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The other side of the Sahulian coin: biogeography and evolution of Melanesian forest dragons (Agamidae)

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New Guinea has been considered both as a refuge for mesic rainforest-associated lineages that contracted in response to the late Cenozoic aridification of Australia and as a centre of biotic diversification and radiation since the mid-Miocene or earlier. Here, we estimate the diversity and a phylogeny for the Australo-Papuan forest dragons (Sauria: Agamidae; ~20 species) in order to examine the following: (1) whether New Guinea and/or proto-Papuan Islands may have been a biogeographical refuge or a source for diversity in Australia; (2) whether mesic rainforest environments are ancestral to the entire radiation, as may be predicted by the New Guinea refuge hypothesis; and (3) more broadly, how agamid ecological diversity varies across the contrasting environments of Australia and New Guinea. Patterns of lineage distribution and diversity suggest that extinction in Australia, and colonization and radiation on proto-Papuan islands, have both shaped the extant diversity and distribution of forest dragons since the mid-Miocene. The ancestral biome for all Australo-Papuan agamids is ambiguous. Both rainforest and arid-adapted radiations probably started in the early Miocene. However, despite deep-lineage diversity in New Guinea rainforest habitats, overall species and ecological diversity is low when compared with more arid areas, with terrestrial taxa being strikingly absent.

ADDITIONAL KEYWORDS: Australia – biogeography – ecological diversity – geology – *Hypsilurus* – *Lophosaurus* – New Guinea – over-water dispersal.

INTRODUCTION

The two major subaerial landmasses to the east of Wallace's Line, Australia and New Guinea (together referred to as Sahul), are geologically linked and share many biotic elements (Mitchell *et al.*, 2014; Marki *et al.*, 2017; Tallowin *et al.*, 2018), but they also have highly contrasting climates and geological histories (Nix, 1982; Hall, 2009). Australia is a geologically stable, low-relief landmass that has shown an overall trend towards intensifying aridification since at least the Miocene (Byrne *et al.*, 2008; Andrae *et al.*, 2018). In contrast, New Guinea is both one of the wettest and one of the most topographically and geologically complex places on earth (van Ufford & Cloos, 2005). Thus, as biotic assemblages in Australia were exposed to increasing aridity, lower productivity and stronger seasonality (Byrne *et al.*, 2008), new high-rainfall, high-productivity

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*Corresponding author. E-mail: p.oliver@griffith.edu.au and relatively aseasonal environments were forming in New Guinea or precursor landmasses (Nix, 1982). Historical changes in the configuration and climates of Australia and New Guinea have accordingly played a crucial, and potentially contrasting, role in shaping patterns of biotic dispersal, ecological diversification and extinction across Sahul.

From a biogeographical perspective, it has been hypothesized that much of the New Guinean biota (especially in the mountains) is derived from mesic-adapted Australian lineages, which have tracked their ecological niche northwards as Australia became more arid (Schodde & Calaby, 1972; Moyle *et al.*, 2016). Conversely, other studies show over-water dispersal and colonization (from both Asia and Australia) on terranes (the 'proto-Papuan archipelago') north of the Australian Craton (AC) during the Miocene or even earlier (Jønsson *et al.*, 2010; Oliver *et al.*, 2018b; Tallowin *et al.*, 2018). The uplift of a high (generally > 2000 m a.s.l.) and near-continuous Central Cordillera in New Guinea since the late Miocene has also been linked to vicariance and diversification of formerly continuous populations of lower-elevation taxa (Rawlings & Donnellan, 2003; Oliver *et al.*, 2017).

From an evolutionary perspective, the diverging environmental histories of Australia and New Guinea also provide opportunities to examine how ecological diversification within lineages may be shaped by contrasting environments, one increasingly wet and mountainous, the other flat and increasingly seasonal and dry. Inclusion of taxa from New Guinea in analyses of ecological diversity in Australasia might also provide a more complete perspective on the potential lineage and ecological diversity of mesic habitats in Sahul. For instance, analyses of marsupials have linked variation in brain size and reproductive strategies to seasonality and predictability of food supply, with species in relatively stable and mesic environments in New Guinea having larger brains and more continuous breeding (Fisher *et al.*, 2013; Weisbecker *et al.*, 2015).

The lizard family Agamidae (referred to as 'dragons') includes a moderately species-rich, ecologically and morphologically diverse radiation in Australia of ~100 species (Gray *et al.*, 2019) and a less diverse assemblage in Melanesia (New Guinea and the Solomon Islands) of 23 species (Roll *et al.*, 2017; Uetz *et al.*, 2019). Several phylogenetic studies have demonstrated that Australian and Melanesian agamids are closely related (all are placed the subfamily Amphibolurinae), with the single exception of the enigmatic riparian specialist *Hydrosaurus* (Hugall *et al.*, 2008; Townsend *et al.*, 2011). Although agamids show considerable sympatric diversity in arid areas of Australia (up to 18 species per 9200 km^2 grid cell; Powney *et al.*, 2010), sympatric diversity across Melanesia is considerably lower, with three or fewer co-occurring species in most rainforest areas (P.M.O., S.J.R. and O.J.S.T., personal observation; Fig. 1). The few species that occur naturally across both regions occupy only savannah habitats in New Guinea (Cogger, 2014). The vast majority of Australian agamid species (<95%) have been sampled genetically (e.g. Chen *et al.*, 2012; Supporting Information, Table S1). In contrast, only five of the 18 Melanesian endemic agamids (23%; Denzer & Manthey, 2016) have had their DNA sequenced, raising the possibility that agamid diversity in Melanesia is considerably underestimated, as for many other vertebrate taxa (e.g. Oliver *et al.*, 2013, 2017; Tallowin *et al.*, 2018).

Here, we present an analysis of the evolution, biogeography and ecological diversity of Melanesian Agamidae. We assess genetic diversity and relationships in the poorly known Melanesian taxa in *Hypsilurus* and *Lophosaurus*. We estimate dispersal history and ancestral areas to test whether the Australian Craton or terranes now accreted onto the northern edge of the Australian Craton are supported as the point of origin for Melanesian radiations. Comparisons of divergence dates between populations occurring north and south of the Central Cordillera are used to assess whether and when these major mountain ranges have functioned as barriers to gene flow. We also test whether New Guinean lineages originated in mesic biomes within Australia. Finally, we use ancestral state analyses to visualize how ecological diversity differs across the contrasting biomes that dominate in Australia vs. New Guinea.

MATERIAL AND METHODS

SAMPLING

Frozen or ethanol-preserved tissue samples from Melanesian forest dragons (*Lophosaurus* and *Hypsilurus*) were sampled from collections at the Australian Museum Sydney (AMS), Museum Victoria (NMV), the South Australian Museum (SAMA), Louisiana State University (LSU) and the Western Australian Museum (WAM) (Supporting Information, Table S1). Where possible, we used at least two individuals per species and sampled across known ranges. Including data from GenBank, our final dataset contained 116 *Hypsilurus* and *Lophosaurus* individuals, representing 11 of the 20 currently described species (Manthey & Denzer, 2006; Denzer & Manthey, 2016), in addition to two subspecies of *Hypsilurus papuensis* (for details, see Supporting Information, Table S1). Other taxa of *Hypsilurus* are very rare, including three known only from the type specimens (Meiri *et al.*, 2018), and obtaining tissue samples from these species is not currently feasible. New data were aligned with a concatenated four-gene dataset for Australasian agamids, comprising the coding region of the mitochondrial gene nicotinamide adenine dinucleotide dehydrogenase subunit 2 (*ND2*) and three nuclear loci (nuDNA): brain-derived neurotrophic factor

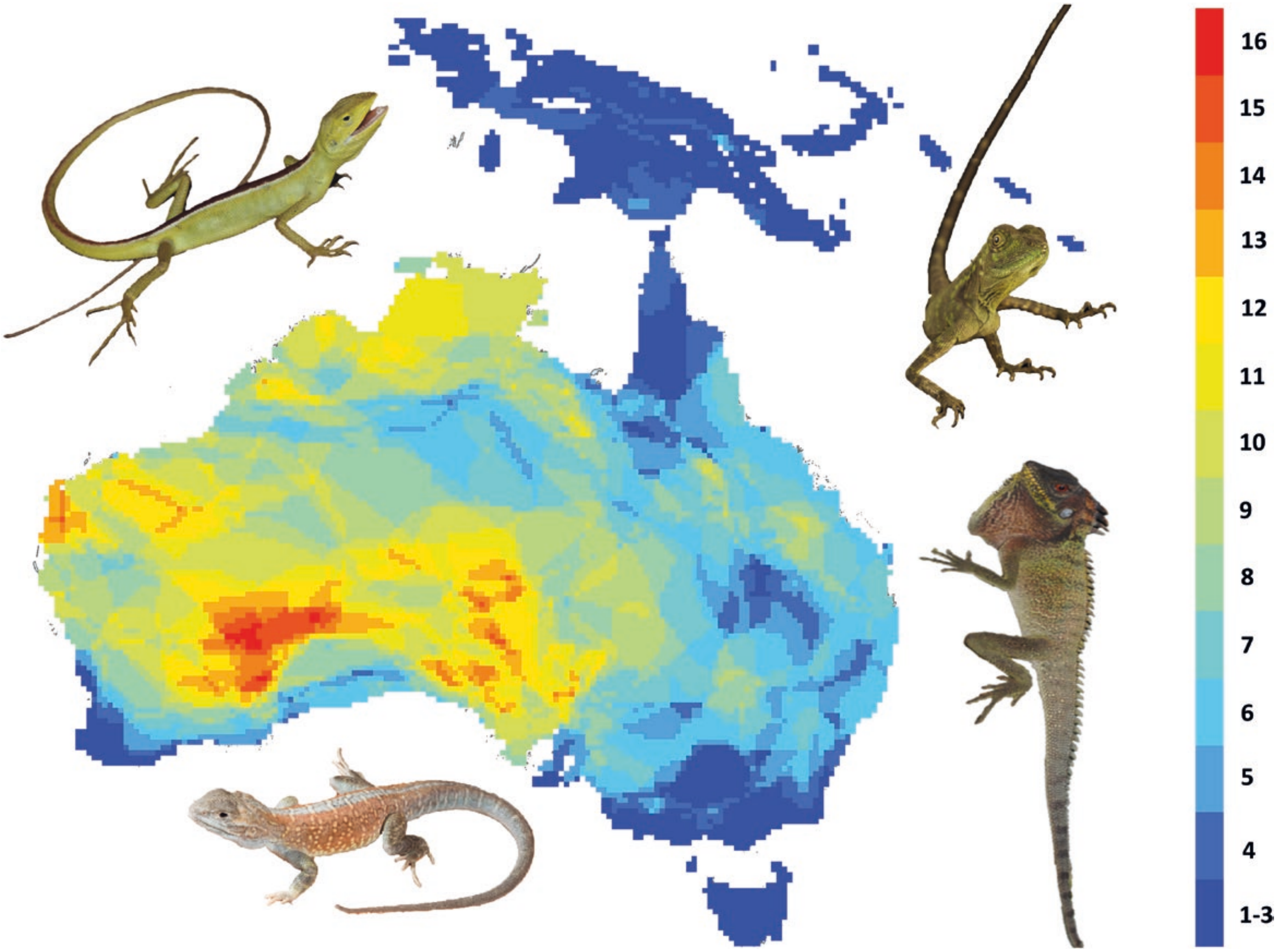

Figure 1. α-Diversity of agamids across Australia, New Guinea and surrounding islands (compiled from Roll *et al.*, 2017). Images, clockwise from bottom left, show examples of two of the most diverse genera of Australian agamids, *Ctenophorus pictus* and *Diporiphora superba*, and two genera of forest dragons, *Hypsilurus modestus* (top right) and *Lophosaurus dilophus* (bottom right). Images by Stewart McDonald, Paul Oliver, Tim Laman and Stephen Richards.

(*BDNF*), oocyte maturation factor Mos (*c-mos*) and recombination activating gene-1 exon (*RAG-1*).

Phylogenetic data generation and alignment

Extraction of DNA and polymerase chain reaction (PCR) amplification of each gene fragment were outsourced (AGRF Adelaide). Sequence data were aligned using MUSCLE v.2.0 (Edgar, 2004) as implemented in GENEIOUS v.6 (Biomatters; http://www.geneious.com). All regions included in alignments were protein-coding sequences and were translated into amino acids to check for nonsense mutations and alignment errors. Our final concatenated alignment of all genes comprised ≤ 3880 bp per sample (*ND2*, 1039 bp; *c-mos*, 930 bp; *BDNF*, 693 bp; and *RAG-1*, 1215 bp).

To investigate phylogenetic structuring and identify major lineages within the forest dragons, we initially analysed an *ND2* dataset including data from 86 *Hypsilurus* and 30 *Lophosaurus* specimens ('all samples'). Subsequently, for broader-scale analyses we used a ('lineages') alignment including 101 terminal taxa, with mitochondrial and nuclear data for exemplars of recognized species and operational taxonomic units (OTUs) identified elsewhere (Manthey & Denzer, 2006; Shoo *et al.*, 2008) or in the present study (see results below). This alignment was used to generate diversification timeframes and estimate patterns of geological dispersal, biome evolution and ecological evolution.

Genetic diversity and lineage delimitation in forest dragons

Our assessment of mitochondrial diversity ('all samples') for forest dragons from Melanesia revealed deep genetic splits within six nominal species (Fig. 2). To identify candidate OTUs for

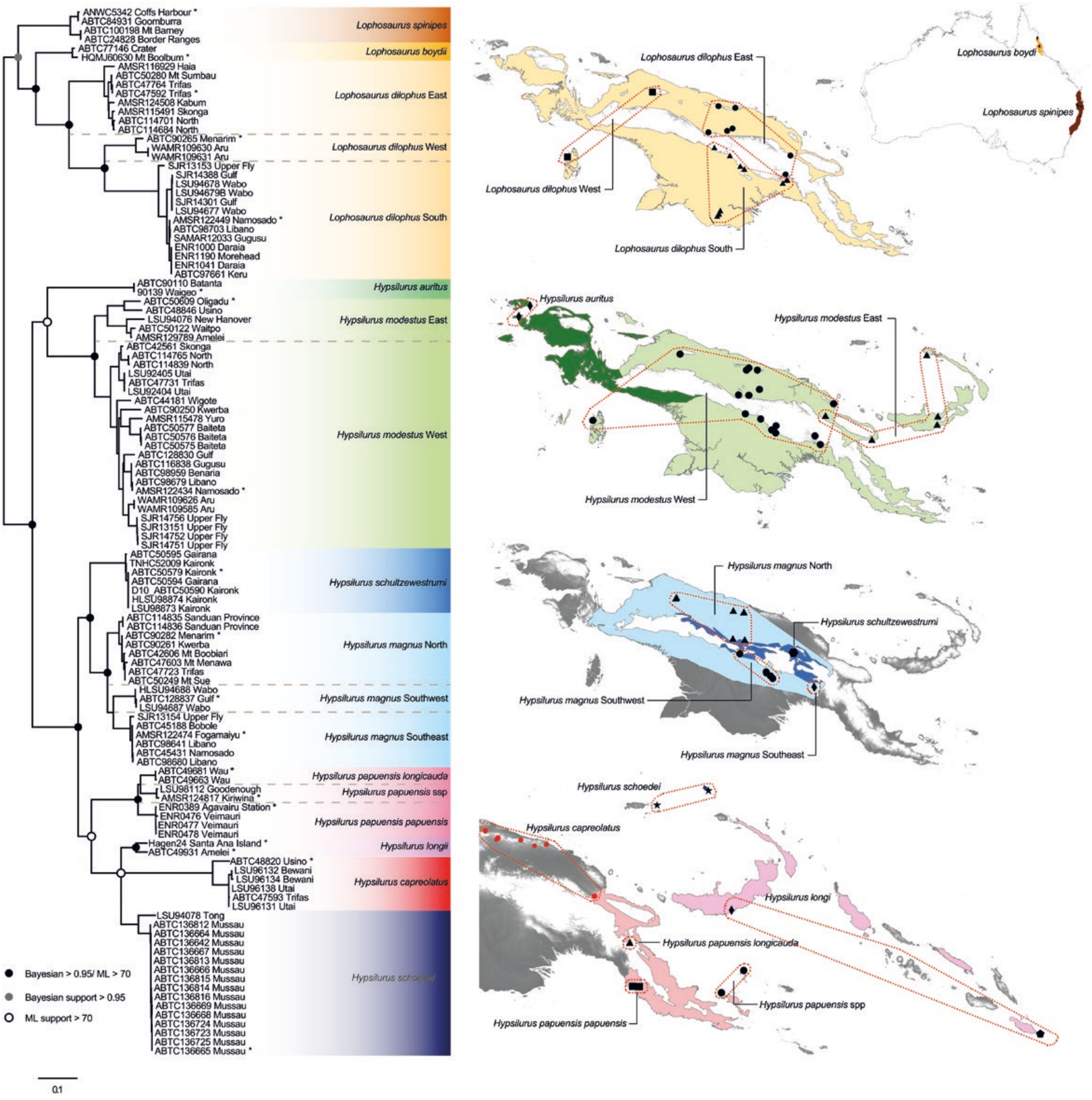

Figure 2. Summary maximum likelihood estimate of phylogenetic relationships and genetic diversity within sampled forest dragons in the genera *Hypsilurus* and *Lophosaurus*. Labelled clades on the tree are key lineages included in downstream biogeographical analyses, and underlying colours demarcate recognized species. Red dotted lines on maps demarcate the span of sampling for each of the same key lineages, and underlying coloured regions or coloured dots demarcate current estimates for the distribution of recognized species.

inclusion in downstream biogeographical analyses, we used a hierarchy of analytical and empirical approaches.

First, we used a multi-rate Poisson tree process (mPTP) to identify populations that might have histories of isolation (Kapli *et al.*, 2017). This non-coalescent, maximum likelihood (ML) method models speciation in terms of the number of substitutions (Zhang *et al.*, 2013). The mPTP has been shown to perform well on single-locus data (Tang *et al.*, 2014) and to outperform other species-delimitation methods when empirical datasets contain incomplete sampling or large differences in effective population sizes (Blair & Bryson, 2017).

Second, we calculated the uncorrected pairwise genetic distance (p-distances) in the coding region of the *ND2* gene between candidate OTUs identified in the mPTP analysis using MEGA7 v.7.0.20 (Kumar *et al.*, 2016). There is no standardized level of genetic divergence that strongly supports or refutes lineage recognition. A recent study on Asian agamids (Welton *et al.*, 2016) considered lineages showing pairwise divergences as low as 4% worthy of further consideration. Here, we found that all morphologically distinct and recognized species and subspecies showed divergence levels around or above 8% and, accordingly, used this as a broad metric for considering clusters as candidate OTUs (Supporting Information, Table S2).

Based on these analyses, for our downstream biogeographical analyses we included lineages that were: (1) supported by mPTP; and (2) showed morphological differentiation and/or sequence divergences close to or above 8%, even if they are considered conspecific under current taxonomic designations (Uetz *et al.*, 2019). We emphasize that the specific status and evolutionary distinctiveness of the candidate OTUs remains to be tested with better geographical sampling and higher-resolution phylogenomic population-level datasets.

PHYLOGENETIC ANALYSES AND DIVERGENCE DATES

We estimated phylogenetic relationships for the all-samples dataset using maximum likelihood (RAxML v.8.1.2: Stamatakis, 2014; IQ-TREE v.1.6.1: Nguyen *et al.*, 2015). For RAxML, we partitioned by codon and used the GTR+G model of sequence evolution (Stamatakis, 2006) as implemented using the RAxMLGUI v.1.5. Optimal partitioning strategies (Supporting Information, Table S3) were selected with PartitionFinder v.2.1.1 (Lanfear *et al.*, 2016) using the Bayesian information criterion (BIC). Best ML trees were determined from 100 randomized maximum-parsimony starting trees. In IQ-TREE, we undertook 1000 ultrafast bootstrap replicates (Hoang *et al.*, 2017), and the best-fitting model (Supporting Information, Table S3) was selected using ModelFinder (Kalyaanamoorthy *et al.*, 2017) as implemented in IQ-TREE.

Phylogenetic relationships within the 'lineages' dataset were estimated using ML (see above) and Bayesian methods (BEAST v.1.8.2: Drummond *et al.*, 2012). The ML analyses used settings and strategies for partitioning as outlined above (Supporting Information, Table S3). Bayesian (BEAST) analyses were run for 150 million generations, sampling every 50 000 generations, and implemented using the CIPRES Science Gateway v.3.1 for online phylogenetic analysis (http://www.phylo.org/index.php/portal/). Posterior trace plots and effective sample-size values of parameters (> 200) for each run were assessed in Tracer v.1.6 (Rambaut *et al.*, 2014), and effective sample-size values > 200 were considered adequate convergence. The first 50 million generations were discarded as burn-in using LogCombiner, and TreeAnnotator was used to infer the ultrametric tree (both in the BEAST package). Nodes are reported if they received ML bootstrap values ≥ 70% and posterior probability (pp) support values ≥ 0.95. The BEAST analyses were run with the relaxed- and strict-clock models and both Yule and birth–death speciation priors. We compared likelihoods using Akaike information criterion (AIC) values as implemented in Tracer. The birth–death model with relaxed clock was favoured.

Divergence dates were estimated in BEAST v.1.8.2 using the 'lineages' dataset. A primary fossil calibration was placed at the putative *Intellagama* stem, based on radiometric dating of sediments from Neville's Garden, Riversleigh (18.0 Mya; Woodhead *et al.*, 2016). A secondary calibration for the crown age of the Amphibolurinae of 30 Mya was derived from earlier studies of agamid phylogenetics (Hugall *et al.*, 2008; Townsend *et al.*, 2011; see Supporting Information, Table S4). We accounted for known uncertainty around secondary calibrations by using age ranges from the relevant original molecular studies (e.g. 95% confidence intervals; see Supporting Information, Table S4).

ESTIMATION OF DISPERSAL HISTORY

To investigate the timing and history of transitions between the Australian Craton and terranes to the north, we assigned all taxa in our 'lineages' tree to either the AC, including Australia and southern New Guinea (Fig. 3), or to the Northern Terranes and microcontinents (NT) of New Guinea, using distributional data from Roll *et al.* (2017) and updated here (see Supporting Information, Table S5). Three sampled taxa (*Hypsilurus modestus* West and two lineages of *Lophosaurus dilophus*; Fig. 2) occur across both regions and were given dual states. Given the low number of taxa and the complicated geology of New Guinea, we did not partition New Guinean taxa more finely.

Ancestral geological range reconstructions were estimated using a two-state model in the package 'BioGeoBEARS' v.1.1.1 (Matzke, 2013) implemented in R (v.3.5.2; R Development Core Team, 2018). According to the standard implementation, we ran three models: dispersal–extinction–cladogenesis (DEC); dispersal–vicariance analysis (DIVA-Like); and Bayesian analysis of biogeography (BayArea-Like). All three models were run with and without modelling founder-effect jump dispersal (the J-parameter; Matzke, 2014). We used the AIC to compare how well different biogeographical models fitted the data (Matzke, 2014).

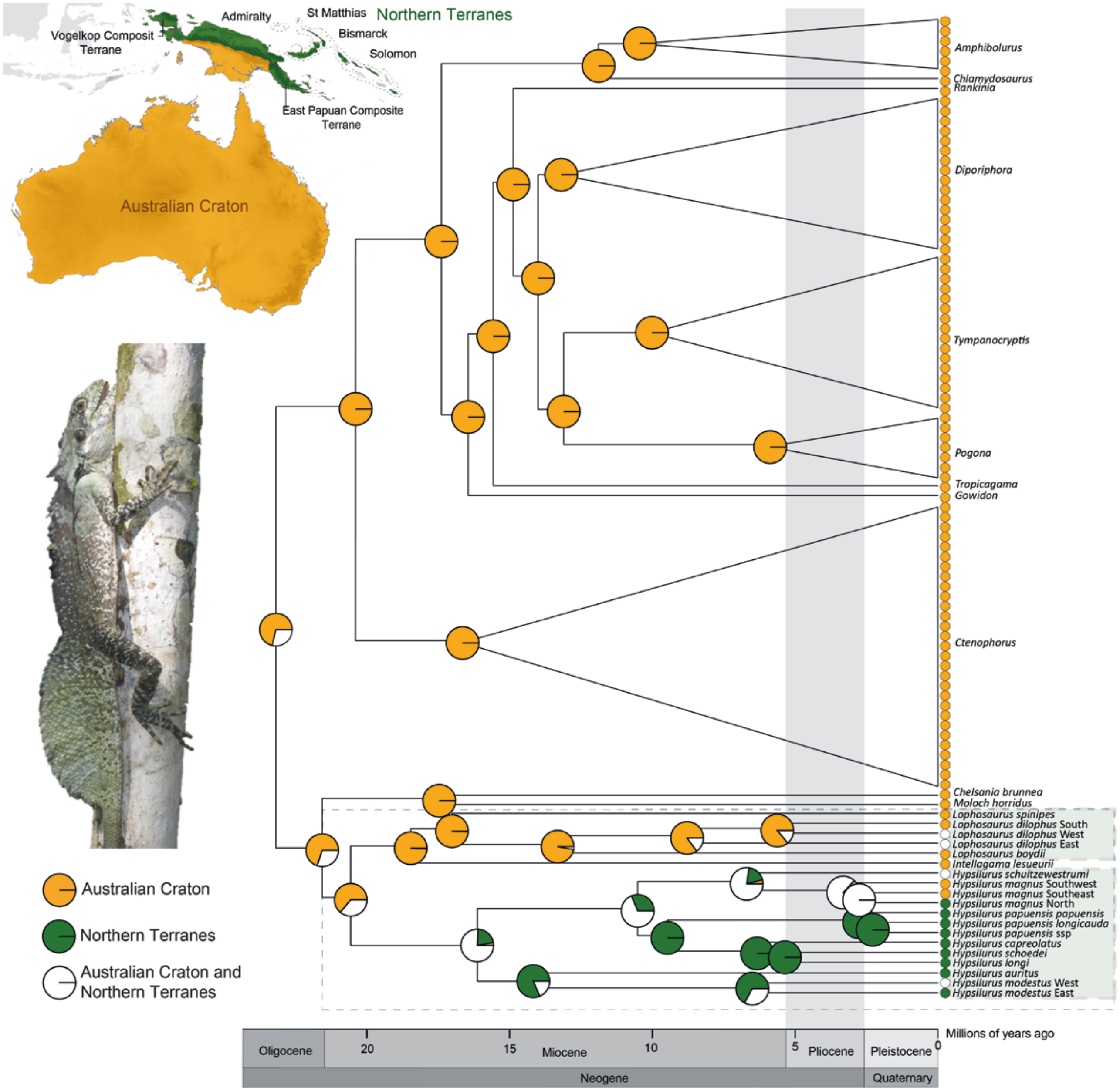

Figure 3. Ancestral area reconstruction of Australo-Papuan agamids using the concatenated lineage BEAST chronogram and a two-state geological model. Pale green boxes highlight the focal genera, *Hypsilurus* and *Lophosaurus*. The image of *Hypsilurus papuensis* was provided by Oliver Tallowin.

BIOME EVOLUTION

Australia and New Guinea were partitioned into five biomes reflecting observed patterns of biological differentiation and a widely used objective climate classification scheme, the modified Köppen–Geiger climate classification (Harvey *et al.*, 2000). The five regions largely follow Brennan & Oliver (2017): (1) savannah, corresponding to the savannah biome in northern Australia and far southern New Guinea; (2) temperate, covering broad areas in south-eastern and south-western Australia; (3) subtropical, including widely isolated areas on the east and west coast of Australia; (4) arid, including both arid and surrounding semi-arid regions and 'grassland' regions (*sensu* Harvey *et al.*, 2000) covering the vast majority of Australia (77.8%); and (5) rainforest, including wet, fire-sensitive forest dotted along the east coast of Australia, but dominating in New Guinea (Byrne *et al.*, 2008, 2011). All taxa were assigned to biome using the Atlas of Living Australia (http://spatial.ala.org.au), and taxa occurring in more than one biome were coded as such (see Supporting Information, Table S5).

We estimated patterns of biome evolution in BEAST, including biome as unordered states with a simple stochastic model of equal probability of all transitions, and otherwise using parameters and settings identical to the dating analyses above. For an independent estimation of the evolution of biome usage, we used the fitDiscrete function in the 'geiger' R package (Harmon *et al.*, 2008a). We compared three potential models using AICc scores: equal rates (i.e. a single probability of transition from any character state to any other state); symmetrical rates (i.e. separate probabilities of transition between each biome, but with no difference in the directionality of transitions); and allowing separate probabilities of transition for each direction between biomes. We reconstructed ancestral states for biome according to the best-fitting model using stochastic character mapping with the make.sim function (1000 simulations) in the R package 'phytools' (Revell, 2012).

ECOLOGICAL DIVERSIFICATION

To visualize ecological evolution of agamids lizards across Sahul, we reconstructed evolutionary patterns of habitat usage. We assigned each taxon to one of the following five habitat categories: (1) terrestrial (lives almost exclusively on the ground, rarely found in rocks or vegetation); (2) semi-arboreal (varies its time between the ground and elevated vegetation); (3) arboreal (lives almost exclusively in elevated vegetation, rarely venturing to the ground); (4) saxicolous (lives almost exclusively on or among rocky substrate); and (5) riparian (taxa typically associated with riparian habitats and foraging and taking refuge in water bodies; Collar *et al.*, 2010). Habitat data were sourced from published literature (e.g. Cogger, 2014) and personal observations (see Supporting Information, Table S5). Models for the evolution of habitat preferences were compared using the fitDiscrete function in the 'geiger' R package (Harmon *et al.*, 2008) as per analyses of biome.

RESULTS

GENETIC DIVERSITY AND DELIMITATION OF OPERATIONAL TAXONOMIC UNITS IN FOREST DRAGONS

Our dataset included 116 samples of Melanesian forest dragons (110 new samples), spanning 11 of the 20 recognized species (Uetz *et al.*, 2019) and three putative subspecies of *H. papuensis* (*H. papuensis papuensis*, *H. papuensis longicauda* and *H. papuensis* ssp.; Manthey & Denzer, 2016). Initial investigation using mPTP identified 22 lineages as candidate OTUs. The mean genetic divergence (p-distances) of lineages (excluding taxa not currently regarded as conspecific) identified by mPTP varied from 2 to 25%. We collapsed lineages that showed low divergence (< 9%) and for which we had no evidence of morphological divergence within four recognized taxa (i.e. *Hypsilurus capreolatus*, *Hypsilurus schoedei*, *Lophosaurus spinipes* and *L. dilophus*), leaving 18 recognized taxa/OTUs for inclusion in downstream analyses (Supporting Information, Table S2). Unrecognized OTUs were concentrated in four nominal species: *Hypsilurus magnus* (3), *H. modestus* (2); *H. papuensis* (3) and *Lophosaurus dilophus* (3). Splits within *L. dilophus* lineages (termed West, North and South) were very deep (18–25%). Two *H. modestus* lineages (East and West) showed splits > 10%, with further intra-lineage variation in both (5–8%). *Hypsilurus papuensis* comprised three moderately divergent lineages (8–11%) corresponding to subspecies and morphotypes identified by Manthey & Denzer (2016). Finally, *H. magnus* comprised three lineages showing divergence between 8 and 10% and minimal intra-lineage structuring (≤ 1%).

We identified four forest dragon taxa with distributions to the north and south of the New Guinea Central Cordillera (Fig. 2), from west to east: *L. dilophus* West, ~4% split between samples from Foja Mountains and the Aru Islands; *H. magnus*, ~9–10% split between two southern lineages and one to the north of the Central Cordillera; *H. modestus* West, ~6% split between multiple samples clustered on adjacent sides of the cordillera; and *L. dilophus* North, 5% split between a single sample from southern Papua New Guinea and many northern Papua New Guinea samples. *Hypsilurus papuensis* samples on the different sides of the Owen Stanley Mountain Range also differed by 10%.

PHYLOGENETIC RELATIONSHIPS AND DIVERGENCE DATING

The monophyly of *Hypsilurus* and *Lophosaurus* was supported in all analyses, as were the majority of intrageneric splits between lineages within both genera (Figs 2, 3; Supporting Information, Figs S1, S2). Conversely, intergeneric relationships between *Hypsilurus* and *Lophosaurus* and other genera of Australo-Papuan agamids were not well supported (Supporting Information, Figs S3, S4).

Lophosaurus showed a stepped distribution of decreasing divergence towards northern latitudes. *Lophosaurus spinipes* from north-east New South Wales and south-east Queensland, Australia is the most southern and divergent taxon. Further north, *Lophosaurus boydii* from the north-east of Queensland, Australia, is sister to the clade of three lineages in the *L. dilophus* complex (New Guinea and Aru Islands).

Within *Hypsilurus*, three major clusters were identified with strong support in both Bayesian inference and ML analyses. The *H. modestus* group comprises moderately sized (snout–vent length < 150 mm), mostly green dragons (*H. modestus* complex and *Hypsilurus auritus*). The *H. magnus* group comprises two species of New Guinea water dragons (*Hypsilurus schultzewestrumi* and the *H. magnus* complex). The *H. papuensis* group comprises the remaining taxa from northern New Guinea (*H. capreolatus*), the Papuan Peninsula (*H. papuensis* complex) and islands of East Melanesia (*Hypsilurus longii* and *H. schoedei*). Within this clade, the position of *H. schoedei* is ambiguous, and it sits on an asymmetrically long branch (Fig. 2; Supporting Information, Figs S1–S4), suggesting a distinctive pattern of molecular evolution (e.g. substitutional bias) in this insular taxon. All analyses inferred the *H. modestus* group as the sister group to remaining *Hypsilurus*, and the *H. magnus* and *H. papuensis* groups were supported strongly as sister lineages.

The 95% posterior distribution for the crown divergence of *Lophosaurus* spans the mid to late Miocene (18.8–14.2 Mya), and the *L. dilophus* complex endemic to New Guinea centres upon the late Miocene (9.8–5.8 Mya). Crown ages for *Hypsilurus* are also Miocene (20.4–11.1 Mya), with ongoing diversification of major species and lineages throughout the late Miocene to early Pleistocene. Genetic divergence north and south of the Central Cordillera within the *H. magnus* and *H. papuensis* complexes was dated at ~3.6–2.4 Mya.

Dispersal history

BioGeoBEARS identified dispersal–extinction–cladogenesis as the model with highest likelihood (Supporting Information, Table S6). Australia, and specifically the Australian Craton, was inferred as the most likely origin of the ancestor for both *Hypsilurus* and *Lophosaurus*, and for the entire Australo-Papuan agamid clade (Fig. 3; Supporting Information, Fig. S5). Within *Lophosaurus*, no lineage is endemic to regions north of the Australian Craton. The ancestral area for the crown radiation of *Hypsilurus* is ambiguous. However, at least four *Hypsilurus* clades are endemic to regions north of the Australian Craton: *H. capreolatus* and *H. modestus* East in northern New Guinea, *H. longii* in the Bismarck and Solomon archipelagos, and *H. schoedei* in the Admiralty Archipelago. *Hypsilurus papuensis* is also principally endemic to the geologically distinct East Papuan Composite Terrane (Fig. 3). Furthermore, for the entire *H. modestus* group, northern terranes are inferred as the ancestral area with mean divergences dating to the mid-Miocene (14.2 Mya; Fig. 3).

Biome evolution

For ancestral state reconstruction of biome, an equal-rates model with a lambda transformation had the highest likelihood (Supporting Information, Table S7). The ancestral biome for the crown radiation of Australo-Papuan agamids is ambiguous in analyses using geiger (Fig. 4) and BEAST (Supporting Information, Fig. S6). *Hypsilurus* and *Lophosaurus* show exclusive histories within rainforest biomes. In contrast, most Australian agamids (including the two most species-rich genera, *Ctenophorus* and *Diporiphora*) are concentrated in a well-supported, species-rich clade dating to the early Miocene, which is most diverse in arid biomes and has no extant representatives in rainforest biomes. The remaining highly divergent and species-poor Australian lineages are as follows: *Intellagama* (forest; riparian, not necessarily rainforests); *Chelosania* (savannah); and *Moloch* (arid).

Ecological evolution

For ancestral state reconstruction of habitat, a symmetric model with an early-burst transformation provided the highest likelihood (Supporting Information, Table S8). Arboreality was inferred as the ancestral state for the primarily Melanesian agamids (*Hypsilurus* and *Lophosaurus*), with a single transition to a riparian lifestyle inferred in the *H. magnus* group. Deeper nodes for the Australian agamids were predominantly reconstructed as terrestrial (Fig. 4) and are concentrated in three ecological niches that are unused in rainforest biomes: terrestrial, semi-arboreal and saxicoline.

DISCUSSION

Lineage diversity and biogeography within Melanesia

We present a DNA sequence-based estimation of diversity and evolutionary relationships among the Melanesian forest dragons *Hypsilurus* and *Lophosaurus*. Monophyly of these respective genera is well supported. Provisionally, we recognize 16 divergent monophyletic lineages among the sampled Melanesian forest dragons, including lineages currently subsumed within four recognized taxa (*H. modestus*, $N = 2$; and *H. magnus*, *H. papuensis* and *L. dilophus*, $N = 3$ within each). Two additional lineages of *Lophosaurus* are present in Australia. Genetic data are still lacking for seven recognized *Hypsilurus* species (some of which are known only

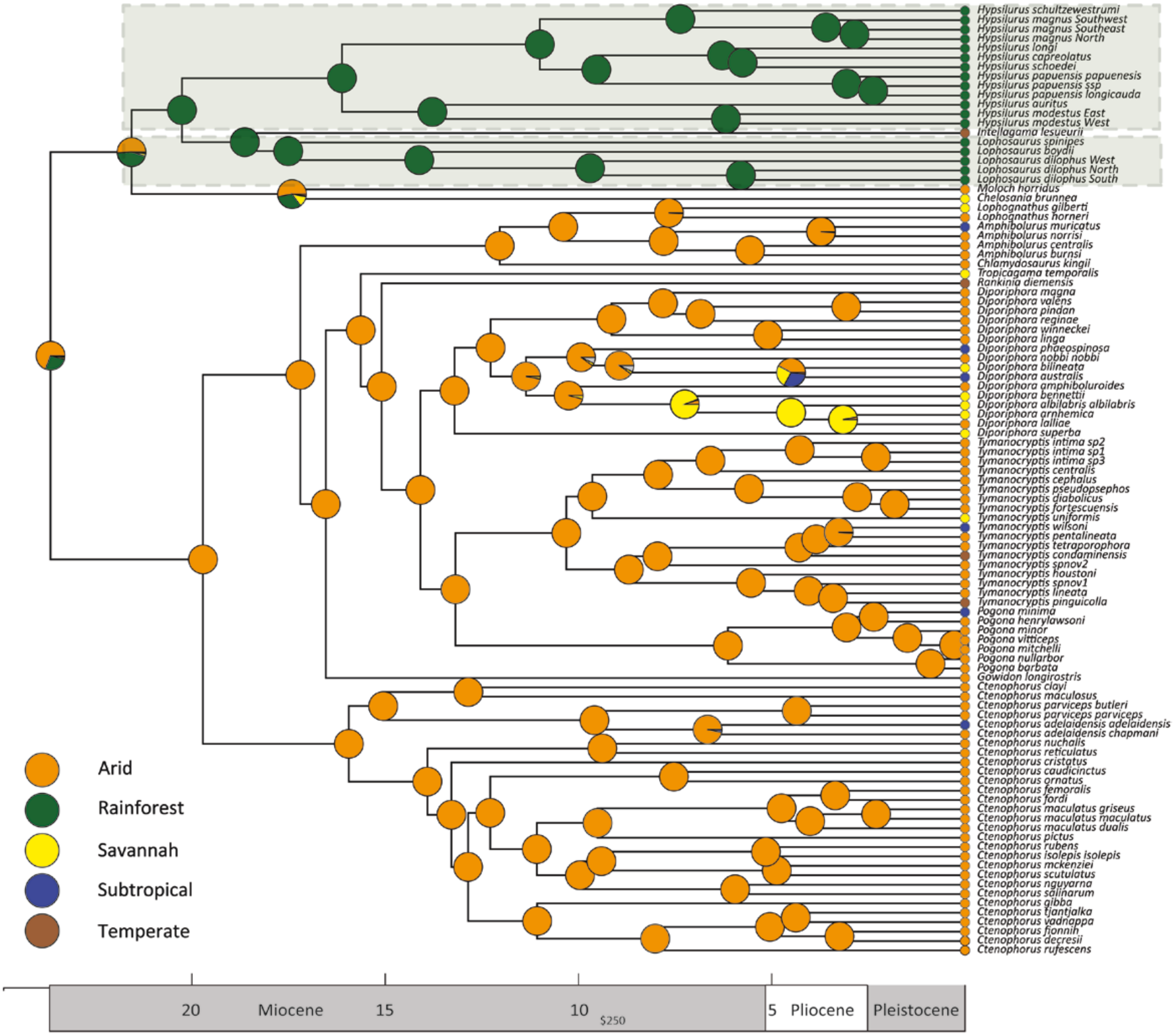

Figure 4. Ancestral state reconstruction of Australo-Papuan agamids for biome occurrence (A) and habitat usage (B). The two main lineages of Australo-Papuan forest dragons are highlighted in pale green. Note the complete absence of terrestrial taxa across divergent genera occurring in rainforest biomes.

from their type specimens; Meiri *et al.*, 2018) and at least two candidate species (Manthey & Denzer, 2016) distributed across New Guinea. Filling these gaps will be an important step towards achieving a full resolution of agamid diversity in these regions, but our study provides a framework for a first biogeographical analysis of the forest dragons.

All forest dragon clades in New Guinea contain widespread taxa, and there is little evidence for micro-endemism. This contrasts with agamids occurring in similar topographically complex rainforest habitats to the west of Wallace's Line, where a number of endemic species with restricted ranges occur (Somaweera & Somaweera, 2009; Wood *et al.*, 2009; Das, 2015; Grismer *et al.*, 2016). Five species or species complexes of forest dragons also show low genetic divergences across the Central Cordillera of New Guinea, indicating that these mountains have become a barrier to gene flow only in recent times. This contrasts with evidence for Melanesian montane radiations of birds, frogs and lizards dating back at least into the early Miocene (Irestedt *et al.*, 2009; Oliver *et al.*, 2017; Tallowin *et al.*, 2018). Together, these data suggest that mountains (with an associated biota) in New Guinea are likely to date back well into the Miocene, but that the current configuration of a long and high Central Cordillera functioning as a barrier to north–south geneflow for lowland taxa is more recent.

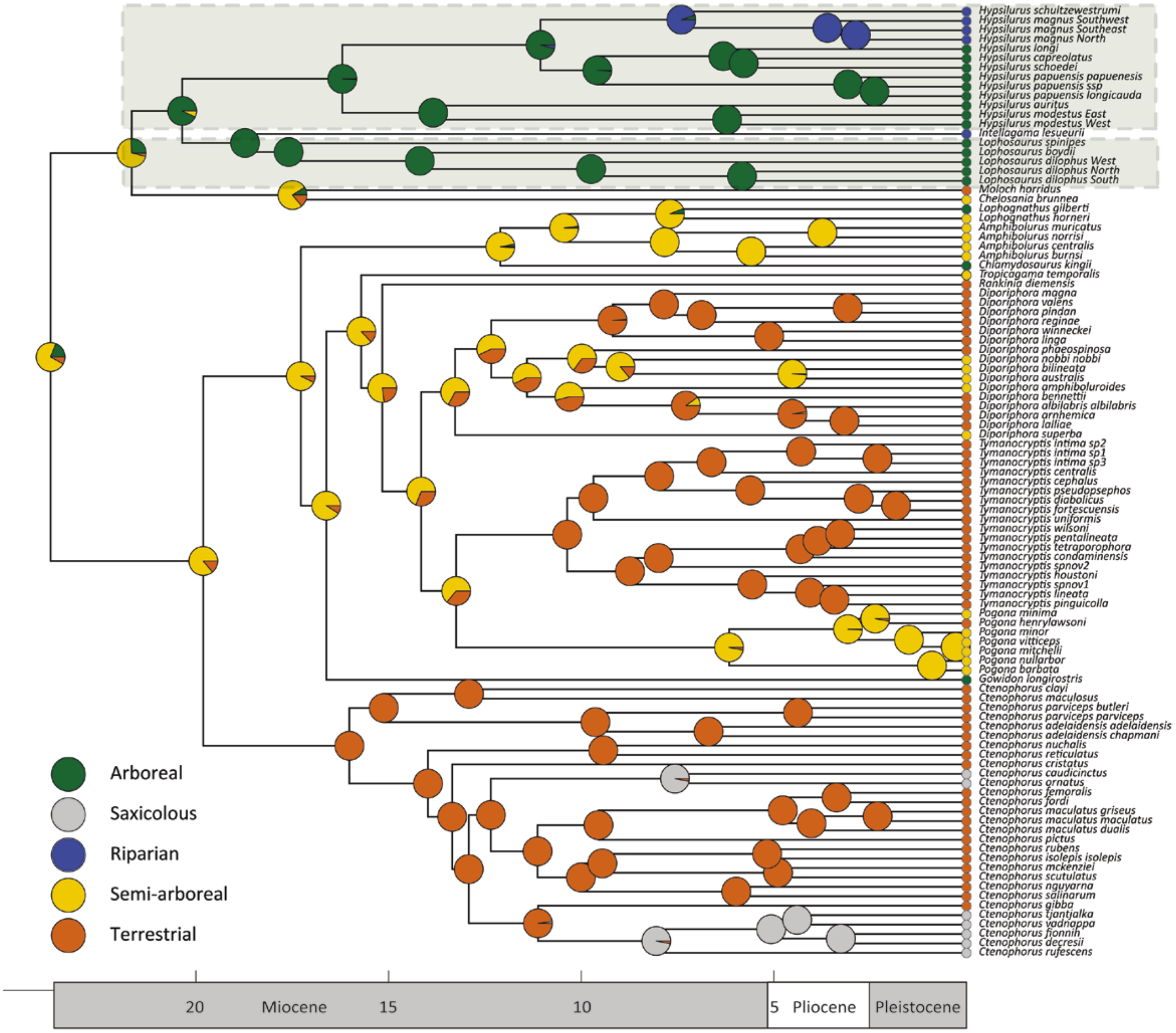

Figure 4. Contiued

We identified clear evidence of past over-water dispersal in *Hypsilurus*. *Hypsilurus modestus* East has dispersed between New Britain, New Ireland and northeast New Guinea, which may itself have been composed of smaller and more isolated islands at various points during the late Cenozoic (van Ufford & Cloos, 2005). Two further lineages are endemic to islands north of New Guinea and show evidence of recent dispersal and possibly also of extinctions across islands. *Hypsilurus schoedei* has a restricted and disjunct range on Tong and Mussau islands, but is unknown from the much larger nearby island of Manus (S. Richards and C. Austin, personal observation; Fig. 2). *Hypsilurus longii* also occurs from New Britain to Malaita, but there are no recent records from the intervening islands of Guadacanal and Choiseul in the Solomon archipelago. However, the inhabitants of Choiseul Island recognize and have a local name for an agamid lizard, suggesting recent extirpation (McCoy, 2006). Another species, *Hypsilurus godeffroyi*, possibly from the island of Palau, has not been recorded since its original description and is possibly extinct (Zug, 2013). The drivers of local rarity/extinction of these island agamids remain speculative; however, in Australia agamids have been shown to persist poorly on small islands compared with other lizards (Palmer *et al.*, 2013).

NEW GUINEA: REFUGE AND CRADLE?

The Australian Craton is inferred to be the ancestral area of *Lophosaurus* and all Australo-Papuan agamids.

Sampling of other *Hypsilurus* taxa, and careful analysis of '*Hypsilurus*' fossils from Australia (Hocknull *et al.*, 2007), might improve the resolution of ancestral area evolution across both regions. Nonetheless, our data suggest that, for forest dragons, New Guinea is home to both lineages that were formerly more widespread in Australia (refuge) and to others that might have deeper origins on islands that formed to the north of the Australian Craton during the Miocene (cradle).

Lophosaurus shows progressively shallower splits between lineages with decreasing latitude, indicating origins on the Australian Craton, with subsequent range contraction. Some birds (Norman *et al.*, 2018) and marsupials (Mitchell *et al.*, 2014) show similar late Miocene splits between Australian and New Guinean lineages, leading to the suggestion that this was a time of major exchange between the two present-day regions, especially for poor over-water dispersers. Future dating analyses of low-vagility rainforest-associated lineages occurring across Australia and New Guinea (e.g. microhylid and myobatrachid frogs, sphenomorphine skinks) might provide additional evidence of late Miocene splits of allopatric Australian and Melanesian populations.

In contrast, *Hypsilurus*, although completely absent from present-day Australia, is clearly able to disperse over marine barriers and shows deeper divergences in the Melanesian region [including inferred mid-Miocene (14.2 Mya) diversification on terranes in the *H. modestus* group]. This age is older than that from some models for the formation of New Guinea (e.g. Moyle *et al.*, 2016); however, over-water colonization with subsequent diversification on islands north of the AC in the mid-Miocene has been inferred in an increasingly diverse array of vertebrate taxa (Jønsson *et al.*, 2010; Oliver *et al.*, 2018a, b, c; Tallowin *et al.*, 2018). Furthermore, within *Hypsilurus*, and especially the *H. modestus* and *H. papuensis* groups, distributions of extant lineages also suggest a history of allopatric diversification on formerly disjunct geological fragments that later accreted together to form New Guinea: the Vogelkop (*H. auritus*), northern terranes (*H. capreolatus* and *H. modestus* East) and the East Papuan Composite Terrane (*H. papuensis* complex). Other recent phylogeographical or biogeographical studies have also identified endemic lineages associated with these distinct regions (e.g. Kalkman *et al.*, 2013; Unmack *et al.*, 2013; Tallowin *et al.*, 2018).

BIOME HISTORY AND ECOLOGICAL DIVERSITY

The pattern of biome evolution inferred for the Australo-Papuan agamids suggests rainforest associations that date back to the earliest Miocene, consistent with the general model of ancestrally mesic Australian lineages contracting or adapting in response to the spread and intensification of aridification (Byrne *et al.*, 2008, 2011). However, our data also imply a similar long history in other biomes, with the most diverse extant non-rainforest clade originating around the early Miocene. Miocene or earlier diversification and radiation away from rainforest habitats has now been inferred for a number of species-rich Australian animal and plant radiations (Toon *et al.*, 2015; Brennan & Oliver, 2017). These data all lend growing support to inferences from palaeoclimatic data that although rainforest might well be ancestral for many Australian radiations, semi-arid or seasonal environments also have a long history in Sahul (Sniderman *et al.*, 2016).

Finally, the inclusion of Melanesian taxa emphasizes how the great ecological diversity of Australo-Papuan agamids (Pianka, 1986; Melville *et al.*, 2001; Collar *et al.*, 2010) is non-randomly distributed across major biomes. In the Australian arid and semi-arid zones, dragon assemblages include a suite of terrestrial or near-terrestrial species, including burrowers, stone mimics and grass dwellers (Melville *et al.*, 2001; Collar *et al.*, 2010). Such ground-dwelling specialists, which are also common in central and Western Asia and Africa, are strikingly absent from terrestrial environments in the rainforests of Sahul, where agamids have not moved out of the putatively ancestral arboreal/riparian niche, despite a long history in this biome. In Australia alone, this lack of ecological diversity could be explained by extinction, because rainforest is highly limited and relictual. However, in New Guinea the rainforest is extensive, and forest dragons are moderately diverse, show localized sympatry and have a long history, but apparently have not specialized to use terrestrial niches (although the ecology of some taxa remains poorly known). Furthermore, with a small number of potential exceptions (e.g. some *Ceratophora* and *Otocryptis* from Sri Lanka and southern India; Somaweera & Somaweera, 2009), few terrestrial agamids are present in Asian rainforests. These data all suggest that low ecological and species diversity of agamids in Sahulian rainforest biomes is not only a function of past extinction, but also reflects fundamental differences in how these lizards diversify in dry vs. wet habitats. Adverse abiotic conditions, such as reduced solar radiation and basking opportunities in rainforests, could impact heavily terrestrial agamids, particularly heliothermic species. A complementary hypothesis might be that agamids are excluded from terrestrial environments in mesic biomes by biotic interactions, such as predation (e.g. by mammals or varanids) and/or competition (e.g. with skinks that are better adapted to shady microclimates).

CONCLUSIONS

An improved understanding of Melanesian forest dragon diversity and inclusion of these taxa into a phylogenetic framework indicates that one lineage shows evidence of retreat as Australia became more arid through the Miocene, whereas another shows evidence of over-water dispersal and diversification on islands to the north of Australia by the mid-Miocene or earlier. Rainforest biomes might be ancestral for some Australian agamid lineages, but there is also strong evidence of early Miocene adaption to and extensive radiation within more arid biomes. Finally, striking differences in agamid ecological diversity between rainforest areas and more arid biomes emphasizes how the contrasting environments across Australia and New Guinea have shaped divergent evolutionary trajectories, even in radiations with a relatively close relationship.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Australo-Papuan agamid specimen numbers, museum accession information, collection localities and GenBank accession details for all the samples included in our analyses.
Table S2. Pairwise sequence divergence between the 18 recognized and putative species of *Lophosaurus* and *Hypsilurus* included in biogeographical analyses.
Table S3. Information on the phylogenetic analyses, partitions, models and parameters.
Table S4. Phylogenetic dating calibrations for Australopapuan agamids used in this study.
Table S5. Character state traits, body-size measurements, geological region, biome and habitat preference information for all samples used in the ancestral state and area analyses.
Table S6. Results of likelihood comparisons of dispersal models implemented in BioGeoBEARS on a reduced Australo-Papuan agamid concatenated genetic dataset and geological categories.
Table S7. Results of fitting various macroevolutionary models of the discrete biome to the Australo-Papuan agamid phylogeny.
Table S8. Results of fitting various macroevolutionary models of the discrete trait habitat preference to the Australo-Papuan agamid phylogeny.
Figure S1. Maximum likelihood phylogeny of Australo-Papuan forest dragons (*Hypsilurus* and *Lophosaurus*) inferred from mitochondrial DNA using RAxML.
Figure S2. Maximum likelihood phylogeny summarizing the diversity of Australo-Papuan forest dragons (*Hypsilurus* and *Lophosaurus*) inferred from mitochondrial DNA using IQ-TREE.
Figure S3. Maximum likelihood phylogeny for Australo-Papuan agamids inferred from mitochondrial and nuclear DNA using IQ-TREE.
Figure S4. Maximum likelihood phylogeny for Australo-Papuan agamids inferred from mitochondrial and nuclear DNA using RAxML.
Figure S5. Ancestral geological range reconstructions of the Australo-Papuan agamids.
Figure S6. Bayesian inference chronogram estimation of Australo-Papuan agamid species and candidate species using a concatenated lineage dataset and posterior probabilities indicated at each node. The 95% highest posterior density (HPD) distributions are shown at the nodes. The colour of the branches indicates the biome.