



Paleoenvironmental models for Australia and the impact of aridification on blindsnake diversification

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Abstract

Aim: Shifts in diversification rates of Australian flora and fauna have been associated with aridification, but the relationship between diversification rates and aridity has never been quantified. We employed multiple approaches to reconstruct paleoenvironments of Australia for the first time. We used this information, and phylogenetic-based analyses, to explore how changes in temperature and increasing aridity during the Neogene influenced the diversification of the Australian blindsnakes. We tested whether diversification rates differ between arid-adapted and mesic-adapted lineages.

Taxon: Typhlopidae, *Anilius* blindsnakes.

Location: Australia.

Materials and Methods: We estimated the historical biogeography of blindsnakes using BioGeoBEARS. We synthesised multiple approaches to reconstruct paleotemperature and paleoaridity of Australia during the Neogene. We fitted several birth-death models and estimated diversification rates under paleoenvironmental conditions using RPANDA. We further compared diversification rates between arid-adapted lineages versus mesic-adapted lineages using ClaDS and GeoHiSSE.

Results: Ancestral area estimation indicated Australian blindsnakes have tropical grassland origins. We found that Australia-specific regional paleotemperature and paleoaridity provided a better explanation for diversification rate variation than global paleotemperature. Specifically, our best-fitting model indicated that speciation rates of blindsnakes decreased with increasing aridity. We found no difference in diversification rates between arid- and mesic-adapted lineages.

Main Conclusions: Soon after dispersing to Australia, the common ancestors of Australian blindsnakes diversified rapidly in mesic habitats during the early Miocene. However, as the continent became increasingly arid, diversification rates decreased. We found that shifts in the environment led to the emergence of two major clades: one remaining in primarily mesic habitats and the other adapting to the expanding arid biome. Our results emphasise the importance of both arid and tropical biomes as sources and sinks of diversification.

KEYWORDS

BioGeoBEARS, diversification, GeoHiSSE, paleoenvironment, Scolecophidia

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1 | INTRODUCTION

The present-day distribution of extant species can provide clues about their biogeographic history and insight into the tempo of their diversification. In particular, one major aim of evolutionary biology is to understand the role that environmental factors have played in shaping rates of species diversification. A variety of environmental correlates have been associated with diversification processes across clades, including elevation (Boschman & Condamine, 2022; Esquerré et al., 2019), CO₂ concentration (Kergoat et al., 2018), microhabitats (Bars-Closel et al., 2017), temperature (Condamine et al., 2013, 2019; Mayhew et al., 2012; Ricklefs, 2006; Rolland & Condamine, 2019; Sun et al., 2020a), and aridification (Catullo & Keogh, 2014; Deepak & Karanth, 2018; Pepper, Ho, et al., 2011; Rabosky et al., 2007). However, despite advancements in our understanding of the evolutionary relationships and divergence times of many clades, our knowledge of the impact of paleoenvironmental change on these clades remains limited, particularly in regard to the regional scale at which many clades radiate (Eyes et al., 2021). As such, it remains a key challenge to combine regional paleoenvironmental histories with molecular phylogenies to understand the drivers of diversification over deep-time scales.

The Australian continent has one of the most diverse reptile faunas on the planet and this may have been driven by its rapid environmental change during the Neogene. After a long period of relatively stable climate and mesic habitats, the aridification of continental Australia began around 20Ma (mega annum) with the development of pockets of aridity (Byrne et al., 2011; Martin, 2006). Subsequent extreme warming and cooling periods in the last ~5Ma created what is now known as the “outback” (Byrne et al., 2008; Pepper & Keogh, 2021). During this period, as aridification progressed, arid-adapted vegetation expanded while mesic biomes became increasingly fragmented (Crisp & Cook, 2013; Martin, 2006). This shift in the environment also led to a radiation of some reptile clades, such as elapid snakes and skinks, which diversified into morphologically and ecologically distinct lineages (Lee et al., 2016; Rabosky et al., 2007; Sanders et al., 2008). Conversely, other reptile clades, such as blindsnakes and geckos, remained morphologically conserved and were thought to be species-poor until recent molecular data suggested otherwise (Marin, Donnellan, Hedges, Puillandre, et al., 2013; Moritz et al., 2018; Zozaya et al., 2019). Furthermore, shifts in diversification rates due to changes in Australian temperature and aridity have been reported in some squamate reptile clades including skinks (Rabosky et al., 2007) and geckos (Fujita et al., 2010; Oliver, Couper, et al., 2014; Oliver, Smith, et al., 2014; Pepper, Ho, et al., 2011; Pepper, Fujita, et al., 2011) as well in frogs (Catullo & Keogh, 2014; Vidal-García & Keogh, 2015), insects (Owen et al., 2017; Toussaint et al., 2015), and plants (Crisp & Cook, 2013; Kadereit et al., 2010; Miller et al., 2013). Yet, the role of aridification and temperature changes on diversification is highly variable, with some arid-adapted vertebrates radiating following aridification (Brennan & Oliver, 2017; Pepper, Fujita, et al., 2011; Rabosky et al., 2007) while other mesic-adapted groups have had suppressed

diversification or been driven to extinction (Bryant & Krosch, 2016; Cardillo et al., 2017; Owen et al., 2017). Whether environmental change in Australia has had generally positive or negative influence on diversification rates in squamate reptiles is still unknown.

Today, the arid zone covers roughly 70% of the Australian landscape and provides habitat to 43% of all of Australia's terrestrial reptiles (Byrne et al., 2008). Of these, roughly a quarter of the snake species diversity in Australia is represented by blindsnakes of the genus *Anilius*, which currently comprises 47 described species (Tiatragul et al., 2023; Uetz et al., 2021). All but three species of formally described *Anilius* are endemic to Australia, *A. torresianus* and *A. leucoproctus* also occur in southern parts of New Guinea, while *A. eryncinus* has only been recorded in New Guinea and the Maluku Islands. Some species of blindsnakes are morphologically similar, and previous phylogenetic and morphological studies have revealed that the true species diversity is underestimated (Ellis, 2019; Hedges et al., 2014; Marin, Donnellan, Hedges, Puillandre, et al., 2013; Pyron & Wallach, 2014). The diversification of *Anilius* in Australia is reported to have originated from a single dispersal event by a mesic-adapted ancestor from Southeast Asia or Indonesia between 39 and 19Ma (Marin, Donnellan, Hedges, Doughty, et al., 2013; Vidal et al., 2010). However, phylogenetic analyses from Tiatragul et al. (2023) indicated that the closest relative to all *Anilius* is *Ramphotyphlops multilineatus*, a species that occur in Western New Guinea, Kai Islands and Salawati, suggesting the Australian radiation may have a Melanesian origin. Despite representing a substantial portion of snake diversity, we know little about the macroevolutionary dynamics of blindsnakes. The monophyly of the genus makes *Anilius* well suited to test hypotheses about how lineages diversified with dramatic environmental changes during the Cenozoic because they are geographically restricted and can be found in every biome on mainland Australia.

Advances in phylogenetic comparative methods and paleoenvironmental reconstructions allow us to better understand regional diversification dynamics. The influence of temperature on diversification rates has been empirically tested with birth-death models (Condamine et al., 2013, 2019; Kergoat et al., 2018; Rolland & Condamine, 2019). Global paleotemperature data for these analyses were first presented by Condamine et al. (2013), where the relative proportions of different oxygen isotopes in samples of benthic foraminifer shells (Zachos et al., 2008) across geological time were converted to absolute temperature using a formula derived from Epstein et al. (1953). The relationship between diversification rates and aridity, however, has been attributed to some proxies such as the timing of aridification or global temperature, rather than quantifying the extent of regional aridity itself (Catullo & Keogh, 2014; Crisp & Cook, 2013; Deepak & Karanth, 2018; Dorn et al., 2014; Fujita et al., 2010; Oliver, Couper, & Pepper, 2014; Oliver, Smith, et al., 2014; Owen et al., 2017; Pepper, Ho, et al., 2011; Pepper, Fujita, et al., 2011; Toussaint et al., 2015). To our knowledge, no study has assessed aridity as a continuous variable in an environment-dependent birth-death model framework, probably due to the difficulty of quantifying

paleoaridity. However, recent developments in spatially explicit paleoenvironmental reconstructions from the lithological and fossil record as well as global circulation models (GCMs) now enables us to estimate paleotemperature and paleoaridity data specific to Australia in the time span of interest. The use of these data sets allows us to conduct empirical analyses of the impacts of regionalised environmental changes on diversification rates over time for the first time.

In this study, we aimed to infer the historical biogeography of the Australian blindsnake radiation and investigate the impact of paleoenvironmental changes, specifically changes in temperature and aridity associated with Neogene aridification, on diversification rates within this group. To do this, we fitted several birth-death models with reconstructed paleotemperature and aridity and estimated diversification rates under these models. Additionally, we compared diversification rates between arid-adapted lineages versus mesic-adapted lineages to investigate if lineages that inhabit the arid biome have undergone faster or slower diversification. We predicted that arid-adapted lineages would have higher diversification rates compared to mesic-adapted lineages. This expectation is based on the hypothesis that aridification can cause fragmentation of continuous habitats, leading to isolated populations in distinct microhabitats and refugia in arid areas, which may lead to greater species-level divergence (Brennan & Keogh, 2018). Additionally, the ecological opportunities or selective pressures resulting from aridification may drive the evolution of specialised traits in mesic-adapted ancestral species, enabling them to exploit previously unoccupied niches and promote speciation.

2 | MATERIALS AND METHODS

2.1 | Phylogenetic hypothesis and taxon sampling

We used the most updated phylogeny for *Anilius* and closely related outgroups from Tiatragul et al. (2023). The species tree was built with the shortcut coalescent method in ASTRAL III (Zhang et al., 2018) using maximum likelihood gene trees inferred in IQTREE from 4930 loci (322 Anchored Hybrid Enrichment loci, 4574 ultraconserved elements, and 34 legacy genes) for 35/47 recognised *Anilius* species. Tiatragul et al. (2023) time-calibrated the phylogeny using 27 outgroup squamate fossils as primary calibrations using MCMCTree from the PAML package (Yang, 2007). Phylogenetic data in Tiatragul et al. (2023) suggest the existence of at least three genetically distinct undescribed species, so we followed their designation and adjusted our taxon sampling fraction to 38/50 species. The genetically distinct OTUs that are not formally described species include three '*Anilius grypus*' (two in Western Australia and one in Queensland) and two '*Anilius ligatus*' (one from the eastern part of the range and one from the northern part; Tiatragul et al., 2023). For ancestral biome estimation analyses, we included three outgroup blindsnakes species from Southeast Asia, Indonesia and Melanesia, where the ancestor of *Anilius* has been hypothesised to have originated

(Tiatragul et al., 2023; Vidal et al., 2010). The three species include *Ramphotyphlops multilineatus* (Western New Guinea, Kai Island, and Salawati), *Sundatyphlops polygrammicus* (Moyo Island, Indonesia), and *Acutotyphlops subocularis* (Bismarck Archipelago). We were not able to include *Ramphotyphlops* from continental Southeast Asia in the time-calibrated phylogeny because insufficient data was available for divergence time estimation.

2.2 | Biogeography and biome transitions

To investigate the biogeographic history of blindsnakes, we used the R package 'BioGeoBEARS' v.1.1.2 (Matzke, 2013). BioGeoBEARS provides a flexible, likelihood-based framework that models how branches in the phylogeny (representing extant taxa and their ancestors) have shifted among a set of discrete biomes over time. These shifts in biomes can occur within a single branch (anagenetic events, including processes such as dispersal and extinction) or at the time of branching (cladogenetic events involving sympatric, vicariant and founder-event speciation). We divided Australo-Papua into nine discrete biomes and assigned each Australian species to one or more biomes based on their occurrence records from the Atlas of Living Australia database (ALA). Biome classifications were based on the World Wildlife Fund's (WWF) Terrestrial Ecoregions of the World data set (Olson et al., 2001) and followed the nomenclature of published Australia-specific studies (Cardillo et al., 2017; Pavón-Vázquez et al., 2021).

Using the phylogeny and distribution data, we fitted three models that vary in the kinds of cladogenetic and anagenetic events they model, including likelihood implementations of Dispersal-Vicariance Analysis (DIVALIKE; Ronquist, 1997), Dispersal-Extinction-Cladogenesis (DEC; Ree & Smith, 2008), and BayArea (BAYAREALIKE; Landis et al., 2013) in BioGeoBEARS (Matzke, 2013). We also fitted these three models, with two additional relevant free parameters, both singly and together, for a total of 12 alternative models. The first additional parameter, *j*, assigns per-event weight to founder events (Matzke, 2014), and the second parameter, *x*, multiplies the probability of dispersal by distance to the power of *x* (Van Dam & Matzke, 2016; see Table S1). We used likelihood ratio tests to determine if the additional free parameter was a justified improvement over the simpler base models and selected the model that best fitted the data based on corrected Akaike information criterion (AICc) scores. Based on the best model, we ran an additional 50 biogeographic stochastic maps to account for uncertainty in ancestral biome estimation and transition between biomes and to estimate the frequency and direction of dispersal events across biomes (Matzke, 2013).

2.3 | Paleoenvironmental reconstruction

We used two alternative approaches to estimate paleoclimate in Australia from 40Ma to the present-day. The first approach used information derived from paleo-Köppen climate bands from

Scotese (2021). Köppen bands are estimated from different fossil and lithological indicators and give a broad categorisation of spatial variation in major climate types (tropical, sub-tropical arid, warm temperate, cool temperate and polar). We obtained estimated Köppen climate bands at 5 Ma intervals from 40 Ma to 0 Ma and used the sub-tropical arid Köppen band as a binary aridity index. We removed sites found in the ocean by using digital elevation models (DEMs) to mask sites below sea-level. To account for uncertainty in paleogeographic reconstructions of continental movements and sea-levels, we used two alternative DEMs (Scotese & Wright, 2018; Straume et al., 2020) to mask the ocean sites and provide two estimates of paleoaridity. To estimate paleotemperature from the Köppen bands, we followed the method of Scotese (2021) as implemented by Hagen et al. (2021). Here, each Köppen climate band was assigned a temperature value based on present-day averages of those climate bands (tropical=26, sub-tropical arid=22, warm temperate=16, cool temperate=5, polar=-20). To account for global fluctuations in temperature, we then modified these values with a global temperature curve estimate from oxygen isotope data (Song et al., 2019). Finally, to account for the change of temperature with elevation, we used a lapse rate of 9.8°C/km. Following Hagen et al. (2021), we model variation in the intensity of temperature oscillations during the Pleistocene. We also used the two alternative DEMs to give two alternative temperature curves using this approach (Scotese & Wright, 2018; Straume et al., 2020).

The second approach used a GCM to obtain a model-based estimate of paleotemperature and paleoprecipitation (Valdes et al., 2021). The paleoclimatic data is based on a HadCM3L model, which couples ocean, atmosphere and vegetation and are simulated at 5 Ma intervals based on the palaeogeography of Scotese (2021). To make it comparable with the binary aridity index derived from the Köppen band approach, we converted the paleoprecipitation into an aridity index by thresholding the precipitation data. We applied a threshold of 500 mm/year, below which is considered arid, above which was considered non-arid (Holzapfel, 2008; Walton, 1969). Each of the three global paleoaridity and paleotemperature maps, from the two approaches, were projected into a Behrmann equal-area projection using a spatial resolution of 110 km x 110 km. We then temporally interpolated the data from 5 Ma intervals to 100 ka using bilinear interpolation. Finally, we subset the data to include only the continent of Sahul from 40 Ma to the present-day. From these maps, we obtain multiple Sahulian curves for paleotemperature by taking the mean, minimum and maximum values within Sahul at each timestep. For paleoaridity, we took the mean value, as minimum and maximum showed little variation in the binary metric.

2.4 | Time- and environment-dependent diversification analyses

To evaluate how diversification rates correlated with climate and aridity through time, we fitted several time- and environment-dependent

likelihood diversification models using the `fit_bd` and `fit_env` functions in the R package 'RPANDA' v.2.0 (Morlon et al., 2016) to the *Anilius* phylogeny. Specifically, we fitted different combinations of pure-birth and birth-death models with speciation and/or extinction rates being constant or otherwise varying linearly or exponentially with paleoenvironment as described above. We fitted 12 diversification models based on reconstructed paleoenvironmental data to the phylogeny including three paleotemperature (mean, minimum, and maximum) and the paleoaridity index from each paleoenvironmental reconstruction method. We also fitted an additional environmental-dependent diversification model with the widely used mean global paleotemperature data set (Condamine et al., 2013) to provide comparison to our reconstructed paleoenvironmental data. To account for missing taxa, we used the fractioning function ($f=38/50$) in RPANDA. We then assessed which diversification model best fit the data based on AICc scores.

2.5 | Geographic range and rates of diversification

To test whether diversification rates differ between arid-adapted and mesic-adapted lineages, we used two approaches. First, we estimated speciation rates at the origin of each branch (henceforth branch-specific rates) using `ClDS` function in the Julia package PANDA v.1.6.1 (Maliet & Morlon, 2022). `ClDS` is designed to capture frequent shifts in speciation rates with small effects. At each speciation event, daughter lineages are assigned its own speciation rate sampled from a distribution parameterised on the parental rate (Maliet & Morlon, 2022).

In the second approach, we fitted four state-dependent speciation and extinction (SSE) models to the phylogeny and geographic range data under the `GeoSSE` (Goldberg et al., 2011) and `GeoHISSE` (Caetano et al., 2018) framework using the R package 'hisse' v.2.1.9 (Beaulieu & O'Meara, 2016). Since these SSE models only allow two states, we restricted our geographic states to arid and mesic. Based on the same categories we used in our BioGeoBEARS analyses, we classified species that primarily occur in the arid biome as arid (State 0; $n=8$), species that occur primarily in other biomes as mesic (State 1; $n=25$), and those that occupy both the arid and mesic biomes as widespread (State 01; $n=5$).

The four SSE models differed in whether they allowed diversification rates to be dependent on geographic states (range-dependent) or independent of them (range-independent), and whether they allowed an unmeasured trait ('hidden state') to influence diversification rates (Beaulieu & O'Meara, 2016; Caetano et al., 2018). Model 1 assumed equal diversification rates regardless of geographic state. Model 2 allowed geographic range to affect diversification rates. Models 3 and 4 were based on models 1 and 2, but they also allowed a hidden state to contribute to diversification rates. By incorporating hidden states, we could assess whether geographic range or an unmeasured trait contributed more to the observed diversification. For each model, we assumed uniform taxon sampling for 89% of arid lineages, 71% of mesic lineages, and 83% of widespread lineages,

based on the number of species in the phylogeny and all currently described species of *Anilios*. We then calculated AIC to identify the best-fitting models. Following the approach by Caetano et al. (2018), we averaged the estimates of diversification parameters across all models according to their AIC weights.

PANDA was implemented in Julia v.1.8.1 (Bezanson et al., 2012), all other analyses were performed in R v.4.2.1 (R Core Team, 2022). Figures were prepared using 'ggplot2' v.3.4.0 (Wickham, 2016). All map graphics were created using the Free and Open Source QGIS v.3.6. We arranged and finalised all figures using Adobe Illustrator v2022.

3 | RESULTS

3.1 | Ancestral biome estimation and transitions

Our BioGeoBEARS analyses all inferred tropical grassland as the ancestral biome of *Anilios*, but the ancestral biome for the common ancestor between *Ramphotyphlops multilineatus* and *Anilios* is ambiguous (Figure 1a; Figure S1). We found that the DEC+*j*+*x* model was the best-fitting biogeographical history model (Δ AICc = -4.47, Table S2). A likelihood ratio test (LRT) showed that both founder events (+*j* parameter) and distance between biomes (+*x* parameter) together provide statistically significant improvements over the simpler models (χ^2 , df = 2, *D*-statistic = 26.7, *p*-value < 0.001).

Based on 50 BioGeoBEARS biogeographic stochastic mappings (BSM) of the DEC+*j*+*x* model, we estimated that an average of 71.2 ± 1.3 (mean \pm SD) total biome shifts occurred throughout the phylogeny (see Table S3). Of these 40 ± 0 were cladogenetic (branching) events compared to 31.2 ± 1.3 anagenetic (within a single branch) dispersal events. Out of the 40 branching events, in 23.8 ± 2.1 events sister species maintained their ancestral biome ("narrow sympatry") and in 5.2 ± 2.3 events one sister species maintain their ancestral biome while the other sister occupies only a subset of the ancestral range ("subset sympatry"). The remaining branching events were made up by 6.1 ± 1.5 founder events where one of the sister species occupies a new range, and 4.9 ± 1.3 vicariance events where the sister species split their ancestral range. Our model also indicate that range expansion is expected to decrease as distance increase (free parameter *x* = -1.3).

Based on current distributions from ALA, most *Anilios* species are found entirely or partially in the tropical grassland biome (*n* = 20) followed by the arid biome (*n* = 13) and Mediterranean biome (*n* = 10). Apart from *A. silvia*, *A. leucoproctus*, and *A. proximus* that appeared to form independent divergent lineages (Figure 1a), we identified divergent biogeographic transitions between two major groups of species, which we refer to as Group 1 (*n* = 21 lineages) and Group 2 (*n* = 14 lineages). The common ancestor of Group 1 remained mostly in the tropical grassland biome, then 12/21 lineages expanded or transitioned into other biomes. The common ancestor of Group 2 first transitioned into the arid biome, four lineages remained in the

arid biome while 10 lineages transitioned or expanded into other biomes.

The tropical grassland biome is the largest source of outward dispersal (16.2 ± 4.9 events; 46.6%) followed by the arid biome (9.7 ± 3.2 events; 26%; Figure 1b). On the other hand, the largest sinks for all inward dispersals are the tropical forest biome (7.9 ± 4.2 events; 21.2%) and the Mediterranean biome (7.0 ± 2.9 events; 18.8%). The greatest directional transition is from the arid biome to the Mediterranean biome (5.3 ± 1.5 events) and from the tropical grassland biome into the temperate forest biome (5.1 ± 1.3 events; Figure 1c).

3.2 | Paleoenvironment estimates

Paleotemperature estimates for Australia differed between the three different methods (Figure 2a). However, all three paleotemperature models indicate Australia was hotter than the average global temperature (Figure 2a; Figure S2). Paleotemperature in Australia were also relatively constant compared to global temperature until the Plio-Pleistocene, a period characterised by fluctuations corresponding to the glacial cycles. Reconstructions of paleoaridity differed slightly between the two Köppen band methods, but these differed substantially from the aridity index derived from the GCM data (Figure 2b). Both Köppen band-based aridity indices show increasing aridity from 10Ma.

3.3 | Environment-dependent diversification

Among all the birth-death, time-dependent and environment-dependent models fitted in RPANDA, we found that environment-dependent models were preferred. Of the fitted environment-dependent models, we found the exponential environment-dependent speciation and constant extinction (BEnv + DCST (EXPO)) model based on paleoaridity estimated by Scotese and Wright (2018) provided the best fit to the phylogeny (AICc = 238.43; see Table 1). This best-fitting model indicates that an increase in aridity is exponentially associated with a decrease in speciation rate ($\lambda = 1.32$, $\alpha = -0.14$) and a constant background extinction rate ($\mu = 0.23$; Figure 3). The second and third most competitive models (Δ AICc < 2) also found that an increase in aridity is exponentially associated with a decrease in speciation rate, but without estimating extinction (see Table 1). Among the exponential environment-dependent models, we found that Australia-specific paleotemperature data provided a better fit to our phylogeny than global paleotemperature data (Table S4).

3.4 | Diversification rates between arid- and mesic-adapted lineages

We applied ClADS and SSE models to evaluate whether diversification rates differ between lineages in arid, mesic, and widespread

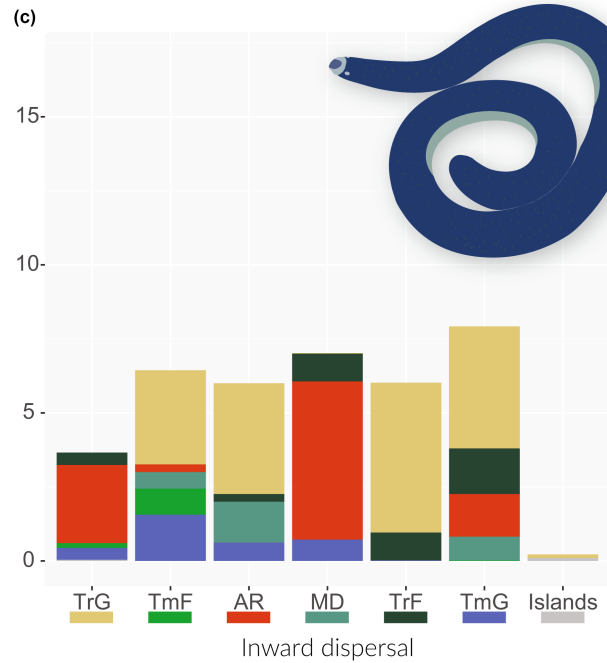
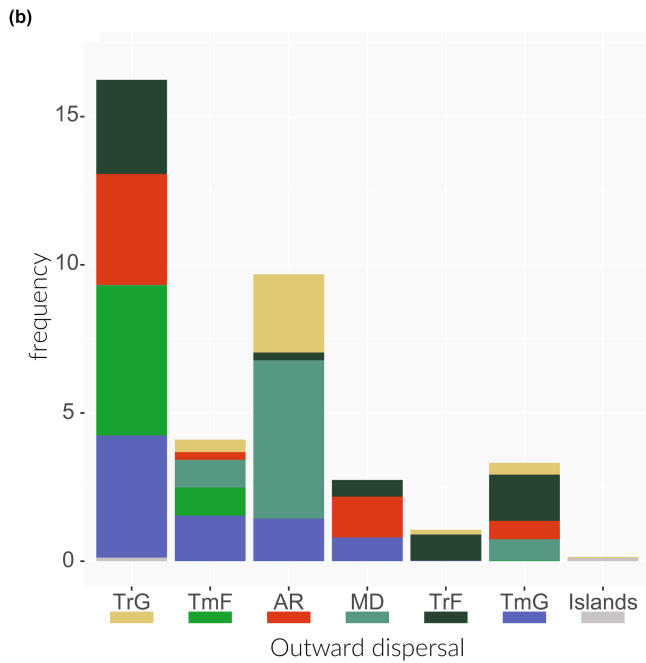
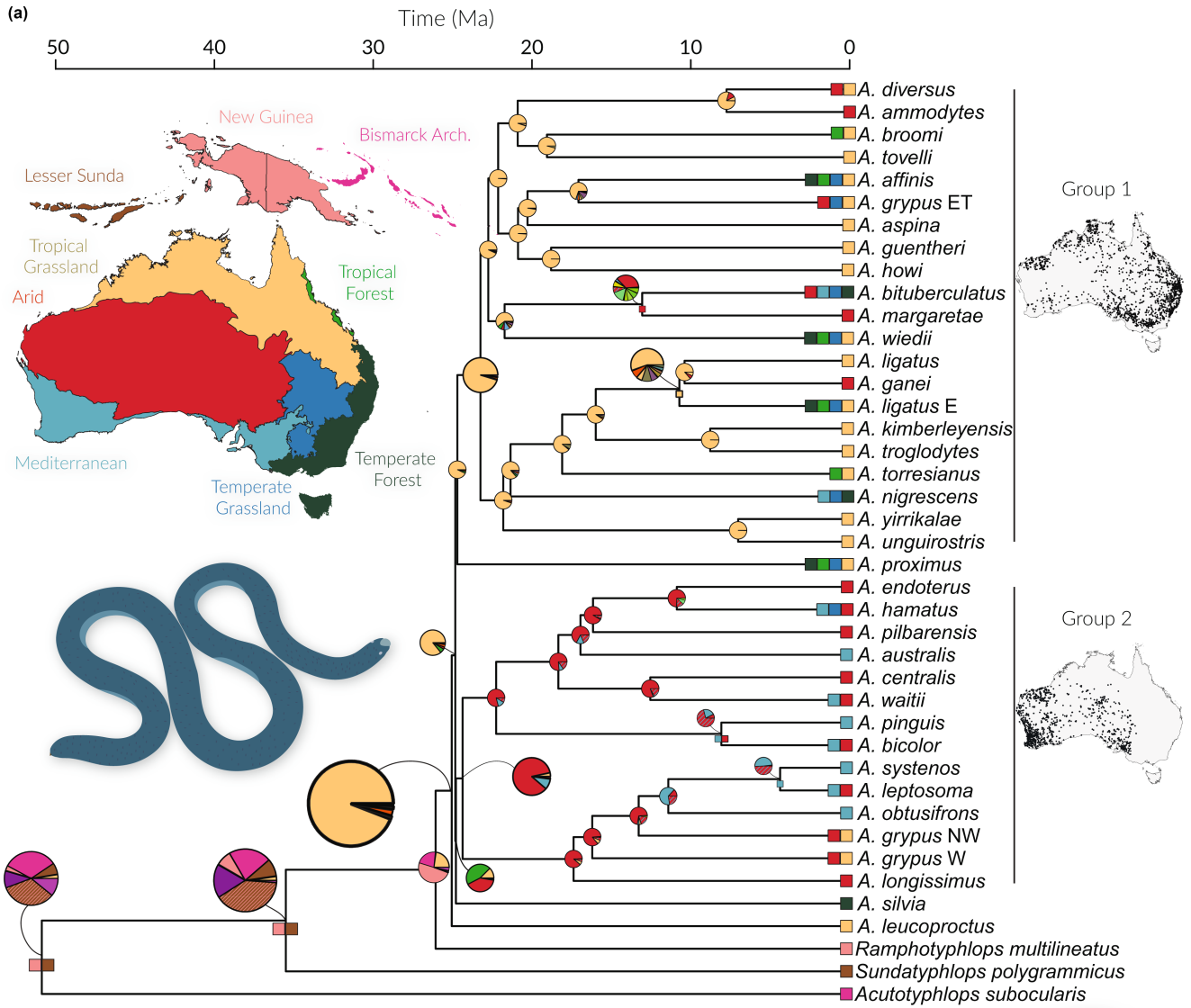


FIGURE 1 Ancestral biome estimation and transitions of Australo-Papuan blindsnakes in BioGeoBEARS, using the DEC+ $j+x$ model. (a) Inset map (left) shows biome classifications of the regions considered in this study. Coloured boxes at the tips correspond to biomes on the map. Pie charts represent ancestral biome reconstruction based on 50 biogeographic stochastic maps (BSM) for each node. Colours present on the pie charts but not in the biome map indicate mixture of more than one biome. Coloured boxes below pie charts indicate the most probable biome(s) at visually ambiguous nodes. Inset maps (right of the phylogeny) shows distribution of species in Group 1 and Group 2. (b) Bar plot showing frequency and composition of outward transitions and (c) inward transitions from Australian biomes and combined non-Australian islands. AR, arid; MD, Mediterranean; TmF, temperate forest; TmG, temperate grassland; TrF, tropical forest; TrG, tropical grassland.

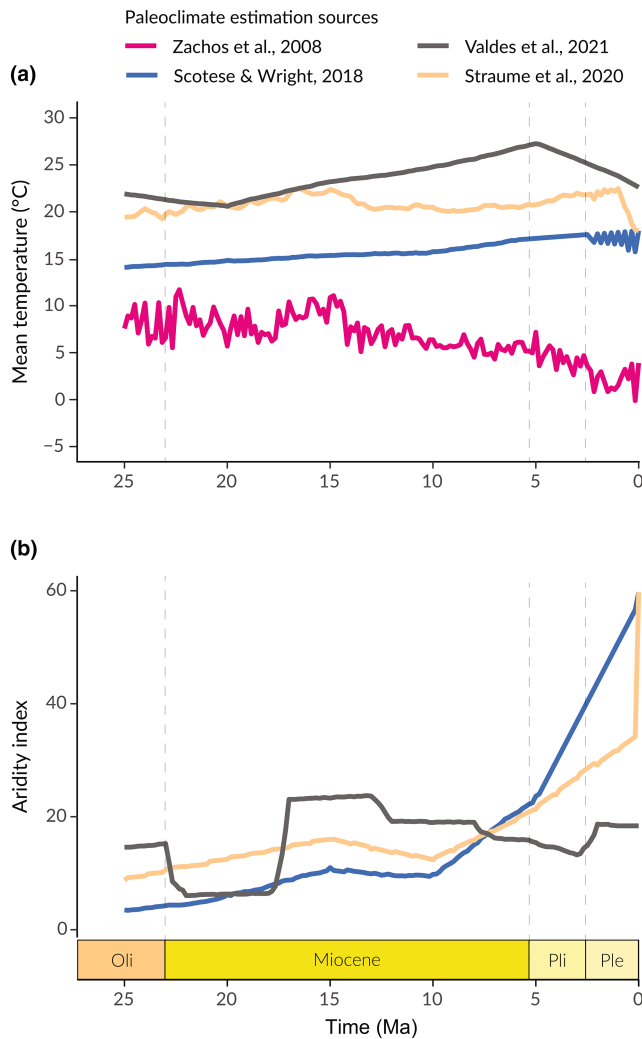


FIGURE 2 Global paleoclimate estimation derived from oxygen isotope data (pink=Condamine et al., 2013) and Sahulian paleoclimate estimation from a global circulation model (GCM) approach (black=Valdes et al., 2021), and two paleo-Köppen climate band approaches (orange=Straume et al., 2020; blue=Scotese & Wright, 2018). (a) Estimated mean temperature over time in Australia compared to global paleotemperature data (pink). (b) Estimated mean aridity index over time based on precipitation threshold (arid <500mm/year). Oli, Oligocene; Ple, Pleistocene; Pli, Pliocene.

ranges (Figure 4). Results from our ClADS analysis show branch-specific diversification rates was high when the genus first diversified and gradually decreased towards the present (Figure 4b). ClADS also indicate mean branch-specific rates did not differ significantly between the geographic ranges (Figure 4c).

In our SSE analyses, we found that the range-independent model fit the data better than models where diversification rates were dependent on geographic range (Table 2). The best-fitting geographic range-independent model included a hidden unobserved state, indicating that diversification rates are better explained by this hidden state. Compared to the three other models, the best-fitting model accounted for 95% of the AIC weight and had an AIC value 7.02 units lower than that of the second best-fitting model (Table 2). The weighted average parameter estimates from all models indicate that both speciation rates and turnover rates did not differ between arid and mesic ranges (Figures S3 and S4; Table S5).

4 | DISCUSSION

With 47 recognised species, the mostly Australian-endemic blindsnake genus *Anilius* is currently the most diverse genus of Scolecophidia in the world. In this study, we estimated that the ancestral species in Australia occupied the tropical grassland biome, most likely as a result of dispersal from other tropical-mesic areas including New Guinea, Bismarck Archipelago and the Lesser Sundas. Within a few million years, this ancestral lineage split, with one group staying in the tropical grassland biome while the other group transitioned into the arid biome. Subsequent biome transitions in these two groups resulted in the distribution of biomes we observed across the phylogeny today. We also found that the paleoaridity index provides the best fit to the diversification dynamics observed in our time-calibrated phylogeny. Although aridification has been linked to elevated diversification rates in other plants and animals (Brennan & Oliver, 2017; Hernández-Hernández et al., 2014; Jha et al., 2021; Rabosky et al., 2014), our results suggest that aridification decreased diversification rates for Australian *Anilius* blindsnakes.

4.1 | Historical biogeography of *Anilius*

Our result supports the hypothesis that the ancestor of the Australian clade first dispersed to the mesic part of the Australian continent, which is consistent with previous studies (Marin, Donnellan, Hedges, Doughty, et al., 2013; Vidal et al., 2010). The observed pattern where the ancestral lineage first inhabited tropical-mesic regions before later expanding into other biomes as they emerge has also been documented in other radiations of Australian squamates (Chapple & Keogh, 2004; Melville et al., 2011; Oliver & Hugall, 2017). Many Australian groups originated in Eurasia and crossed into Australia

TABLE 1 Results of the 10 most supported RPANDA diversification models on the Australian blindsnake radiation.

Models	Parameters	logL	AICc	λ	α	μ	β	Paleoenvironment
BEnvVar+DCST (EXPO)	3	-115.86	238.43	1.32	-0.14	0.23		Arid ¹
BEnvVar (EXPO)	2	-117.87	240.08	11.00	-0.34			Arid ²
BEnvVar (EXPO)	2	-117.97	240.27	0.60	-0.20			Arid ¹
BEnvVar+DCST (EXPO)	3	-116.95	240.61	11.50	-0.24	0.28		Arid ²
BEnvVar+DEnvVar (EXPO)	4	-116.19	241.60	3.80	-0.22	0.00	0.20	Arid ²
BEnvVar (EXPO)	2	-120.08	244.50	27700.00	-0.83			Mean temperature ¹
BEnvVar+DEnvVar (EXPO)	4	-117.97	245.14	0.60	-0.20	0.00	-0.11	Arid ¹
BEnvVar (LIN)	2	-121.25	246.85	3.21	-0.13			Maximum temperature ¹
BEnvVar+DEnvVar (LIN)	4	-118.96	247.13	0.55	-0.01	0.07	-0.01	Arid ¹
BEnvVar+DCST (LIN)	3	-120.72	248.14	1.10	-0.06	0.01		Mean temperature ¹

Note: The table includes the models (BEnvVar=Speciation rate varying with environment; DCST=Constant extinction rate; DEnvVar=Extinction rate varying with environment; EXPO)=rates varying exponentially with environment; (LIN)=rates varying linearly with environment) number of parameters, the estimated log-likelihood (logL), the corrected Akaike information criterion (AICc), and corresponding parameter estimates (λ =speciation rate at present, α =parameter controlling the dependency of speciation rate on time or paleoclimate, μ =extinction rate at present, β =parameter controlling the dependency of extinction rate on time or paleoclimate). Sources of paleoenvironment presented in the table: ¹Scotese and Wright (2018) and ²Straume et al. (2020).

after the continental plates collided and caused the uplift of a number of 'stepping stones' including the Sunda islands, New Guinea and the Soloman islands. Our historical biogeographic estimation of *Anilius* is consistent with the hypothesis that this group arrived in Australia during the Miocene, first occupying tropical grasslands of Northern Australia before diversifying throughout the continent. However, whether the Australian radiation was a result of an oceanic dispersal from Southeast Asia, as proposed by Vidal et al. (2010), is equivocal. Our results indicate the common ancestor of Australian *Anilius*, *S. polygrammicus*, *R. multilineatus* and *A. subocularis* most likely occurred either in the Bismarck Archipelago or New Guinea. Increasing taxonomic sampling, particularly by including the New Guinean endemic *Anilius erycinus* and more species from *Ramphotyphlops* and *Acutotyphlops* will enable us to make more informed inferences about the origin of the group prior to colonising Australia. Our BioGeoBEARS analyses suggest that *Anilius* gradually diversified in the tropical grassland (Group 1) and arid biome (Group 2) during a time when Australia was relatively wet and humid (Byrne et al., 2008). This indicates that many species found in arid biomes, particularly in Group 2, diversified in the arid biome prior to the onset of widespread aridification in the late Miocene (Byrne et al., 2008).

We hypothesise that the contemporary distribution of *Anilius* and other blindsnakes in arid biomes is explained by pre-adaptation to living in such environments. Blindsnakes have been found in xeric areas around the world, such as *Rena humilis* in the desert of North America and *Myriopholis macrorhyncha* in semi-arid areas from east Africa to the Middle East (Sindaco et al., 2013). These arid-adapted blindsnake species share specialisations in diets and morphology with Australian *Anilius*, including a diet of pupae and larvae of social insects (Cundall & Greene, 2000; Webb & Shine, 1993), smooth scales that protect them from biting adult ants/termites, relatively small body size compared to other snakes, and fossorial lifestyle. A

combination of these traits allows blindsnakes to avoid direct heat exposure and desiccation in harsh arid environments.

4.2 | Regional vs global paleoenvironment

Our reconstructed Australia-specific paleotemperature data provided a better fit to the environment-dependent diversification models we considered in RPANDA than the global temperature data set (Condamine et al., 2013), although models that used paleoaridity provided better fit (Table 1; Table S4). In the context of our birth-death models, the absolute value of temperature might not have made much of a difference because our environment-dependent models fit the spline rather than absolute temperature. However, models that take in account thermal niche tolerance, such as NEMo (Hua et al., 2022), will benefit from paleoclimate reconstructions such as these to inform limits (boundaries). As it stands, current estimates of climate at deep timescales are still developing and we see strong differences in climate estimates from different approaches. For example, while both GCM-based and Köppen band-based approaches showed a gradual increase in temperature from 25 to 5 Ma before a decrease from the Pliocene to the present-day, the GCM-based approach showed a much sharper increase in temperature (Figure 2a). Similarly, aridity estimates from the GCM-based approach were starkly different to the Köppen band approaches (Figure 2b). This may be because deep-time GCM models are currently aimed at estimating general global fluctuations in climate, rather than regionally specific ones, which may be poorly approximated. Instead, the Köppen band approach is data driven and is based on known indicators of aridity from around the world (Boucot et al., 2013). This could explain why the Köppen band approach for aridity provided the strongest explanation for the diversification rate data. Because climate estimates can vary widely, we suggest future studies that aim to understand how aridification

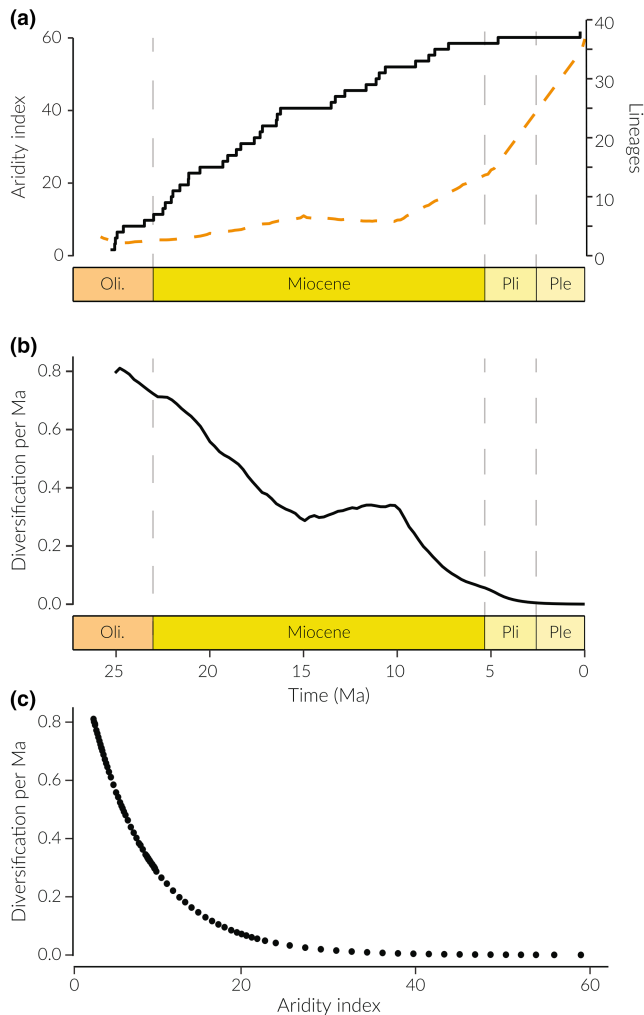


FIGURE 3 Effect of aridity change on the net diversification of *Anilius* estimated from the phylogeny. (a) The aridity index through time calculated from reconstructed paleoclimate (dashed line), and lineage through time estimated from the phylogeny (solid line). (b) Fitted net diversification rates through time reconstructed from parameter estimates ($\lambda = 1.32$, $\alpha = -0.14$, $\mu = 0.23$) from the best diversification model (speciation rates vary exponentially with paleoaridity and constant extinction rate; “BEnvVar + DCST (EXPO)”). (c) Fitted net diversification rates at different aridity index values calculated from parameter estimates of the previous model. Increased aridity is associated with decrease net diversification rates in this model.

affects diversification rates in Australia consider using these (and other) paleoclimate models to inform model inferences.

4.3 | Aridification and diversification rates

Our best-fitting diversification model shows that speciation is negatively associated with aridity (Figure 3c). Our reconstructed paleoaridity index data indicate that aridity increased from ~25 Ma following the opening of the Southern Ocean and the onset of the Antarctic circumpolar current (Byrne et al., 2008). A particularly sharp increase from 10 Ma followed from the “Hill Gap” period of cooling

(Hill, 1994), and intensification from 5 Ma onwards following the Pliocene transition to a contemporary arid Australian climate (Byrne et al., 2008). Out of the 38 lineages we considered, 5/35 divergence events occurred in the last 10 Ma when the continent intensively aridified. In contrast, 31/35 divergence event occurred between 25 and 10 Ma when the continent was getting warmer but not entirely arid. Indeed 12/16 lineages that have current distributions in the arid biome diverged before 10 Ma. This pattern is consistent with other studies on vertebrates that have shown that the divergence time for some arid-adapted taxa pre-dated the intense aridification in the last 5 Ma (Byrne et al., 2008; Catullo & Keogh, 2014).

The observed decrease in diversification rate with increasing aridification may be linked to decreasing speciation rates or increasing extinction rates. One hypothesis is that mesic-adapted ancestral blindsnakes may have been widespread in the past, but populations later became extinct due to extreme aridity in the last 5 Ma (Byrne et al., 2011; Fujioka et al., 2009). An extensive population genetics study of blindsnake by Marin, Donnellan, Hedges, Puillandre, et al. (2013) proposed that during widespread aridification, mesic-adapted lineages went extinct or were confined to mesic refugia, such as the Pilbara and Kimberley, where they became pre-adapted to seasonal aridity, which enable subsequent invasion into more arid environments. We note that isolation in mesic refugia may also promote diversification in mesic taxa. Additionally, long naked branches in our current phylogeny, particularly in Group 1, suggests past extinction events or intraspecific diversity not yet recognised. Our best-fitting models of diversification support constant extinction rates with decreasing rates of speciation. However, the lack of *Anilius* fossils makes extinction rates difficult to estimate (Louca & Pennell, 2021; Rabosky, 2010). An alternative explanation for the negative relationship between aridification and diversification is decreasing speciation rates through time. This could be driven by the indirect effect of aridification on population size (Goldie et al., 2010). More arid sites have lower primary productivity and may support smaller population sizes. Under the integrated evolutionary speed hypothesis (Gillman & Wright, 2013; Rohde, 1992), smaller population sizes are predicted to have slower rates of molecular evolution and subsequently lower rates of speciation. Lower rates of molecular evolution have been found in Australian arid zone plants compared to mesic zone plants (Goldie et al., 2010). Yet, here we found no difference between speciation rates in arid- and mesic-adapted lineages which is inconsistent with this hypothesis. Finally, another potential explanation for the negative correlation between diversification and aridity is the limited sampling of Australian blindsnakes, particularly in major sand deserts (Pepper & Keogh, 2021) or even in areas of high cryptic diversity such as the Kimberley (Ellis, 2019). The current phylogeny is missing 12 described species (Tiatragul et al., 2023), such as the arid-adapted *A. fossor* and *A. minimus*, and the true diversity has been estimated to exceed 56 species (Ellis, 2019; Marin, Donnellan, Hedges, Doughty, et al., 2013; Marin, Donnellan, Hedges, Puillandre, et al., 2013). It is possible that unrecognised species may be hidden under nominal species and that these missing lineages have diversified more recently when aridity is high.

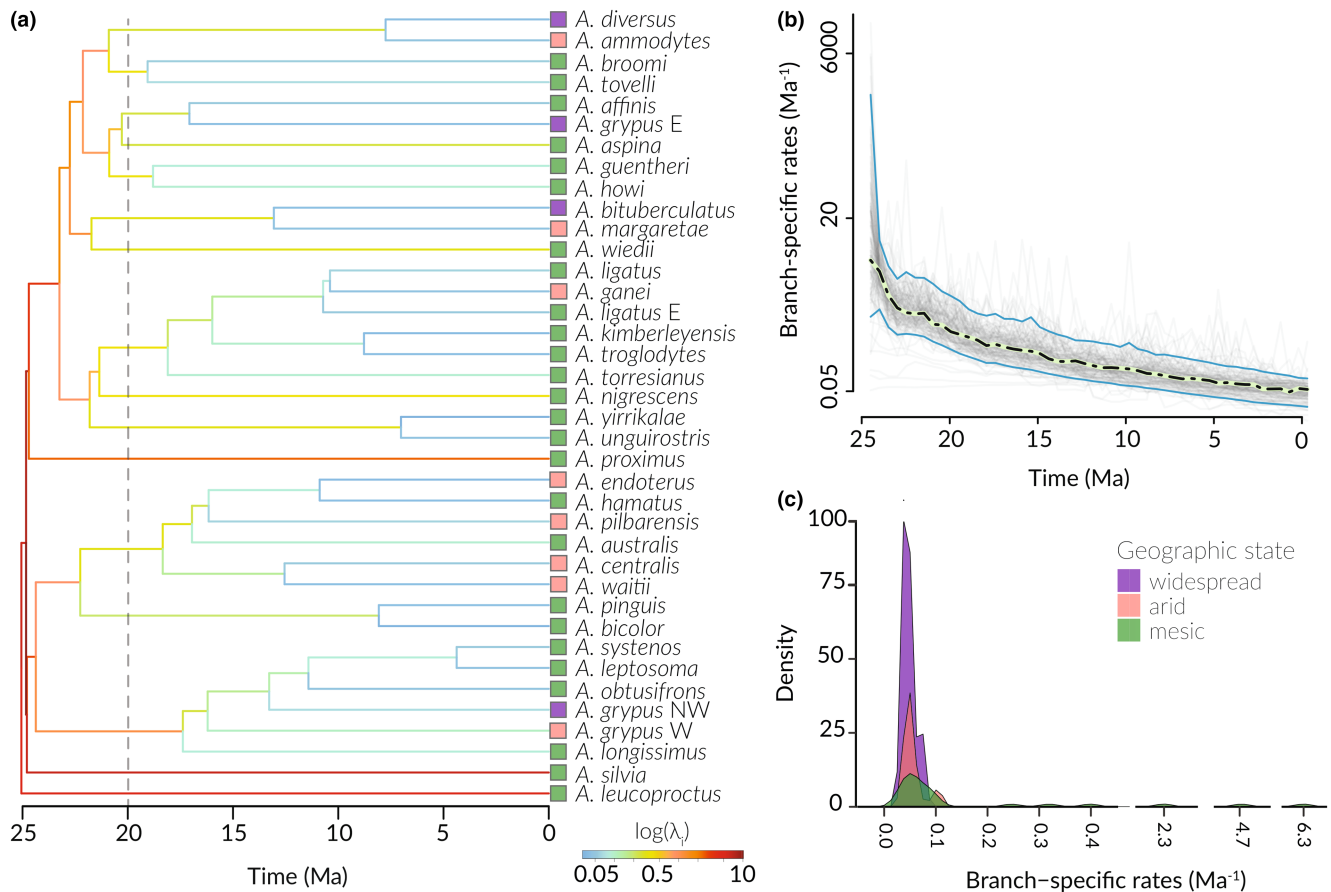


FIGURE 4 Diversification rates estimates from ClADS analysis. (a) Branch-specific rates ($\log(\lambda_i)$) across the phylogeny. (b) Mean branch-specific rates over time. Thin grey lines: individual draws from the MCMC. Blue lines: 95% credibility interval in the MCMC. Dotted green line: inferred mean rate through time estimated from the MCMC iterations. (c) Density plot of branch-specific rates by geographic range from ClADS analysis.

Description	Range effect	Hidden state	No. parameters	AIC	Δ AIC	AIC weights
GeoSSE	No	No	6	350.37	7.67	0.021
GeoSSE	Yes	No	7	356.24	13.54	0.001
GeoHiSSE	No	Yes	18	342.70	0.00	0.950
GeoHiSSE	Yes	Yes	20	349.72	7.02	0.028

Note: AIC scores and AIC weights indicate which models best fit the data.

If all suspected cryptic OTUs were treated as recognised species, we could see a different relationship with aridification.

4.4 | Diversification rates between arid- vs mesic-adapted lineages

Several studies have shown that arid-adapted species originated either from a single ancestor present in Australia before the Miocene, or through multiple independent expansion into the arid zone (Byrne et al., 2008). Our ancestral biome analyses show that several mesic ancestors of *Anilius* blindsnakes have diverged into the arid zone evident by multiple arid species throughout the phylogeny. This pattern

is consistent with several other groups of reptiles that started to diversify in the Miocene including monitor lizards (Brennan et al., 2021; Pavón-Vázquez et al., 2022), *Sphenomorphus* and *Eugongylus* skinks (Skinner et al., 2011), elapid snakes (Sanders et al., 2008), pythons (Esquerré et al., 2020, 2022) and several geckos (Ashman et al., 2018; Fujita et al., 2010; Oliver, Couper, & Pepper, 2014).

For these terrestrial reptiles, increased rates of speciation for arid-adapted taxa have been attributed to species filling niches in the saxicolous and xeric habitats that emerged with the contraction of mesic forest throughout the Miocene (Hugall et al., 2008; Sanders et al., 2008). Contrary to our predictions, results from our analyses on the Australian blindsnake phylogeny revealed no differences in speciation, extinction and turnover rates between arid and mesic

lineages. This suggests that the influence of aridity on diversification rates is more complex and does not follow the pattern we expected if species are filling new niches. Several factors may explain the lack of difference in diversification rates between biomes. One possible biological reason is that ancestral mesic-adapted blindsnakes already possessed specialised traits suitable for both arid and mesic subterranean environments, which reduced the potential for divergent diversification rates. A possible lack of differentiation in prey and availability of these prey items, particularly ant and termite larvae and pupae, in both biomes could also contribute to comparable diversification rates observed. Additionally, all species of blindsnakes exclusively inhabit subterranean environments during the day, which shield them against surface climatic variations such as extreme heat in the arid zone (Ehmann & Bamford, 1993). While other reptiles may seek shade cover, many species must also physiologically adapt to extreme temperatures. Finally, incomplete sampling may obscure the true diversification patterns, particularly because there may be a larger proportion of unrecognised species from the arid zone (Pepper & Keogh, 2021).

4.5 | Limitations

Although we did not detect conflicting signal between our analyses, some of our results, particularly those that estimate diversification rates (GeoHiSSE, ClaDS, and RPANDA), may be biased due to the small sample size of our *Anilius* phylogeny (Caetano et al., 2018; Maliet et al., 2019; Sun et al., 2020b). However, this near-complete phylogeny of *Anilius* is the most comprehensive data set available at this time. We suspect there remains several undescribed species of blindsnakes in Australia and New Guinea that may belong in the genus *Anilius*. Future studies should endeavour to include more samples per species to increase the chance of detecting cryptic OTUs. We also wish to highlight that obtaining genetic data from *A. erycinus* should be a priority as this will allow us to place the species among other *Anilius* and provide a more comprehensive picture of the evolution of this genus.

Our BioGeoBEARS ancestral biome estimation is limited by the areas, in this case biomes, to which we can assign our extant species. By following the WWF Bioregions maps, we had to assign species that occur in extremely different habitats in the same biome. For example, *A. longissimus*, a species that has only been collected from 30m underground on Barrow Island located 50km the northwest off the Pilbara coast of Western Australia, shares the same biome with *A. centralis* from the arid interior of the continent. Current methods do not allow us to account for heterogeneity of the biome even though we know the arid biome consists of everything from flat, seemingly featureless, desert in the interior to topologically complex mountain ranges on the fringes (Pepper, Ho, et al., 2011; Pepper & Keogh, 2021). However, modern software under development such as PhyBEARS may be able to account for more complex geological processes such as the movement of continents. For our SSE analyses, it is also noteworthy that the lineages we designated as “mesic-adapted” in reality may occupy a variety of biomes with

varying degree of aridity from tropical rainforests to tropical savannah. Finally, (mass) extinction likely played important roles in the pattern of diversity we observed today (Oliver & Hugall, 2017). Out of all our comparative analyses, only the SSE and some RPANDA models estimated extinction rates.

5 | CONCLUSION

As we continue to generate more genetic data to build ever more extensive phylogenies, there is a growing need to develop methods, and complimentary paleoenvironmental data sets, that allow us to test hypotheses about how different macroevolutionary processes influence diversification. We inferred that tropical grassland is the ancestral biome of Australian *Anilius* and acted as a major source of biodiversity to other biomes. Compared to other Australian reptile radiations in the Miocene, we observe a burst of diversification when the lineage first arrived on the continent and gradual decrease in diversification as the continent aridified. We showed that regionalised paleoaridity data provides a better fit to our Australian blindsnake phylogeny than global paleotemperature, highlighting the need to include and improve estimates of continental scale paleoenvironmental data in diversification analyses. To our knowledge, this is the first study that empirically fit diversification models to Australia-specific reconstructed paleoenvironmental data. We believe these regional paleoclimate models will be of interest for studies where species are geographically restricted.

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CONFLICT OF INTEREST STATEMENT

No, there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and analyses scripts are available from the Dryad Repository (<https://doi.org/10.5061/dryad.t4b8gtj5x>).

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BIOSKETCH

Sarin Tiatragul is broadly interested in learning about how organisms came to be and their interaction with the environment. This work is part of his PhD work at the Australian National University on the macroevolution of Australian blindsnakes.

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Author Contributions: S.T and J.S.K conceived the ideas; S.T and A.S collected the data; S.T analysed the data; S.T led the writing; A.S and J.S.K edited the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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