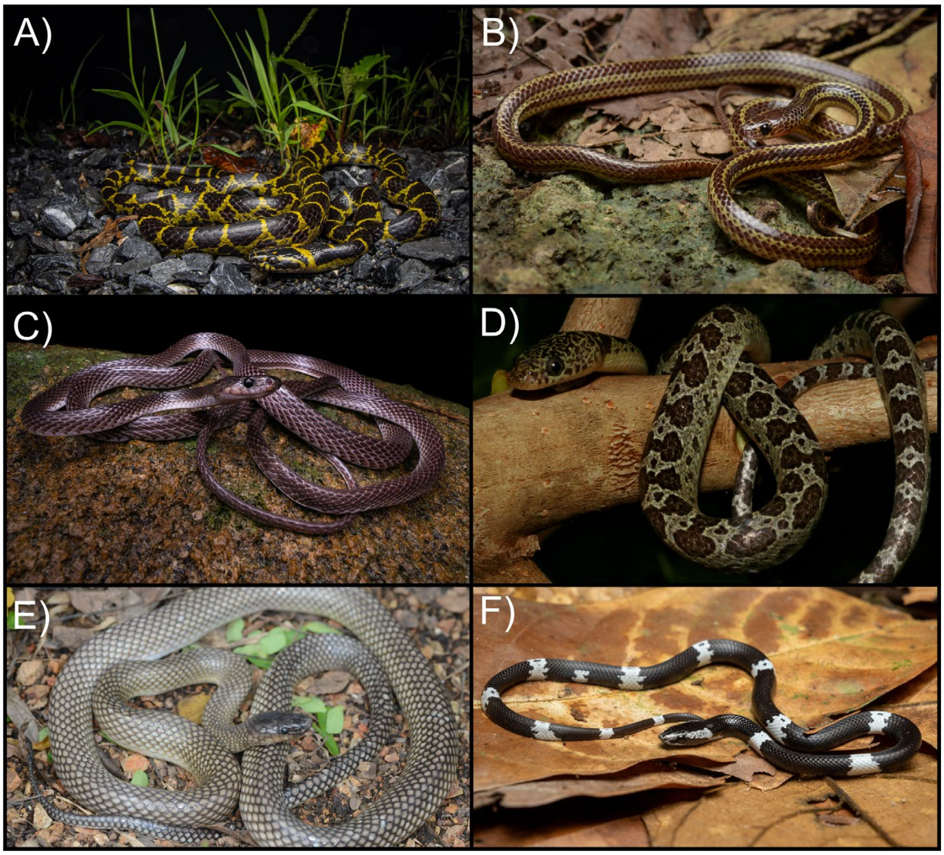

FIGURE 4 | The six genera in this study, showing representative species for each: (A) *Dinodon flavozonatus*. (B) *Dryocalamus tristrigatus*. (C) *Lepturophis albofuscus*. (D) *Stegonotus muelleri*. (E) *Lielaphis reticulatus* (LSUMZ 129283). (F) *Lycodon effraenis*. Photograph credit in panel order: Artur Tomaszek, Chien C. Lee, RajathNJ, Justin M. Bernstein, Christopher C. Austin, Edward Wong.

the Moluccas in Wallacea. Higher species richness estimates were found at higher elevations, with the highest estimates in eastern and western India, Sri Lanka, Bangladesh, Indochina (Cambodia, Laos, Vietnam), northern Philippines and southern Myanmar and Thailand on the Thai-Malay Peninsula (Figures S3–S8). The stacked distribution model for *Dinodon*, primarily distributed in Indochina, East and Southeast Asia (Greater Sunda Islands, Palawan [Philippines] and the Lesser Sunda Islands [Nusa Tenggara] in Wallacea), also predicts higher levels of diversity at higher elevations. This model identifies elevated richness in eastern India and western Myanmar, and the mountainous regions of Vietnam. *Dryocalamus* is restricted to Indochina and the Greater Sundas based on our sampling. Higher levels of modelled richness were observed in lower elevation areas, with the highest diversity estimates on the Thai-Malay Peninsula just south of the Isthmus of Kra, and northern Borneo and Java. *Stegonotus s.s.* is endemic to the Philippines (and Wallacea—*S. batjanensis*), in which models project higher species richness in southern Luzon (the Bicol Region) and central Philippines (Samar and Leyte). Finally, *Lielaphis*, which is restricted to Australia, New Guinea and some Wallacean islands, showed higher numbers of species at lower elevations, with the Central Cordillera of New Guinea identified as having low habitat suitability. Australia, which only has one species of *Lielaphis*, was also identified as a low richness region for this genus. Higher levels of *Lielaphis* diversity were observed in Maluku (Halmahera) and the Southern Region of Papua New Guinea. The ensemble model that was generated for *Lepturophis*, distributed in Sundaland (Thai-Malay Peninsula and Greater Sunda Islands), showed high levels of habitat suitability throughout its range, with the highest values in eastern Malaysia and northern Borneo.

Variable importance calculations from the ensemble models show that temperature and precipitation are important indicators of species richness across these groups. Models of *Dinodon*, *Lycodon*, and *Lielaphis* had isothermality, mean diurnal range and precipitation seasonality as the top three (in decreasing order) most important climatic variables (Table S5). The *Dryocalamus* species richness model was most heavily influenced by isothermality, annual precipitation and precipitation of the driest quarter, and the *Stegonotus s.s.* model by precipitation seasonality, precipitation of the driest quarter and annual precipitation. The *Lepturophis* model also had isothermality as the most important predictor variable, followed by precipitation of the driest month and precipitation of the driest quarter.

4 | Discussion

Diversification paradigms in the Indo-Australian Archipelago have often focused on the cyclic nature of land bridge emergence and submergence in the Pliocene and Pleistocene (de Bruyn et al. 2014; Lohman et al. 2011; Oaks et al. 2022). The rise in genomic datasets has provided evidence of much older divergences that predate the inundation of land bridges (Husson et al. 2020), allowing us to test vicariance and dispersal hypotheses from alternative geological influences (Salles et al. 2021). Our study is the first investigation of snakes across the entire IAA, and our results reveal deep divergences that not only warrant taxonomic revision but also identify processes beyond Plio-Pleistocene sea-level fluctuations that shape species distributions. We outline these processes below as alternative hypotheses for subsequent researchers to test.

4.1 | Mechanisms of Dispersal and Diversification in the IAA

4.1.1 | Ancestral In Situ Diversification in East and Mainland Southeast Asia

Our phylogenies support several biogeographic modes of colonisation that explain extant diversity and species distributions across the IAA. Of note, this entire lineage of colubrid snakes has reached its current distributions through overwater dispersals past major biogeographic barriers. As seen in many families of snakes (Bernstein et al. 2023; Deepak et al. 2021; Weinell et al. 2024), the ancestral lineage of *Lepturophis*, *Dinodon*, *Dryocalamus*, *Lycodon s.s.*, *Stegonotus s.s.* and *Lielaphis* originated in Mainland Southeast and East Asia, and Sundaland, when Cenozoic land bridges connected these regions (Hall 2009; Husson et al. 2020). Although it is difficult to determine the exact mechanisms that led to the in situ diversification within this region for *Dinodon* and *Lycodon s.s.* (Figure 2), many geological changes, like tectonic uplift events (Bernstein et al. 2024) and formation and structural changes in drainage basins (Cheng and Faidi 2025) and paleorivers have impacted faunal population dynamics. The roles of river courses, in particular, in shaping biodiversity has long been proposed (Wallace 1854). At the beginning of the Miocene, many of the major rivers in Mainland Southeast Asia changed courses (Lacassin et al. 1998). Some of Asia's largest rivers, such as the Mekong, Salween, Siam and Ayeyarwady Rivers have undergone river catchment/capture events, drained into different basins over time, and/or changed in volume between the Miocene and post-Pleistocene (Carbonnel 1965; Hutchison 1989; Lacassin et al. 1998; Robinson et al. 2014). Corridors and barriers to migration have formed from these paleo-riverine dynamics (Salles et al. 2021) and facilitated diversification in terrestrial vertebrates with low to moderate dispersal capabilities (Klabacka et al. 2020; Lukoschek et al. 2011; Meijaard and Groves 2006). We identify that some of these lineages (*Dinodon*) dispersed into East Asia and diversified in the late Miocene (~5–8–7.5 mya; Figure S1). East Asia has several topographic formations, like the Qinghai-Tibetan Plateau (QTP), that exhibit high levels of diversity that arose due to colonisation events and in situ speciation due to tectonic uplift (Favre et al. 2015; Yang et al. 2009). The Hengduan Mountains had reached near-present elevations by the late Eocene or early Oligocene (Spicer et al. 2025), and there is evidence that rates of in situ diversification of flora have increased significantly more in this region than by nearby mountains (Xing and Ree 2017). The Hengduan Mountains, as well as the Himalayas, have become cradles of biodiversity due to various processes (Feijó et al. 2022; Liu et al. 2016). Our *Dinodon* EDSMs (see *Discussion*: *Environmental Correlates of Species Richness*) estimate the highest patterns of species richness in eastern India and northern Myanmar at the borders of the QTP, Hengduan Mountains and Himalayas (Figure 4). It is possible that the formations of mountains or presence of mountains that have been long present have helped shape present-day species distribution patterns. In addition to vicariant processes arising due to rivers and geological uplift, we also identify range expansions facilitated through Cenozoic land bridges.

4.1.2 | Cenozoic Land Bridges and Range Expansion

Southeast Asia and Australasia show the greatest extent of Cenozoic land bridge by area in the world. Inundation and emergence of these land bridges occurred both ephemerally and cyclically (Chappell and Shackleton 1986; de Bruyn et al. 2014; Voris 2000) and for long spans of time (millions of years; Husson et al. 2020). We find that several species of *Lepturophis* (*L. albofuscus*), *Dinodon* (*D. subcinctus*; *D. sealei*), *Dryocalamus* (*D. tristrigatus*; *D. subannulatus*) and *Lycodon s.s.* (*L. capucinus*; *L. effraenis*) have dispersed between Mainland Southeast Asia and the Greater Sunda Islands throughout the Miocene, and, though to a much lesser extent, between New Guinea and Australia (*Lielaphis australis*; Figure 2; Figure 3A). Historical land bridge dispersal events between the mainland and islands in the IAA during sea-level minima are one of the most significant biogeographic paradigms of distribution patterns in the region (Jiang et al. 2019; Li and Li 2018; Othman et al. 2020; Tougard 2001; Wüster et al. 2005). Our finding of Southeast Asian origins for many South Asian species (Figure 2) supports previous studies on snakes and plants (Bernstein et al. 2023; Liu et al. 2021). We emphasise the importance of Southeast Asia (including the IAA) as acting as a species source for adjacent biogeographic realms. Our study expands on knowledge gaps of IAA dispersal patterns in understudied groups, particularly snakes. We do not find sea-level fluctuations as the primary drivers for species diversity, and we provide data and findings for future studies investigating how different historical land bridge connections might influence diversification and genetic patterns (Cros et al. 2020).

4.1.3 | Crossing the Line(s) and Island Hopping Through Asia

Some of the most famous demarcations of faunal boundaries are present in the IAA, namely Wallace's and Huxley's lines (Huxley 1868; Müller 1846; Wallace 1863) through the Lombok Strait (between Bali and Lombok) and Makassar Strait (between Borneo and Sulawesi), and Lydekker's Line (Lydekker 1896) delineating Wallacea and the Sahul Shelf (but see Ali and Heaney 2021) (Figure 1). These lines were originally described to demarcate turnovers between Asian and Australian assemblages, resulting in the description of Wallacea as a transition zone (Dickerson 1928). Wallacea was never connected to the Sunda Shelf, even at sea-level minima at the Last Glacial Maximum (Voris 2000). Crossing the deep Makassar Straight over Wallace's Line, which has been supported for several groups in prior studies (Bernstein et al. 2023; Brodie et al. 2018; Letsch et al. 2020), allowed species to enter the Wallacean realm of smaller, lower-area, more isolated, scattered islands. Interestingly, crossing Wallace's line has been linked to tolerance in precipitation (Skeels et al. 2023), which was among the most important climatic factors in all genera analysed in this study (Table S5). Our ancestral range estimations suggest that the movement of these lineages (*Stegonotus s.s.* + *Lielaphis*) into Wallacea opened opportunities for further dispersal into the adjacent regions of the Philippines and Australasia, with subsequent diversification.

As lineages dispersed through Wallacea, the common ancestor of *Stegonotus s.s.* entered the Philippines through the southern colonisation route (Figure 3B), via the Wallacean Islands (Brown, et al. 2013), evidenced by *S. batjanensis* (endemic to Maluku) being recovered as the sister taxon to all other *Stegonotus s.s.* (endemic to the Philippines; Figure 2). The Philippines has four major colonisation pathways into the archipelago (Brown and Siler 2013; Diamond and Gilpin 1983)—north: Taiwan; two island arcs/chains form 'umbilici' from the west (Brown and Guttman 2002): Palawan and the Sulu Archipelago; south: Wallacea. A majority of colonisation scenarios in the Philippines have Mainland Southeast Asian origins and have occurred through the southwestern umbilici (Brown, et al. 2013), with only few studies finding evidence of dispersal into the Philippines from Wallacea (Evans et al. 2003; Jones and Kennedy 2008; Setiadi et al. 2011). Our recovery of *S. batjanensis* as the sister to all other Philippine species supports long-standing hypotheses that small islands in Wallacea, like Sangihe and the Talaud Islands, might serve as entry ways into the Philippines (Diamond and Gilpin 1983; Dickinson et al. 1991; Inger 1954). We identify subsequent dispersal and in situ diversification as lineages within *Stegonotus s.s.* island hopped from the southern to northern Philippines over the last ~10 million years during periods of high tectonic movement as islands arranged themselves into their current geographic configuration (Hall 1996, 2009; Yumul et al. 2008) (Figure 3B). Although we identify more ancient processes that explain species distributions and diversity, land bridges in the Philippines during the Pleistocene likely explain population structure at shallow timescales. It is very likely that Pleistocene sea-level fluctuations also facilitated movement through the archipelago when island groups were connected to one another (Pleistocene Aggregate Island Complexes [PAIC]; Brown and Diesmos 2009; Heaney 1985). This stepping-stone dispersal through the Philippines terminated at the northernmost island group in the archipelago, the Babuyan Islands, in the Pliocene (Figure 3B). We note that greater geographic sampling is needed to identify inter- and intra-PAIC (e.g., Mindanao, Samar and Leyte) relationships and dispersal patterns within the Philippines. We also acknowledge that additional sampling from Borneo, which harbours other species not sampled here (e.g., *S. caligocephalus*), would clarify if *Stegonotus s.s.* have used other dispersal routes into the Philippines, such as Palawan or the Sulu Archipelago. However, our results provide insight into evolutionary patterns across these islands. The Philippines is known for its rich and endemic fauna, especially amphibians and reptiles, with the documented herpetofaunal diversity growing each year (Meneses et al. 2024). The only endemic snake genera in the Philippines are *Hemibungarus* and cyclocorid snakes (Weinell and Brown 2018). Although *Stegonotus batjanensis* is distributed outside the archipelago, our finding of *Stegonotus s.s.* diversifying within the Philippines further demonstrates the autochthonous endemicity of many elements in Philippine herpetofauna.

We find an increase in speciation during the Miocene, when the ancestor of *Stegonotus s.s.* dispersed out of Wallacea and into the Philippines (~11 mya; Figure S1). We also observed increased speciation in the common ancestor of *Lielaphis* upon arrival into

New Guinea (Figure 2). Only ~10% (10 species) of all *Lepturophis*, *Dinodon*, *Dryocalamus*, *Lycodon s.s.*, *Stegonotus s.s.* and *Lielaphis* are found in Wallacea. Speciation was low in Wallacea until colonisation of island-rich archipelagos (Philippines; *Stegonotus s.s.*) or large land masses (New Guinea and Australia; *Lielaphis*). The lack of land bridges and the small size of Wallacean islands likely explain the lower levels of diversity in this region. These islands have remained small throughout their geological history, and the largest, Sulawesi, only attained its current size in the last 3–5 million years from the amalgamation of smaller paleo-islands (Nugraha and Hall 2018).

Our findings suggest that Wallacea served primarily as a conduit for eastward dispersal through Southeast Asia (Reilly et al. 2022). However, the species that are found in Wallacea are often endemic to single islands or island groups. Ancestral range analysis on our species tree identifies multiple back-dispersals of *Lielaphis* over Lydekker's Line into Wallacea during the Pliocene, ~3–4 mya (Figure 2), resulting in single-island endemics. These founder event scenarios represent interesting systems for future studies investigating dispersal capabilities across physical geographic barriers in reptiles. The Indonesian Throughflow (ITF) is a strong current that arises due to the imbalance in sea level between the Indian and Pacific Oceans, causing water to flow through and around the Lesser Sundas (Godfrey 1996). This current may represent a barrier between Australia and Wallacea (Karin et al. 2020), but we find that *Lielaphis nancuro* (Timor-Leste) and *L. keyensis* (Kei Islands) may have dispersed over the ITF. Our results do not resolve whether these species crossed Lydekker's Line (and the ITF) from New Guinea or from Australia, and thus finer-scale studies are needed.

4.1.4 | Long-Distance Dispersal and Microcontinental Rafting

Our results support prior studies that show short- and long-distance dispersals in the IAA (Grismer et al. 2022; Kuhnhäuser et al. 2025; Linkem et al. 2013; Reilly et al. 2023, 2025; White et al. 2021). Of all genera in this study, only *Lycodon* extends its range beyond the Himalayas and further into South Asia. We identify the geographic origin of *Lycodon* in Southeast Asia (Figure 2), with expansion into South Asia. However, with our current sampling limited to Mauritius, we are unable to determine the mechanism of dispersal (e.g., westward expansion through South Asia or long-distance dispersal). The migration of *Lycodon s.s.* into Mauritius is only represented by *L. aulicus*, where we recover a divergence of ~6.1 mya, but more sampling of these lineages are needed to examine population structure that would pinpoint how these they ended up at their present-day distributions and if it was through natural (e.g., rafting) or human-mediated dispersal. In the case of a long-distance rafting scenario, this would have had to occur over a distance of ~4000 km (Figure 3A). Although this spans a great distance, dispersals of greater distances have been inferred in recent systematic studies of iguanas in Madagascar (Welt and Raxworthy 2022) and Fiji (Scarpetta et al. 2025), with the latter involving long-distance dispersal of more than 8000 km. Additionally, an alternative hypothesis is that *L. aulicus* dispersed into South Asia (e.g., Indian subcontinent; absent in our sampling) and subsequently got to Mauritius from a long-distance dispersal event. With our current sampling, we refrain from suggesting a particular scenario of dispersal as our divergence date reflects lineage diversification of our included samples and may not be the date of dispersal to Mauritius. Future work should focus on filling in taxonomic and geographic sampling gaps of South Asian *Lycodon* species and populations to confirm or refute these biogeographic inferences.

We find that land bridges and rafting scenarios were important dispersal mechanisms in the early evolutionary phases of this group. We find that all *Stegonotus s.s.* lineages in the Philippines diversified through island hopping. However, one other species, *Dinodon sealei*, is endemic to one of the western Philippine umbilici, Palawan (Figure 1). Surprisingly, we find *D. sealei*, to be distantly related from the Philippines-endemic *Stegonotus s.s.*, a result that might reflect the geological history of their known distributions. Faunally, the Palawan island group has allied with islands in Sundaland in some studies (Boulenger 1984b; Brown and Alcala 1970; Esselstyn et al. 2004; Everett 1889, but see Esselstyn et al. 2010), a pattern which led to Huxley modifying Wallace's line to wrap around Palawan (Huxley 1868). These faunal relationships are rooted in Palawan's geological origins; the Palawan group is comprised of old continental crustal rock and recent oceanic crust which has drifted away from the South China continental crust of the mainland during the mid-Oligocene to early Miocene (32–17 mya; Hall 2002; Heaney 1986; Holloway 1982; Taylor and Hayes 1980) (Figure 3). It is likely that *D. sealei* and *D. subcinctus* had diverged from their common ancestors in Mainland Southeast Asia, and rafted to their current distribution in the late Miocene (Figure 2; Figure 3B). *Dinodon subcinctus* is found on the mainland, as well as the Greater Sunda Islands (Borneo), and more sampling is needed to look at population-level relationships of *D. subcinctus* and *D. sealei* (the former of which we find the Borneo samples are likely *D. sealei*; Figure S1), to better understand the divergence times and mode of dispersal. Our results are supportive of the 'Palawan Ark Hypothesis' (Blackburn et al. 2010; Hall 2002), as has been found for other species groups (Blackburn et al. 2010; Brown et al. 2016; Esselstyn et al. 2004; Siler et al. 2012), but future studies that include more samples might find support of alternative hypotheses, such as Borneo origins and dispersal into Palawan (Figure 3B).

4.2 | Environmental Correlates of Species Richness

We used ensemble niche models to test if Wallacea was environmentally less suitable across all genera in this study, and to identify potential areas of high diversity. Our ESDMs yielded no broad patterns that would identify Wallacea as a climatically poor region for species richness (Figures S3–S8). This might indicate that the smaller land area and absence of land bridges in Wallacea are contributing factors to the lower species-level diversity in this region. Despite this, we identify patterns of species richness broadly consistent with the known distributions of each genus and related environmental factors (see Figures S3–S8 for individual models and regions of high estimated species richness). Our assessments of variable importance for the ESDMs identify precipitation as an important factor predicting species richness (Table S5). Environmental correlates (including precipitation) to species richness and diversification have been identified for most vertebrate groups, including reptiles (Lewin et al. 2016; Qian 2010; Soares and Brito 2007), and can impact dispersal into new regions (Skeels et al. 2023). The IAA consists of a wide range of low- and high-elevation habitats, and land masses with large differences in land area (Philippines: ~116,000 km^2; Wallacea: ~347,000 km^2; Sundaland: ~1.85 million km^2; Sahul: ~10.6 million km^2), creating an environmentally heterogenous archipelago due to latitudinal and topographic effects on climate, especially seasonality of monsoons (Dalsgaard et al. 2014). Such environmental heterogeneity has historically impacted distributions (Myers et al. 2019), particularly in Southeast Asia when tropical rainforests expanded from and contracted into refugia during sea-level oscillations and when savanna corridors were widespread through Sundaland (Bird et al. 2005). Floral demarcations in Southeast Asia have become known biogeographic barriers, such as the Isthmus of Kra and Kangar-Pattani Line (Parnell 2013; van Steenis 1950). Our niche models show that *Lepturophis* and *Dinodon* have higher habitat suitability and species richness estimates south of the Kangar-Pattani Line and north of the Isthmus of Kra (Figures S3 and S4), respectively, and *Dryocalamus* has greater estimates between these two geographic features (Figure S5). Many floral and faunal species have their northern or southern limits at these boundaries (Chai et al. 2025; De Bruyn et al. 2005; Hinckley et al. 2020; Hughes et al. 2011, 2003), which are associated with changes in climatic zones, geological history and community composition of ecosystems (Hughes et al. 2011; Parnell 2013). In addition, we find that elevation plays an important role in shaping distributions in the IAA. Although we did not include elevation as a layer in our niche models, we find evidence that genera like *Lielaphis* and *Dryocalamus* have lower habitat suitability at higher elevations (Figures S5 and S6), whereas *Lycodon s.s.* and *Stegonotus s.s.* have their highest species richness estimates in regions of high-elevation, mountainous terrain (Figures S7 and S8). This shows that both geological history and the environment are not mutually exclusive factors in explaining diversity and distributions. Dramatic geological shifts and topographic changes can alter local and regional climates and population structure at biogeographic barriers can also reflect differences in the environment, not just the barrier itself (Meijaard and Groves 2006; Yuan et al. 2016).

Lastly, the timing of colonisation events can have a large impact on subsequent community diversity levels and species richness patterns (Liu et al. 2021). Most likely, the distributions of these snakes in the IAA were formed due to a combination of complex geological histories and environmental conditions (Woodruff 2010). Indeed, ecological niche models for predicting species distributions are influenced by a variety of factors, both biological (e.g., occurrence data) and methodological (sampling effort, sample bias, model parameters, algorithm, data errors). We take an ensemble niche modelling approach to account for variation obtained through different model algorithms. Our ensemble models had high overall and individual AUC and kappa values (Table S4) and did not result in any richness predictions that were questionable when considering the extant species distributions. We acknowledge that our approach is heavily reliant on publicly available data and thus took a conservative approach of only using research-grade observations (iNaturalist) and/or vouchered specimen locality data from natural history collections. Additionally, we used only a subset of the known diversity of *Lepturophis*, *Dinodon*, *Dryocalamus*, *Lycodon s.s.*, *Stegonotus s.s.* and *Lielaphis* to remain conservative while interpreting our niche models. Downstream research would benefit from the inclusion of occurrence data from additional species once available (and greater taxon sampling in subsequent phylogenetic reconstruction). Many of the taxa in these genera are known from very few samples. For example, in this study, only 23 of the 59 unsampled *Lycodon s.l.* and 2 of the 18 unsampled *Stegonotus s.l.* have enough occurrence records to include in the niche modelling analyses, with most species having 0–9 occurrence records. With more species sampled in future studies, this may improve model performance, as we found that Maxent consistently performed poorly in our analyses (Table S4), likely due to overfitting of data. We find that, for all algorithms and genera, Maxent had a ~50% rate of model specificity, but high model sensitivity. This indicates that Maxent can likely detect species occurrences but is underestimating species richness in regions with lower estimated richness values. Additionally, the Cohen's kappa values (which range from −1 to +1) for *Dryocalamus* and *Stegonotus s.s.* were greater than +1; while a high kappa value represents high model agreement, this inflated value might also suggest overfitting of the models.

Nonetheless, we note that our occurrence records from multiple taxa span across all bioregions (and subregions within) based on other faunal groups in the IAA (Oong et al. 2026), capturing the environmental heterogeneity across landscapes. Additionally, our stacked model approach combines several ensemble models of different species into a single stack; if a species is not sampled, another species that lives in that region for which we have records for will still provide habitat suitability information to the stacked model, providing a level of robustness to our framework. Overall, our AUC values and agreement of species richness estimates with the known distributions of these genera make us confident in the interpretation of our models.

4.3 | Taxonomy in Light of Genomics

In this study, we focus on the biogeography of several lineages previously included in *Lycodon s.l.* and *Stegonotus s.l.* The non-monophyly of both genera, however, means taxonomic revision is necessary to better reflect the evolutionary history and biogeography of these snakes. As we could only include 38 of the 107 species presumed from this entire group, we recommend our phylogeny be used as a baseline for which to add molecular data of additional, unsampled species as they are obtained. We resurrect and reorganise the following taxa for *Lycodon s.l.* and *Stegonotus s.l.*: *Lepturophis* Boulenger, 1900—*Lepturophis albofuscus*; *Dinodon* Duméril, Bibron & Duméril, 1854—*Dinodon flavozonatus*, *Dinodon septentrionalis*, *Dinodon ruhstrati* comb. nov., *Dinodon sealei* comb. nov., *Dinodon subcinctus* comb. nov., *Dinodon fasciatus* comb. nov., *Dinodon gongshan* comb. nov.; *Dryocalamus* Günther, 1858—*Dryocalamus davisonii*, *Dryocalamus tristrigatus*, *Dryocalamus subannulatus*; *Lielaphis* Günther, 1863—*Lielaphis derooijae* comb. nov., *Lielaphis diehli* comb. nov., *Lielaphis melanolabiatus* comb. nov., *Lielaphis aplini* comb. nov., *Lielaphis iridis* comb. nov., *Lielaphis admiraltiensis* comb. nov., *Lielaphis heterurus* comb. nov., *Lielaphis guentheri* comb. nov., *Lielaphis nancuro* comb. nov., *Lielaphis keyensis* comb. nov., *Lielaphis australis* comb.

nov., *Lielaphis reticulatus* comb. nov.; *Lycodon Fitzinger*, 1826—*Lycodon stormi*, *Lycodon effraenis*, *Lycodon laoensis*, *Lycodon jara*, *Lycodon zawi*, *Lycodon aulicus*, *Lycodon capucinus*; *Stegonotus* Duméril, Bibron & Duméril, 1854—*Stegonotus muelleri*, *Stegonotus philippinensis* comb. nov., *Stegonotus alcalai* comb. nov., *Stegonotus chrysoprateros* comb. nov., *Stegonotus bibonius* comb. nov., *Stegonotus solivagus* comb. nov.; (Fig. 4). This paper is registered for nomenclatural purposes under Zoobank urn:lsid:zoobank.org:pub:6BAE4B4A-B5B5-4B95-8F49-AC58F974D26D. The genera *Lepturophis*, *Dinodon* and *Dryocalamus* are considered valid taxa by Wallach et al. (2014), but are not often used in current research compared with *Lycodon*. Our study is not the first to suggest genus-level revisions of these snakes. The synonymisation of *Lepturophis* and *Dyrocalamus* with *Lycodon* by Figueroa et al. (2016) is considered premature and consisted of sampling with divergent lineages that may require future taxonomic revision (Wostl et al. 2017; Vogel and David 2019). Morphology also suggests the distinct nature between genera (Günther 1864; Pauwels et al. 2006; Wickramasinghe et al. 2020), and molecular studies have reconstructed phylogenies that support the distinctiveness of these genera (Zaher et al. 2019). Our study is the first to provide genomic evidence, which helps to resolve long-standing taxonomic debates of these lineages. Considering the deep divergences found here (minimum *cytochrome-b* divergence [~1100 bp] between revised genera = 14.7%), and regional distributions of these taxa, distinct genera for these snakes is warranted and we encourage others studying these groups to use this more phylogenetically accurate taxonomy.

Indeed, accurate taxonomic revision requires sampling of the type species of the respective genera. Our revision is supported by the inclusion of several type species in our sampling and their recovery as distinct linages from each other: *Lepturophis* (*L. albofuscus*), *Lycodon s.s.* (*L. aulicus*), *Dryocalamus* (*D. tristrigatus*), *Stegonotus s.s.* (*S. muelleri*) and *Lielaphis* (*L. modestus*). Our *post hoc* phylogenetic analysis of *L. modestus*, while having weak support at deeper notes, recovered this species with strong support as part of the Australasian clade previously referred to as *Stegonotus s.s.*, supporting the Australasian+Wallacean clade as *Lielaphis* (Figure S9). Unfortunately, we could not get samples of *D. rufozonatus*, the type species of *Dinodon*. The taxonomic stability of *Dinodon* and *Lielaphis* will benefit if future works include modern samples for type species in subsequent phylogenetic efforts.

Our phylogenetic trees (Figure S1) also indicate taxonomic changes at the species level are needed for a few taxa in the Philippines. *Lycodon dumerilii* Boulenger, 1893 was found in the *Stegonotus muelleri* Duméril, Bibron & Duméril, 1854 clade, supporting that these two species are the same taxon. Furthermore, our generic revision and assignment of all Philippines lineages to the genus *Stegonotus s.s.* (except *Dinodon sealei*) necessitates further revision—this taxonomic change of *Lycodon muelleri* Duméril, Bibron & Duméril, 1854 results in a case of secondary homonymy with *Stegonotus muelleri* Duméril, Bibron & Duméril, 1854. Boulenger (1893:368) likely found *Lycodon muelleri* Duméril, Bibron & Duméril, 1854 as a distinct taxon that should be in the genus *Stegonotus s.l.* However, the name *Stegonotus muelleri* was already in use (*S. muelleri* Duméril, Bibron & Duméril, 1854)—to avoid secondary homonymy, Boulenger (1893) likely named *Stegonotus dumerilii* as a replacement name. Thus, we synonymise *L. dumerilii* Boulenger, 1893 with *S. muelleri* Duméril, Bibron & Duméril, 1854. To avoid secondary homonymy due to genus-level revisions, we designate the population previously considered *Lycodon muelleri* Duméril, Bibron & Duméril, 1854 to *S. philippinensis* comb. nov. (Griffin, 1910). Following the distributions of Leviton et al. (2018), we restrict *S. philippinensis* comb. nov. to populations on the islands of Batan, Catanduanes, Luzon, Marinduque, Mindoro and Polillo, and *S. muelleri* to the islands of Basilan, Dinagat, Leyte, Mindanao, Samar, and Siargao.

5 | Conclusions

The Indo-Australian Archipelago and its mosaic of geological histories, topographies, climatic zones and faunal and floral communities make it a model system for studying insular evolutionary dynamics (De Bruyn et al. 2005; Lohman et al. 2011). We show here that the divergences among *Lepturophis*, *Dinodon*, *Dryocalamus*, *Lycodon s.s.*, *Stegonotus s.s.* and *Lielaphis* predate the more recent Plio-Pleistocene inundation of Cenozoic land bridges. We emphasise the importance of six modes of oceanic landmass colonisation, ancient geological processes, diverse topographic features and environmental conditions that have generated biodiversity and regional distribution patterns in the IAA—all of which allows us to confidently reject the major predictions of the single (or few) shared mechanisms paradigm and the species pump model of diversification as providing sufficient explanatory power to understand this remarkable radiation of snakes. It is important to note that our results and interpretations do not mean that Plio-Pleistocene sea-level fluctuations had no impact on diversity and distributions. Several studies have found that biodiversity is highly correlated to historic land connectivity or estimated migration events during times of land bridge reemergence (Wüster et al. 2005; Chan et al. 2020; Bernstein et al. 2021; Shiba 2021; Prasetya et al. 2023). We encourage more population-level studies with dense sampling to more accurately identify how these land bridges impacted faunal assemblages in the IAA at shallow time scales.

We acknowledge that our sampling of these genera is incomplete in our study, with our species-level representation at 29% of *Lycodon s.l.* and 58% of *Stegonotus s.l.* (these percentages are greater, though, after generic revision). Although more sampling will be needed to determine the taxonomic identity of lineages at the generic level, our study provides a base phylogeny to aid in systematic and taxonomic efforts of *Lepturophis*, *Dinodon, Lycodon, Dryocalamus, Stegonotus* and *Lielaphis* for further taxonomic and biogeographic hypothesis testing. The number of species for *Lycodon* in particular increases each year based on single gene/loci datasets with mitochondrial data (Naveen et al. 2025; Nguyen, Poyarkov, et al. 2025; Nguyen, Lee, et al. 2025). While these studies are valuable for species richness estimates of these snakes, taxonomic instability may persist if species are described as *Lycodon* but are more closely related to a different genus (i.e., *Dinodon, Dryocalamus, Lepturophis*). Our phylogeny consists of the most comprehensive sampling of these genera to date. Additionally, our reconstruction was performed using thousands of publicly available nuclear loci which have aided in resolving topologies that were difficult to resolve using mitochondrial data (Bernstein et al. 2023;

Roberts, Kraus, et al. 2024; Roberts, Bernstein, et al. 2024). Indeed, morphological diagnostic characters are prevalent in the literature for some of these taxonomic groups. Subsequent research investigating morphology with dense sampling schemes would benefit the taxonomic efforts of the genera in this study. Finally, future studies at the population level would provide greater resolution of some biogeographic scenarios that we are unable to test here due to sampling (e.g., *D. sealei* on Palawan and Borneo; dispersal of *Lycodon* to Mauritius).

Despite sampling gaps, our included taxa and use of publicly available data have expanded our knowledge of IAA biogeography. While public occurrence records must be curated prior to analyses and handled with caution, our use of these records provides insight into climatic factors towards species distributions across the IAA. Indeed, the use of patterns in genomic and climatic data as evidence of specific geological influences on speciation must be considered carefully (Fu and Wen 2023); high-resolution genomic data with fine-scale population level sampling is needed for greater confidence in testing biogeographic hypotheses, as is the inclusion of both speciation and extinction processes (Herrera-Alsina et al. 2024). This will be particularly important for islands which are undersampled (e.g., Borneo). Overall, we provide a baseline phylogeny and identify biogeographic patterns, as well as formulate hypotheses, to be tested in subsequent evolutionary works involving these taxa in this model archipelago.

Author Contributions

All contributions are stated under Contribution Roles Taxonomy (CRediT). Justin M. Bernstein: conceptualisation; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; visualisation; writing – original draft preparation. Christopher C. Austin: conceptualisation; funding acquisition; investigation; project administration; resources; validation; writing – reviewing and editing. J. Angel Soto-Centeno: formal analysis; methodology; writing – reviewing and editing. Tianqi Huang: writing – reviewing and editing. Jackson R. Roberts: resources; writing – reviewing and editing. Jimmy A. McGuire: resources; writing – reviewing and editing. Djoko T. Iskandar: resources; writing – reviewing and editing. Bulisa Iova: resources; writing – reviewing and editing. Jeffrey H. Frederick: resources; writing – reviewing and editing. Marites B. Sanguila: resources; writing – reviewing and editing. Jeffrey L. Weinell: investigation; resources; writing – reviewing and editing. Rafe M. Brown: funding acquisition; investigation; resources; writing – reviewing and editing. Sara Ruane: conceptualisation; funding acquisition; investigation; project administration; supervision; validation; writing – reviewing and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw sequence data (target capture) for this project has been submitted to NCBI's Sequence Read Archive under BioProject ID PRJNA1337899 (outgroups for this study under BioProject ID PRJNA790029). Publicly available data (e.g., GBIF) DOIs are provided in Table S2. All relevant code and scripts for analyses are on JMB's GitHub (DOI: 10.5281/zenodo.17245566).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Details on library preparation and genomic sequencing for this study. **Figure S1:** Concatenated phylogeny (revised taxonomy), concatenated phylogeny (previous taxonomy), species tree and time-calibrated phylogeny. **Figure S2:** Ancestral range estimation results for the best-fitted models (DEC and DEC + J) from *BioGeoBEARS*. **Figure S3:** Ensemble niche model for *Lepturophis*. Map on the left shows sampling included in the ensemble species distribution model (ESDM). Points in map represent occurrence records. Species-specific occurrence dataset DOIs are found in Table S2. Results of the ESDM are shown in the species richness map on the right. **Figure S4:** Ensemble niche model for *Dinodon*. Map on the left shows sampling included in the ensemble species distribution model (ESDM). Points in map represent occurrence records; all species are various shades of the same colour—species-specific occurrence dataset DOIs are found in Table S2. Results of the ESDM are shown in the species richness map on the right. **Figure S5:** Ensemble niche model for *Dryocalamus*. Map on the left shows sampling included in the ensemble species distribution model (ESDM). Points in map represent occurrence records; all species are highlighted various shades of the same colour—species-specific occurrence dataset DOIs are found in Table S2. Results of the ESDM are shown in the species richness map on the right. **Figure S6:** Ensemble niche model for *Lielaphis*. Map on the left shows sampling included in the ensemble species distribution model (ESDM). Points in map represent occurrence records; all species are highlighted various shades of the same colour—species-specific occurrence dataset DOIs are found in Table S2. Results of the ESDM are shown in the species richness map on the right. **Figure S7:** Ensemble niche model for *Lycodon*. Map on the left shows sampling included in the ensemble species distribution model (ESDM). Points in map represent occurrence records; all species are highlighted various shades of the same colour—species-specific occurrence dataset DOIs are found in Table S2. Results of the ESDM are shown in the species richness map on the right. **Figure S8:** Ensemble niche model for *Stegonotus*. Map on the left shows sampling included in the ensemble species distribution model (ESDM). Points in map represent occurrence records; all species are highlighted various shades of the same colour—species-specific occurrence dataset DOIs are found in Table S2. Results of the ESDM are shown in the species richness map on the right. **Figure S9:** Maximum likelihood gene tree using cytochrome-b for a subset of individuals in this study, focusing on *Lielaphis*. Numbers at divergences represent ultrafast bootstraps. Scale bar in substitutions per site. *Lielaphis modestus* RMNH43599 is the type species of the genus. **Table S1:** Metadata for specimens used in this study. Taxonomic designations before and after this study are provided based on our phylogenomic efforts. Barcode and adapter sequences for bioinformatic processing of ultraconserved elements (UCEs) are provided. **Table S2:** Digital object identifiers (DOIs) from the Global Biodiversity Information Facility (GBIF) for occurrence data downloads in this study. Taxon searched are given as the exact taxonomic search criteria for the DOI; updated genera and species are provided as per phylogenomic results. **Table S3:** (Top) Model statistics for *BioGeoBEARS*. Log-likelihood (LnL), number of parameters (numparams), dispersal rate (d), extinction rate (e), founder-event speciation (jump dispersal) rate (j), corrected Akaike Information Criterion (AICc) and AICc weight are given for each model. The best fitted models are shaded in green. (Bottom) Likelihood ratio test for all models; green shaded row indicates no significant different between the alternative and null models. **Table S4:** Model performance statistics for ensemble species distribution models in this study. Area under the receiving operating characteristic curve (AUC), algorithm sensitivity and specificity and the mean Cohen's Kappa (individual Kappa for *Lepturophis*, the only non-stacked model) are shown. For mean Cohen's Kappa values, the standard deviation is given parenthetically. **Table S5:** Variable importance for ensemble models of *Lepturophis*, *Dinodon*, *Dryocalamus*, *Lycodon*, *Stegonotus* and *Lielaphis*. Mean and standard deviation of variable importance is provided. For *Lepturophis*, axis evaluation is provided.