Limited dispersal and differing evolutionary trajectories across geographically proximate continental and insular regions in an Australasian lizard radiation (*Gehyra*).

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Abstract.

**Introduction**

In biogeographic comparisons between islands and continents, the former have been characterised as both biogeographic dead ends and hotspots of ecological release and innovation (MacArthur, 1967; Whittaker et al., 2017). However, while there is abundant evidence to support these general trends, real-world patterns of dispersal and diversification across islands and continents show considerable nuance and often challenge neat characterisation. For instance, islands can be important sources of diversity for nearby continents (upstream colonisation or reverse colonisation) (Bellemain & Ricklefs, 2008; Jønsson et al., 2011). Likewise, comparisons of key traits such as body size and shape and ecological niche breadth across related insular and continental radiations have emphasised both divergence and overlap, sometimes even within the same radiation (Huie et al., 2021; Patton et al., 2021). The dynamic, complex, and poorly understood geological histories of many island systems can further confound understanding of their role in shaping regional biotas (Whittaker et al., 2017).

The “island continent” of Australia and nearby Melanesia (centred on the world’s largest and highest tropical island of New Guinea) provide opportunities for focused comparison of patterns of biotic radiation and dispersal across geographically proximate continental and insular regions. These two regions share many lineages (Heinsohn & Hope, 2006; Letsch et al., 2023; Mitchell et al., 2014; Pavón-Vázquez et al., 2022; Tallowin et al., 2020), but are also each characterised by their own rich and highly endemic biotas (Joyce et al., 2021; Prasetya et al., 2023). Australia and Melanesia are also dominated by strongly contrasting environments – the former is predominantly arid, flat and relatively temperate; while the islands of Melanesia (and especially New Guinea) are wet, tropical and generally much more mountainous. These two broad areas provide an opportunity to examine the extent to which increasing geographic proximity may or may not enable taxa to overcome environmental differentiation and niche conservatism, and disperse between regions.

The geological history of the islands of Melanesia is complex, and their proximity to the main landmass of Australia has likely varied greatly through time (Harrington et al., 2017; Norvick, 2003). During the Plio-Pleistocene, land bridges repeatedly formed across the Arafura Shelf and linked northern Australia with southern New Guinea, forming the paleocontinent of Sahul and potentially allowing overland dispersal (Heinsohn & Hope, 2006; Jones & Torgersen, 1988; Norvick, 2003). Many taxa show divergences consistent with dispersal across these land bridges, especially in rainforest and savannah lineages (Liang et al., 2024; Oliver et al., 2021; Peñalba et al., 2019; Roycroft et al., 2022). However, this Plio-Pleistocene connectivity likely masks a deeper history of geological differentiation. While the southern portions of New Guinea are comprised of the uplifted northern edge of the northwards moving Australian plate, northern and eastern New Guinea and many nearby islands are derived from terranes and associated archipelagos that have likely been at tropical latitudes, and thus some distance from Australia, for more than 30 million years (Harrington et al., 2017). Biogeographic analyses of many Australasian radiations dating back to the Miocene or earlier also show marked differentiation between Australia and islands to the north (Joyce et al., 2021; Oliver et al., 2022), and evidence for long time periods with limited or no dispersal (Pavón-Vázquez et al., 2022)**.**

Environmental differences between predominantly arid Australia and mesic tropical Melanesia may also have presented an important barrier to successful dispersal, especially from the mid-Miocene to the present (Heinsohn & Hope, 2006). Even radiations that do occur across both regions may show divergent patterns of ecological differentiation. For instance, in agamid lizards, certain ecological niches such as terrestriality are absent in New Guinea but common in Australia (Tallowin et al., 2020), while in dasyurid marsupials, it has been suggested that low seasonality and resource-rich environments in New Guinea have mediated the evolution of larger brains (Weisbecker et al., 2015). If signatures of divergent evolution are found to be pervasive, this would support the hypothesis that environmental differentiation between these two regions may have played a key role in limiting biotic dispersal (Heinsohn & Hope, 2006). However, for most taxa shared between Australia and Melanesia, patterns of evolutionary diversification in the two regions, including eco-morphology, have not been compared.

*Gehyra* is a genus comprising around 70 species of scansorial gecko lizards that is widespread across both Australia (~55 species) and the islands of Melanesia and the Pacific (~17 recognised species). It has been hypothesised that south-east Asia is the ultimate point of origin for this genus (Heinicke et al., 2011), although the contemporary fauna of this region includes only five species (Uetz, 2025). The diversity, biogeography, and macroevolutionary dynamics of *Gehyra* in Australia have been characterised by numerous recent studies (Ashman et al., 2018; Oliver et al., 2019; Sistrom et al., 2013; Sistrom et al., 2009). These have revealed a moderately diverse fauna characterised by exceptional levels of cryptic lineage diversity (Kealley et al., 2018; Oliver et al., 2020; Sistrom et al., 2013), morphological conservatism in most aspects except body size (Moritz et al., 2018)**,** and limited ability to disperse between major monsoonal and arid biomes (Ashman et al., 2018).

In contrast, lineage diversity and biogeographic patterns in Melanesian *Gehyra* remain much more poorly known. Recent taxonomic work has increased known diversity (Kraus, 2024; Kraus et al., 2024) and preliminary estimates of divergence times point to the presence of deeply divergent lineages in Melanesia (Heinicke et al., 2011; Oliver et al., 2016). A notable feature of Melanesian *Gehrya* is a suite of species that show relatively large body sizes, especially when compared against *Gehyra* from Australia and Asia (SVL >130 mm and up to nearly 160 mm, versus a maximum of usually <90 mm). The evolution of particularly large-sized taxa has occurred in several island radiations of gekkonids (Heinicke et al., 2023; Oliver et al., 2014; Skipwith & Oliver, 2023), raising the possibility that large *Gehyra* may be showing a differing evolutionary regime to their continental relatives.

Here we aim to a) understand patterns of dispersal in *Gehyra* across continental Australia and insular Melanesia with a particular focus on assessing support for contrasting broader biogeographic narratives of high or low connectivity between these two regions, and b) to contrast patterns of evolutionary diversification in body size, with a particular focus on the evolution of “giant” species of Melanesia. To undertake these analyses, we first assembled an expanded mitochondrial genetic sampling of taxa from the poorly known Melanesian region and used this to identify divergent lineages. We then collected exon-capture data for these samples and combined this with recently published data for Australian taxa to generate a robust tree for Australasian *Gehyra*. This tree was then used to infer and contrast patterns of dispersal and body size evolution across Australasia using Bayesian approaches.

**Methods**

**Taxon sampling and lineage diversity in Melanesia**

Australian *Gehyra* have been the focus of extensive taxonomic work over the last decade, resulting in the description of numerous new species, and the elucidation of additional lineage diversity within nominal species. A phylogenomic tree including the vast majority of recognised species of Australian *Gehyra,* plus divergent intraspecific lineages based on exon-capture data, has also recently been made available (Lau et al., 2024).

Melanesian *Gehyra* have also been the focus of some recent taxonomic work (Kraus, 2024; Kraus et al., 2024; Oliver et al., 2016; Skipwith & Oliver, 2014), however they remain more poorly known. For an initial assessment of evolutionary diversity in Melanesian *Gehyra* we sequenced the full mitochondrial ND2 gene. For these analyses our sampling of *Gehyra* from Melanesia and other regions outside of Australia included 154 unique individuals, of which the majority were newly sequenced in this study (Additional file 1). Within the mitochondrial dataset, we used the divergence between lineages in the *Gehyra oceanica* group that have elsewhere been identified as candidate species based on population genetic approaches (Tonione et al., 2016) as a yardstick for picking lineages to include in downstream exon-capture and macroevolutionary analyses. We emphasise that our priority here was to ensure that we sampled the maximum possible diversity of Melanesian *Gehyra*. Further work is required to test the hypothesis that these lineages warrant recognition as distinct species. Where possible, we matched these lineages to recognised species; however, for unnamed or taxonomically ambiguous lineages we used code names.

**Exon-capture, alignment and selection**

Where possible, we selected multiple geographically dispersed individuals from each candidate lineage for genomic analysis via exon-capture. The final exon-capture dataset included 51 samples from outside Australia. This data was integrated with exon-capture data for Australian *Gehyra* that have already been published (Ashman et al., 2018; Lau et al., 2024; Moritz et al., 2018; Oliver et al., 2019). Methods for generating and processing exon-capture data, and consequently constructing phylogenetic trees from this data, largely follow those outlined in the aforementioned papers. To briefly summarise, raw sequencing reads were cleaned and trimmed using the pre-cleanup and scrubReads scripts of the SCPP pipeline (Peñalba et al., 2014). Cleaned reads were assembled into contigs using a pipeline described by Bragg et al. (Bragg et al., 2016), filtered to base quality >20 and sequence coverage >20, and then individually assembled, phased, aligned, and concatenated as described in Moritz et al. (2018).

**Species tree estimation**

Where possible, two representative individuals with the highest average read coverage were selected for each species/OTU, and h0 haplotypes were produced for use in multi-species coalescent analyses via the EAPhy pipeline v1.2 (Blom, 2015). In cases where only one sample was available for a particular OTU and the sample had >20x average coverage, both the h0 and h1 haplotypes from EAPhy were included for the sample to try and ensure two representatives for all taxa. Single exon alignments (1473 in total) were then produced for the representative samples using EAPhy, after which neighbour-joining trees were created for each exon in PAUP\* v4.0.b10 (Swofford, 2002) using the HKY substitution model. From these NJ trees we randomly selected 100 loci that satisfied criteria appropriate for a StarBEAST2 analysis (200–500 bp, sequences with at least 90% complete alignments and at least 95% taxa, no paralogs). These loci were then concatenated, and an initial maximum-likelihood tree was created using RAxML (Stamatakis, 2014) with a GTR-G model and boot-stopping criterion to check topology. This initial tree was not rooted. Following this, each locus alignment was also checked by eye in Geneious v6.1.8 (http://www.geneious.com, Kearse et al., 2012) and cleaned – remaining gene paralogs, low quality individuals (high rates of Ns due to low sample coverage), chimeric/contaminated individuals (haplotypes of incorrect species, often associated with chimeras) – were removed from the data. Post-cleaning, the top ranked 100 loci were again concatenated, and an ML tree was produced in RAxML.

To conduct the multi-species coalescent analyses, we used the algorithms implemented in BEAST2 v2.4.8 (Bouckaert et al., 2014; Drummond & Bouckaert, 2015), as StarBEAST2 v0.14 (Ogilvie et al., 2017), with all xml files set up using BEAUti v2.4.8 (Bouckaert et al., 2014). Following Ashman et al. 2018 and to overcome the computational limits on taxa numbers, we employed a “divide and conquer” strategy (sensu Antonelli et al., 2016). We identified five strongly supported subclades with many closely related lineages from initial RAxML concatenated trees, and removed them for smaller, subclade-specific StarBEAST2 analyses. When a subclade was removed, at least two lineages delimiting the subclade were retained in order to represent the subclade’s root node; any lineages that are phylogenetically isolated, or have highly uncertain placement, are also left in the remaining “skeleton tree”.

Each subclade analysis and the skeleton tree analysis were set up to run using a linked strict clock model across all exons with a 1/X prior setting, and estimated the clock of each gene relative to the overall mean clock. The data was partitioned by locus with substitution models set to HKY+G, overall constant populations model, and a Birth-Death speciation model. Each subclade analysis was set with a relative date for tree height by placing a tight Normal(1,0.001) prior on the root node to facilitate easy integration back into the skeleton tree. Two independent analyses were conducted for each subclade and the skeleton tree, with a chain length of 1.0x109, logging every 1.0x105, and results were combined after 20% burn-in was removed. The largest internal clade required four independent runs to ensure adequate ESS values (>200) for all parameters (assessed using Tracer v1.7; Rambaut et al., 2018b).

After the StarBEAST2 analyses were completed, the trees sampled from the posterior of each subclade analysis were integrated with trees sampled from the posterior of the skeleton tree analysis, by replacing each pair of subclade-delimiting lineages with a sampled full subclade tree, with branch lengths scaled to match the subclade root date of the sampled skeleton tree. The new collection of dated trees contains all lineages, and was treated (with caveats) as a posterior distribution of dated species trees, and summarised as a Maximum-Clade Credibility tree calculated with TreeAnnotator v2.4.8 (Rambaut & Drummond, 2002-2017).

For all macroevolutionary analyses, we used the coalescent species tree as the basic framework. We calibrated the Maximum-Clade Credibility tree into a timeframe of millions of years before present by assigning a crown age of 24 million years to the well supported note comprising of the two main Australia radiation and the two large bodied Melanesian radiations (see results below). This age constraint broadly matches with results from fossil-calibrated nuclear-gene-based dating analyses (Gamble et al., 2015; Oliver et al., 2017).

Four additional taxa for which exon sequences were not available were imputed into the dated tree based on their phylogenetic position and inferred ages in mitochondrial analyses. Specifically, these were two divergent lineages within a currently unrecognised clade that occur across Cape York and far southern New Guinea ‒ CYsp 2A and CYspB, *Gehyra corona* from an island north of New Guinea, and *Gehyra fehlmanni* from mainland Asia (Heinicke et al., 2011; Kraus et al., 2024; Oliver et al., 2019). This resulted in a phylogeny with a total of 97 terminal taxa.

**Biogeographic analyses**

Patterns of dispersal across Australasia and the Pacific were estimated on this fixed 97-taxon tree using BEAST X (Bouckaert et al., 2014) treating distribution area as a discrete general-time-irreversible character (i.e., with separate forward and reverse relative rates between areas. This biogeographic model is analogous to the GTI DNA substitution model, which has 12 relative rates for forward and reverse changes between nucleotides and an absolute substitution rate. The ancestral areas for each node, and the number of transitions of each type, were recorded for each MCMC sample (using the ancestralTreeLikelihood and MarkovJumps functions); convergence was monitored in Tracer v? (Rambaut et al., 2018a) and results were collated and visualised using LogCombiner v? and TreeAnnotator v? in the BEAST v? package (Suchard et al., 2018). In total, 4 runs of each analysis were performed, and the details of the MCMC parameters are in the supplied xml scripts, with relevant annotations (Supplementary Information X).

To test whether dispersal probability between Australia and New Guinea varied across time slices, a 2-epoch clock was employed, with overall dispersal rates estimated separately for two time slices: 0-10 and >10 million years; see justification below. Ten million years ago was chosen as the breakpoint as it roughly corresponds with the estimated end of the most extensive recent widespread inundation of the New Guinea region (Harrington et al. 2017). Over the period from 10 million years till the present, New Guinea was increasing in areal extent, while the width of sea barriers between New Guinea and Australia was likely diminishing, and at multiple times these were completely severed by land bridges (Norvick, 2003). If land area and barrier size are primary determinants of dispersal probability, it would be predicted that after correcting for extant lineage diversity in the relevant timeslice, dispersal rates between Australia and New Guinea should be much higher in the more recent time period.

We ran two biogeographic analyses. First, to visualise histories of dispersal and diversification across contemporary geographical regions, we used a “detailed” six-region coding system: 1) Australia - corresponding to the boundary of contemporary Australia and not including New Guinea (Oliver et al., 2023); 2) New Guinea - the contemporary islands of New Guinea and nearby land bridge islands; 3) Asia and the Sunda Shelf; 4) East Melanesia - the islands of the south-west Pacific that are largely underpinned by the Vitiaz Arc, namely Manus, New Britain, Solomons, Fiji and Vanuatu; 5) Wallacea - broadly referring to the islands between Wallace’s Line and Lydekker’s Line; and 6) Pacific - more isolated islands in the south-west Pacific that are not part of the Vitiaz Arc systems, including parts of Micronesia (Palau) and Polynesia (e.g. Tonga and Samoa).

The second analysis was explicitly designed to visualise timeframes and number of shifts between Australasia and adjacent islands (i.e. those east of Wallace’s line) and used a “simple” three-state coding system: 1) Australia (as above); 2) Asia and the Sunda Shelf (as above); and 3) the remaining four insular regions described above lumped together.

Given the overall small number of lineages in many regions, we caution that these analyses are likely to lack power with respect to estimating ancestral areas or precise absolute rates of dispersal. It is for these reasons that we did not follow recent analyses of other Melanesian geckos (Oliver et al., 2024) and break New Guinea up into its constituent regions, such as the East Papuan Composite Terrane and Northern Terranes. While some *Gehyra* taxa do appear to be associated with some of these regions, the low number of lineages makes our dataset suboptimal for testing for regions of origin and patterns of dispersal at this finer scale. In a similar vein, in the absence of outgroups and given poor sampling of the small number of Asian lineages of *Gehyra*, we refrain from making any comments about the ancestral area for the entire *Gehyra* radiation. Rather, our analyses are designed to highlight relative patterns of dispersal and diversification across insular Melanesia and continental Australia.

**Comparing macroevolutionary regimes for body size**

Body size analyses were performed on a pruned version of the 97-taxon species tree: thirteen lineages or species for which we were unable to obtain body size data were pruned for the phylogeny used in this analysis. Typical maximum body size (snout-vent length) for all others was obtained from published literature (most species) or through direct measurements of museum material (**see Table X**).

Shifts in body size optima (OU theta parameter) were estimated using a relaxed Ornstein–Uhlenbeck (OU) model (Uyeda & Harmon, 2014) as implemented in RevBayes (May & Hoehna, 2022). Snout-vent length was log10-transformed before all analyses. The settings in the model RevBayes script (May & Hoehna, 2022) were used with the following modifications. The burnin, MCMC run length, and sampling interval were increased tenfold, to ensure convergence and stationarity. The lower bound of the prior on the sigma2 distribution was lowered to 10-5, because the sampled parameter estimates abutted the original lower limit of 10-3. Four runs were performed, convergence was monitored using Tracer (Rambaut et al., 2018a), and a maximum clade credibility tree computed using TreeAnnotator in the BEAST X package (Suchard et al., 2018).

**Results**

*Species groups in* Gehyra *and lineage diversity in Melanesia*

All analyses of both mtDNA (ND2) and exon capture data identified six major lineages of *Gehyra*. The *variegata* group (here expanded to include *G. xenopus*) and *australis* groups are endemic, or nearly endemic to Australia, with only a single taxon (CYsp) within the *australis* group occurring in the savannahs of the Trans-Fly region of far southern New Guinea. Within CYsp ND2, diversity is strongly concentrated in northern Australia and low in southern New Guinea. Diversity and relationships within these Australian groups are discussed in more detail elsewhere (Moritz et al. 2018; Ashman et al. 2018; Oliver et al. 2019).

The remaining four lineages consist of: 1) the *mutilata* group, including at least three species that together have a huge distribution spanning across Asia, the Pacific and the Indian Ocean; 2) the *vorax* group – three described species and one candidate taxon distributed from Manus Island to Fiji; 3) the *membranacruralis* group – three recognised species known from across eastern New Guinea and Sudest Island in the Louisiade Archipelago; and 4) the *oceanica* group – at least nine recognised species (plus several candidate taxa) distributed from Wallacea, across New Guinea, and much of the tropical west Pacific (Fig. 1).

Mitochondrial and exon-capture-based analyses highlighted the presence of additional lineage diversity not captured by current taxonomy. Particularly striking are divergent (e.g., late-Miocene origins) lineages in the *oceanica* group from Maluku and the Solomon Islands. Conversely, other previously recognised taxa or candidate taxa in the *oceanica* group were found to be less divergent (e.g. *G. brevipalmata* and lineages within the *G. oceanica* species complex from across the Pacific).

A diagram of a lizard

AI-generated content may be incorrect.

Figure 1 \*BEAST topology and support values for *Gehyra*, and distribution of main species of *Gehyra* groups that occur east of Wallace’s Line. The distribution of the *G. mutilata* group is not shown because the extent of the natural versus introduced range of that species group is unclear.

*Phylogenetic relationships*

Topological relationships were broadly similar across RAxML, BEAST, and \*BEAST analyses, although there were some key differences. We only focus on relationships between the six major species groups here. A sister-taxa pairing of the larger-bodied insular taxa in the *membranacruralis* and *vorax* groups was strongly supported in concatenated BEAST and coalescent analyses. In Maximum in maximum likelihood analyses of the concatenated data the basal realtionships of the two giant lineages was unresolved (**Figure SX-X**). These two large-bodied insular species groups also always formed a strongly supported clade with the *australis* and *variegata* groups from Australia. In concatenated datasets, the two Australian lineages tended to form a clade, while in coalescent analyses the two Australian lineages and the clade comprising the two large-bodied insular lineages essentially formed a polytomy. In all analyses of exon-capture data, the *mutilata* and *oceanica* groups clustered together with strong support.

*Biogeography*

Both the “detailed” (6-state) and “simple” (3-state) **(Figure S5)** biogeographic analyses revealed limited numbers of shifts between Australia and islands to the north, with an especially low number of jumps over the most recent time period (i.e., the last ten million years). Focusing on the 6-state analysis, the most probable ancestral states suggest that Australia was colonised either twice or only once with an early outwards shift **(Figure 2)**. However, our data cannot robustly distinguish between these two options due to uncertainty around the basal area state for *Gehyra*. The only other well-supported shift between these regions occurred much more recently in CYsp and involves a species that occurs across both Australia and the savannahs of far southern New Guinea, with the inferred shift being most likely out of Australia.

The Markov-Jumps shift counts result in slightly higher average numbers of shifts, due to a scattering of low-probability shifts occurring in any single MCMC sample; these are distributed across different branches in different samples (always at low probability) and thus do not appear in the consensus ancestral reconstructions. Ancestral reconstructions on the detailed 6-state analysis infer ~2.8 shifts between Australia and islands to the north, and 1.9 shifts from islands into Australia. In contrast, at least 12.3 dispersals between island systems to the north of Australia that have likely never been connected by land are inferred, with the most frequent shifts being from East Melanesia into New Guinea, and from New Guinea into East Melanesia and Wallacea.

*Body size*

The relaxed OU analyses on the \*BEAST phylogeny found the biggest shift in body optima between the clade comprising the *vorax* (East Melanesia) and *membranacruralis* (New Guinea) groups and all other taxa. This is consistent with the larger body sizes observed in all members of these two species groups (max SVL between 129–155 mm; **Fig 3**). There was also a subtler increase in the *oceanica* group, and nested within this clade, a further increase in the lineage leading to *marginata* from Wallacea (SVL 142 mm). The Australian lineages show no evidence of marked shifts in optima either when compared against each other or against the baseline for the genus.

**Discussion**

We present a phylogeny including nearly all recognised species of Australasian *Gehyra* based on a large (100 locus) nuclear gene dataset and coalescent analyses. This phylogeny emphasises that *Gehyra* radiations from Australia are highly discrete from those from New Guinea and other islands of Melanesia, and that successful dispersal has been very rare despite the proximity of these regions, especially since the mid-Miocene. Some, but not all, lineages of Melanesian *Gehyra* also show evidence of a shift in body size optima towards very large size. Below, we discuss the significance of these results both for understanding the biogeographic history of Australasia, and the factors that may mediate patterns of dispersal and ecological diversification across insular and continental regions.

**Phylogeny of *Gehyra***

This study represents the most complete and gene-comprehensive phylogeny of *Gehyra* published to date. The six major species groups of *Gehyra* identified here are well-supported and robust, as are most shallower relationships, although the latter were not the primary focus of this paper (see (Ashman et al., 2018; Oliver et al., 2019). Our sampling also supports the distinctiveness of most recognised Melanesian species and further highlights divergent lineages that are either unnamed or for which the correct name is uncertain. Resolving the status and ecology of these potentially unnamed taxa is a priority for ongoing work, however, documentation of this Melanesian diversity will probably not change our broad-scale understanding of the biogeography of *Gehyra* in Australasia.

In contrast, the shortage of genetic (and especially genomic) data for the small number of *Gehyra* endemic to Asia, and the absence of matching genomic data for probable outgroups in the genera *Hemiphyllodactylus* and *Perochirus* (Heinicke et al., 2011) are major constraints on our understanding of the deep-scale relationships and biogeography of *Gehyra*. Most notably, relationships of the *oceanica* and *mutilata* groups vary in our analyses when compared against phylogenies (using concatenation) with more outgroups (Heinicke et al., 2011; Title et al., 2024). Alternative positions for these species groups and the addition of missing Asian taxa may also be the difference between inferring whether *Gehyra* have deep Oligocene origins on Island Arcs in the south-west Pacific (like some other co-occurring Australasian squamate taxa (Oliver et al., 2018); , or conversely, are more recent colonists from the Asian continental shelf (Oliver & Hugall, 2017). Filling these data gaps should be a priority area for further research, although we reemphasise that new data is unlikely to change our interpretation that the well-sampled Australian and Melanesian radiations of *Gehyra* have largely independent and distinctive histories (see below).

**Island to continent dispersals in Australasia**

Understanding the degree to which the biotas of Australia and Melanesia (and especially New Guinea) are shared has been a theme in Australasian biogeography for over 150 years (Heinsohn & Hope, 2006; Wallace, 1876). Our data indicate that dispersals between Australia and islands have played a limited role in shaping the contemporary diversity of *Gehyra*. Furthermore, the probability of dispersal is inferred to be lower in the last ten million years, despite the increasing extent of land in the New Guinea region and formation of land bridges through this time (Harrington et al., 2017). In contrast, frequent and often long-distance overwater dispersals have clearly occurred in several Melanesian lineages of *Gehyra* (e.g., (Oliver et al., 2016; Tonione et al., 2016). Indeed, our coding for regions across Melanesia and Wallacea certainly underestimates the frequency of overwater dispersal because it lumps together islands that have likely never been connected by land (e.g. Manus versus Fiji/Vanuatu within East Melanesia) or landmasses such as New Guinea that are comprised of formerly discrete islands (Pigram, 1987). These data indicate that, at least for Melanesian *Gehyra*, an inability to disperse overwater cannot be invoked to explain the low rate of dispersal into northern Australia, especially over the last ten million years.

A possible explanation for limited dispersal by *Gehyra* between Australia and Melanesia is niche conservatism (Crisp et al., 2009). Studies of Australian *Gehyra* have emphasised that even within this moderately old radiation, only one lineage has been able to shift from monsoonal to arid environments (Ashman et al., 2018), despite having hard shelled eggs and considerable lability in thermal and hydric physiology (Skelton et al., 2024) . Melanesian *Gehyra* are mostly associated with wet rainforest habitats, while the two main Australian *Gehyra* lineages are almost completely absent from rainforest areas. Analyses of other families of Australasian reptiles, including diverse and relatively old radiations associated with arid and savannah environments in Australia, have also found limited or even no evidence for dispersal into New Guinea (Pavón-Vázquez et al., 2022; Skipwith et al., 2019; Tallowin et al., 2020). This suggests that for many taxa, and perhaps ectothermic reptiles in particular, the increasingly close proximity of Australia and New Guinea has not been sufficient to overcome environmental differences and the constraints of niche conservatism.

The rarity of recent dispersal between Australia and New Guinea in *Gehyra* contrasts with some other components of the Australasian biota, including some other lizard radiations (Blom et al., 2019; Probst et al., 2025), rats (Roycroft et al., 2022), pigeons (Oliver et al., 2023), some groups of parrots (Schweizer et al., 2015) and even tropical rainforest plants (Sniderman & Jordan, 2011). These aforementioned studies have all inferred numerous and recent colonisations between Australia and islands to the north, centred on, but not exclusive to, New Guinea. However, in most cases, these lineages are much more closely associated with mesic environments than are typically inhabited by Australian *Gehyra*. To better understand the ecological, taxonomic, or environmental correlates that might mediate varying probabilities of dispersal between Australia and islands to the near north, comparative analyses across multiple taxa are now needed. These results also further emphasise the importance of considering Australia and New Guinea as separate regions in broad-scale biogeographic analyses of the Australasian and Asian biotas (Oliver et al., 2023).

**Single origin of most island ‘giants’**

Our analyses of body size evolution in *Gehyra* support the underlying hypothesis that island regions are characterised by at least one lineage with a larger body size optimum, but with important nuances. *Gehyra* do not show a repeated general shift to gigantism (as optimal body size) on all islands of Melanesia. Rather, there is a single marked shift in body size in a clade comprising the *membranacruralis* and *vorax* groups (which are strongly supported as sister taxa in the focal coalescent analyses), which then dispersed across multiple islands. This pattern stands in strong contrast to the widely studied pattern in *Anolis* lizards, where large-bodied ecomorphs have evolved repeatedly on separate islands (e.g. Losos et al. 1998). One lineage in the *oceanica* group from Wallacea (where the aforementioned two species groups are not present) has also evolved moderately large body size. Most other species on islands (*mutilata* and *oceanica* groups) tend to be similar, or at most *slightly* larger in size than Australian and Asian continental forms.

The limited number of shifts in body size makes it difficult to test whether the larger body size in some island *Gehyra* is due to contingency (large species evolved by chance on islands) or determinism (island environments favour the evolution of large species) (Losos et al., 1998). The trend towards the evolution of large body size in *Gehyra* does however mirror large body sizes observed in several other lineages of forest-associated and generally, *but not always*, insular geckos with distributions occurring across south-east Asia, the south-west Pacific, and even small areas of eastern Australia. This includes taxa in the genus *Gekko*, several lineages in the Melanesian radiation *Cyrtodactylus* (Oliver et al., 2014), and also radiations of diplodactylid geckos on New Caledonia and New Zealand (Heinicke et al., 2023; Skipwith & Oliver, 2023). In Australia, a potential parallel is the large-bodied species of arboreal leaf-tailed geckos in the genus *Saltuarius*. All of these lineages include taxa with maximum snout-vent lengths consistently approaching or above 130 mm. Inasmuch as their ecology is understood, most are also highly arboreal and often found resting on the trunks or branches of large rainforest trees. The combination of large size and a highly arboreal ecology also suggests parallels with the repeated evolution of crown-giant ecomorphs in scansorial *Anolis* lizards that occur in both insular and continental regions of tropical America (Huie et al., 2021).

When viewed in the context of similar large body species observed in other gecko lineages in Australasia, we hypothesise that elements of both contingency and determinism are in play. Most islands and even potentially mainland tropical rainforest areas in Australasia do seem to have at least one or two large-sized arboreal gecko lineages (suggesting determinism); however, which lineage evolves to this large size seems to be somewhat randomised (suggesting contingency). Given that some large-sized species do occur in continental rainforests, we also tentatively suggest that tropical rainforest habitats may be the strongest correlate with this trait. However, we also emphasise that formal comparisons involving more gecko taxa, and at a global scale, are now needed to properly test if there are consistent predictors of the evolution of large body size in geckos.

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