



The Kimberley, north-western Australia, as a cradle of evolution and endemic biodiversity: An example using grunters (Terapontidae)

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Abstract

Aim: To test two prominent, alternate hypotheses that provide explanations for the great accumulation of endemic species in the Kimberley bioregion in north-western Australia, using an extensively sampled, region wide phylogeny of northern Australia's most species-rich freshwater fish family, Terapontidae. Specifically, we test whether the Kimberley may act as (1) a "museum" accumulating taxa and endemic species over time or (2) a "cradle" of more recent diversification and neoendemism.

Location: The Australian monsoonal tropics.

Taxon: Grunters (Terapontidae).

Methods: We obtained a robust and well-supported Bayesian phylogeny for the family using DNA sequences from mtDNA and nuclear gene regions. We performed molecular phylogenetic analyses using species tree methods including molecular dating analysis, ancestral range reconstruction and diversification analysis.

Results: Based on our phylogeny, the combined molecular clock estimates and likelihood-based historical-biogeographic reconstructions suggest that terapontids recently transitioned into the Kimberley from the east during the late-Miocene. We found that 80% of Kimberley terapontids diversified within the Kimberley in the last 3 Ma. Furthermore, diversification analyses identified a single significant shift in diversification rates ~1.4 Ma that corresponds with a change in global climate midway through the Pleistocene that was predominantly driven by speciation in the Kimberley.

Main conclusions: The weight of evidence suggests that the Kimberley has been a "cradle" of evolution for Terapontidae, rather than a "museum". Our analysis provides strong evidence for a geologically recent transition of terapontids into the Kimberley from regions to the east during the late-Miocene followed by a significant increase in speciation rates during the Pleistocene, driven by speciation in the Kimberley. The results provide important insight into the evolutionary and biogeographical processes that have shaped the regions unique biota, which will inform land managers working to protect and conserve both species and the processes responsible for generating and sustaining them.

KEYWORDS

biogeography, diversification, freshwater fish, molecular clock, monsoonal tropics, phylogenetics, range reconstruction

1 | INTRODUCTION

Refugia are environmental habitats that provide protection for biotic communities from changing climatic conditions over evolutionarily significant timescales, allowing them to persist in a landscape where they would otherwise become extinct (Keppel et al., 2012). These habitats may act to conserve associated communities over many millions of years, and as such they are often considered to be “museums” of diversity (Shoo et al., 2013). However, the spatial extent of refugia may change over time with shifting environmental conditions, leading to patterns of connection and isolation (Pepper, Ho, Fujita, & Keogh, 2011). In such cases, refugia can alternatively promote the evolution of divergent lineages, thereby creating a “cradle” that generates diversity (Wiens & Donoghue, 2004). Due to the dual role that refugia can play in conserving and generating biodiversity, identifying and understanding refugia is not only important for understanding biogeographical patterns and the evolution of communities (Bowman et al., 2010; Byrne et al., 2008), but it is also a major conservation priority (Shoo et al., 2013).

The Australian monsoonal tropics (AMT) is a globally significant hotspot of biodiversity and endemism that has been shaped by climate change, although the evolutionary history of its fauna and the phylogeography of the region are poorly studied (Bowman et al., 2010). It is clear that aridification spreading from the continental interior over the last 15 Ma had an overwhelming influence on extinction, persistence and diversification across the region (reviewed in Bowman et al., 2010; Byrne et al., 2008). The importance of long-term refugia in maintaining biodiversity is evident in the distributions and genetic relationships of a number of taxa (e.g. Couper & Hoskin, 2008; Fujita, McGuire, Donnellan, & Moritz, 2010; Oliver, Smith, Laver, Doughty, & Adams, 2014; Pepper, Fujita, Moritz, & Keogh, 2011; Pepper, Fujita, et al., 2011; Potter, Rosauer, Doody, Webb, & Eldridge, 2014). However, a paucity of fossils and palaeoecological and fine-scale genetic studies has meant that the size, distribution and timing of such refugia for the diverse flora and fauna are poorly understood, as is its role in maintaining and/or generating biodiversity.

The Kimberley, in remote north-western Australia, is a unique bioregion within the AMT biome. The region has been of particular interest to biogeographers as it harbours the highest number of endemic species of any bioregion on the continent (see Pepper & Keogh, 2014). There is increasing evidence indicating the accumulation of this extraordinary diversity and endemism is due to the topographically complex Kimberley highlands that are believed to have provided long-term refuge from intense aridity for a number of terrestrial faunal groups (Byrne et al., 2008; Oliver et al., 2014; Pepper, Fujita, et al., 2011; Pepper, Fujita, et al., 2011; Potter et al., 2014).

However, there is uncertainty over the mode of diversification; either the Kimberley is a “museum” acting as a long-term evolutionary refuge that accumulated taxa and endemic species over time, or a “cradle” of more recent diversification and neoendemism, or both (Figure 1).

The concept that the Kimberley is a museum for biodiversity is based on the idea that the region provided long-term refuge for ancient taxa during increased aridity that began during the middle Miocene, thus accumulating diversity over longer time frames (e.g. Oliver, Adams, & Doughty, 2010; Oliver et al., 2014; Pepper, Fujita, et al., 2011; Pepper, Fujita, et al., 2011). Support for this concept would include the following: older lineages in the Kimberley compared to other regions in the AMT, evidence of the steady accumulation of species over time and larger geographical range sizes that positively correlate with the length of time a species has been extant. In contrast, the cradle concept dictates that diversification was driven by frequent (40–100 kyr) and intensifying wet-dry cycles during the late-Pliocene and Pleistocene (3 Ma to present), that led to intermittent connectivity between refuges, ultimately driving more recent vicariant speciation events over geographically smaller areas (Figure 2; e.g. Fujita et al., 2010; Pepper, Ho, et al., 2011; Potter, Eldridge, Taggart, & Cooper, 2012). If the Kimberley is a cradle for biodiversity, we would expect high-speciation rates relative to background rates, adaptive radiations and small range sizes, and

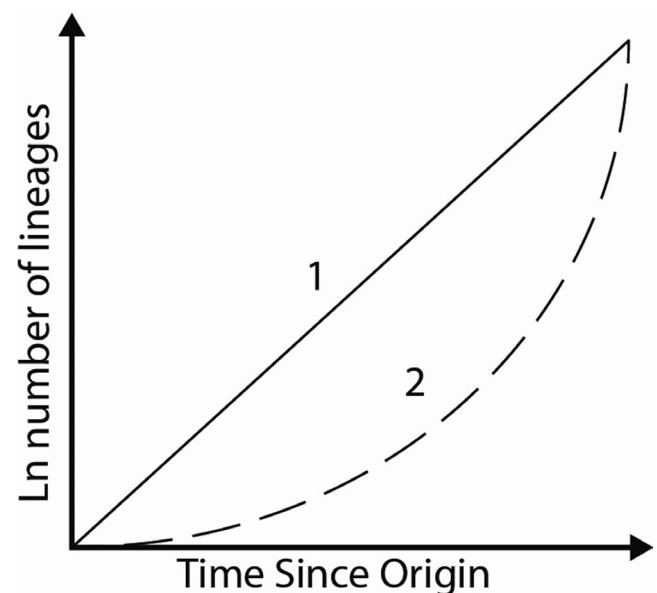


FIGURE 1 Lineage-through-time plots for two alternative modes of diversification of biodiversity in Kimberley Province, north-western Australia: (1) a constant diversification rate, “museum” mode; or (2) an increase in diversification rates since origination with recent radiation; recent “cradle” mode

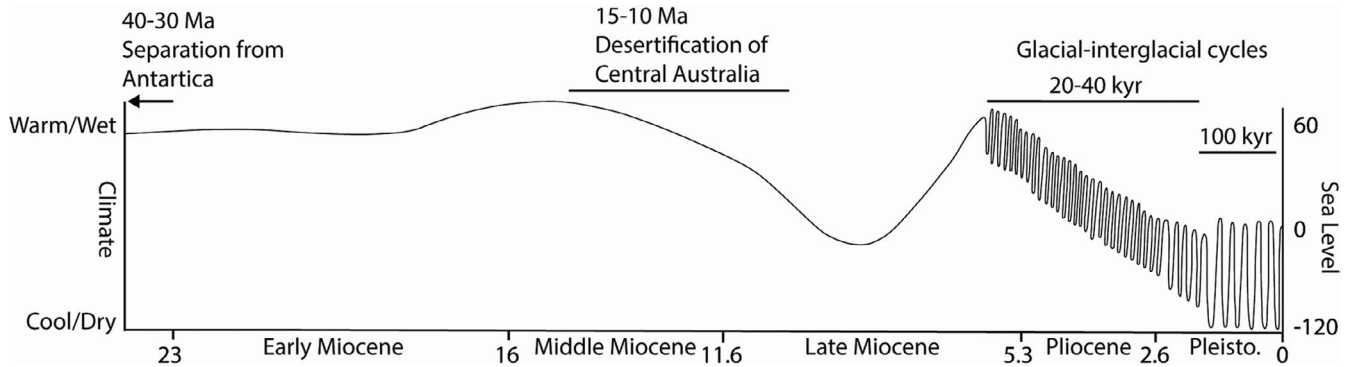


FIGURE 2 Summary of the palaeoclimatic conditions in Australia during the evolution of Terapontidae, 30 Ma to present. The right vertical axis representing sea level is not to scale. The left vertical axis is a rough scale indicating warm/wet to cold/dry climatic conditions. The horizontal axes represent time in the past (Ma). Development of cycling of climatic conditions and sea level changes are evident through the Pliocene and Pleistocene. This diagram is modified from Byrne et al. (2008)

the region acting as a centre of origin for species diversity. There have been few attempts to explicitly test the origin and diversification of the Kimberley's rich endemic fauna, largely due to the historic paucity of molecular data from the region. However, as scientists work towards understanding the distribution and partitioning of species and genetic diversity across this remote region, it is important to now use this information to understand the evolutionary and biogeographical processes that have shaped it. That way land managers can work to protect and conserve not only the unique biota, but the processes responsible for generating and sustaining them (Pepper & Keogh, 2014).

Molecular data for a number of terrestrial Kimberley groups are beginning to accumulate. Most indicate high levels of cryptic diversity and microendemism unlike that seen elsewhere on the continent (Fujita et al., 2010; Moritz, Ens, Potter, & Catullo, 2013; Oliver et al., 2010; Pepper, Ho, et al., 2011). However, geographically fine-scale molecular studies of aquatic organisms remain scant and all studies are restricted to a few opportunistically collected samples with little geographical resolution or continuity (e.g. Davis, Unmack, Pusey, Johnson, & Pearson, 2012; Huey, Cook, Unmack, & Hughes, 2014; Unmack, Allen, & Johnson, 2013; Unmack & Dowling, 2010). If the Kimberley has been a refuge from arid conditions, the influence of palaeoclimate change would leave a strong imprint on obligate aquatic organisms. Recent fine-scale molecular and morphological studies of the freshwater fish family Terapontidae across the Kimberley, and the entire AMT, uncovered 13 new narrow-range endemic species and candidate species (Shelley, Delaval, & Feuvre, 2017; Shelley, Swearer, et al., 2018). When added to the 18 previously described species, this provides the first opportunity to meaningfully investigate the broad patterns of diversification across the Kimberley and the AMT in a comprehensively sampled aquatic group. Here, we combine phylogenetical, biogeographical and diversification analyses of this comprehensive molecular dataset to test whether the museum or cradle hypothesis best explains the diversification of the Kimberley region's rich and highly endemic aquatic fauna.

2 | MATERIALS AND METHODS

2.1 | Study group

The family Terapontidae contains 67 described and candidate species within 16 genera that are distributed across the Indo-west Pacific (Shelley, Swearer, et al., 2018; Vari, 1978). Within the family, there is a marine and a freshwater lineage, the latter containing 52 species and candidate species that are mostly restricted to Australia and New Guinea, with two further representatives in the Philippines and Sulawesi (Eschmeyer, Fricke, & van der Laan, 2017; Shelley, Swearer, et al., 2018). Molecular evidence suggests they might have evolved from a single freshwater invasion (Davis et al., 2012). Within Australia, we herein refer to the distribution of species by the freshwater biogeographical provinces defined in Unmack (2001) and partially revised in (Shelley et al., 2019) as they are the most informative and relevant spatial units in this instance. Of the 38 obligate freshwater terapontid species found in Australia, 32 are shared between the Kimberley Province and Northern Province in the AMT. Given their ubiquitous distribution across northern Australia (Figure 3; Allen, Midgley, & Allen, 2002), Terapontidae provides an ideal study group to test geographical patterns and the tempo of diversification in the Kimberley Province, compared to the rest of the AMT.

2.2 | Molecular dataset and phylogenetic analysis

For this study, we used the STAR BEAST (*BEAST) time-calibrated terapontid phylogeny presented in Shelley, Swearer, et al. (2018). Full details of the underlying molecular dataset are found there. The major focus of this study was the species found within the AMT, although a near complete phylogeny of the family and outgroups was included to investigate the broader evolutionary history of the family. The dataset includes sequences for 53 of the 67 Terapontidae species. Only one species from the AMT (*Scortum neili* – Victoria River, Kimberley Province) was not included due to a lack of material.

Within the obligate freshwater lineage, the following species are missing: *S. neili* (Australia – Kimberley Province), *Hephaestus*

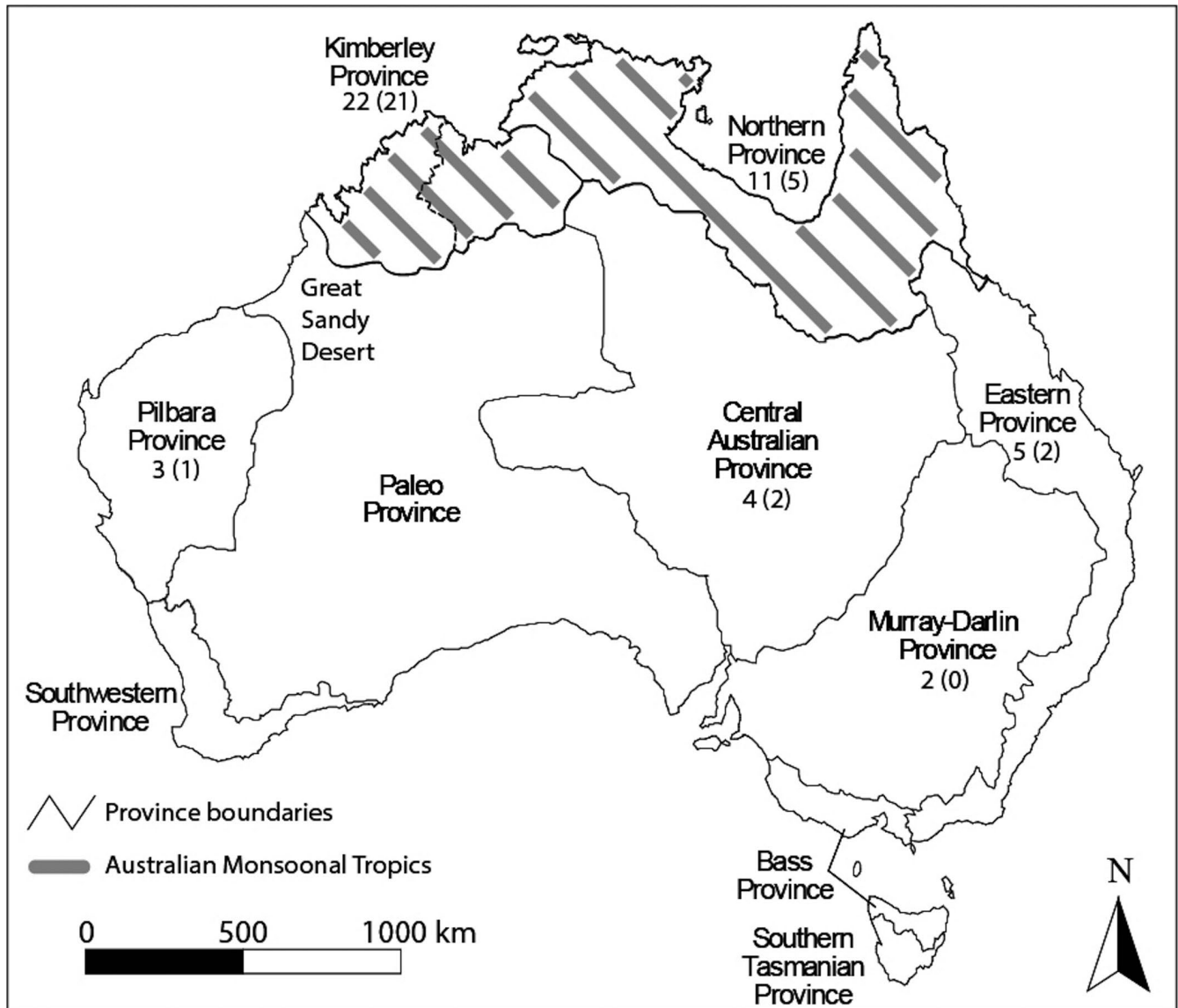


FIGURE 3 Australian freshwater biogeographical regions used in this study, based on Unmack (2001, 2013) and Shelley et al. (2019) (see Materials and Methods), with freshwater terapontid species total richness and endemic richness (in brackets) indicated by number. Some species are found across multiple provinces. The focus of this study, the Australian Monsoonal Tropics, is dashed in grey

adamsoni, *H. komaensis*, *H. lineatus*, *H. obtusifrons*, *H. raymondi*, *H. roemeri*, *H. trimaculatus*, *Variichthys jamaoerensis* (New Guinea) and *Lagusia micracanthus* (Sulawesi). The marine and euryhaline lineages include all but the following four species: *Mesopristes elongatus*, *M. iravi*, *M. kneri*, and *Pelates qinglanensis*. The species within *Hephaestus* that occur in New Guinea form a deep, unique lineage separate to the endemic Australian species and they are suspected to represent a separate genus (Davis et al., 2012; Shelley, Swearer, et al., 2018). It seems likely that the New Guinea species of *Hephaestus*, that make up the majority of missing species from our phylogeny, belong to this lineage. As such, their influence on our phylogenetic interpretation of diversification among the predominantly Australian freshwater lineages is considered minimal. Regardless, our analysis remains open to refinement as new genetic material from these species becomes available.

The dataset included a 2,541 bp sequence of Recombination Activation Gene one (RAG1) from a single representative of each species and 2–3 representative 601 bp sequences of Cytochrome *b* (*cytb*) for each species, except *Leiopotherapon plumbeus* (from the Philippines) for which a sequence of suitable quality could not be obtained. Suspected mtDNA introgression was identified in six species (*Syncomistes kimberleyensis*, *S. rastellus*, *S. holsworthi*, *S. versicolor*, *S. moranensis* and *S. carcharus*) and the relationships for these species observed in the *cytb* tree were in clear contradiction to the RAG1 tree and independent allozyme results presented in Shelley, Swearer, et al. (2018). To overcome the impact that this would have on the combined RAG1 + *cytb* tree, the variable sites from the mitochondrial sequences of individuals with heterospecific mtDNA haplotypes were removed (Shelley, Swearer, et al., 2018). Zheng and Weins (2015) investigated the impact of missing

data on the accuracy of dating analysis with *BEAST, across multiple empirical datasets, and found that significant amounts of missing data (up to 75% missing data in 80% of sampled genes) had little impact on divergence time estimates using the relaxed log-normal dating approach. The mean error created by missing data was particularly minimal when the majority of taxa in the dataset had complete sequences, which is the case in our dataset (46/53 taxa with complete sequences). Therefore, we make the assumption here that our time-calibrated phylogeny is minimally impacted by the removed mtDNA data.

2.3 | Ancestral range reconstruction

To investigate geographical origins of the Kimberley fauna, we reconstructed the ancestral freshwater biogeographical provinces occupied by the members of Terapontidae using the *BEAST tree and the R package "BioGeoBEARS 1.1" (Matzke, 2013). "BioGeoBEARS" uses maximum-likelihood to estimate ancestral areas by modelling transition events between regions onto a phylogeny. We coded all sampled taxa used in the tree based on their contemporary distributions within major freshwater biogeographical provinces for Australian species presented in Unmack (2001, 2013) [(1) Kimberley Province (K); (2) Northern Province (N); (3) Eastern Province (E); (4) Central Australian Province (C); (5) Murray-Darling Province (D); (6) Pilbara Province (P)], or by their broader biogeographical region for non-Australian species [(7) New Guinea (G); (8) Southeast Asia (S); or (9) Marine (M)]. The bioregionalization of freshwater fishes in the AMT, which encompasses the Kimberley and Northern provinces presented in Unmack (2001, 2013), was recently revised in Shelley et al. (2019) and the province boundaries were redefined. Specifically, the boundary of the Kimberley Province was extended east to include the Victoria River Basin (VRB; see Figure 3), whereas the eastern Northern Province boundary was defined by the Great Dividing Range (as far north as the Wenlock River). Catchments to the east of the Great Dividing Range formed a separate province, although the southern extent of the province was not determined as the analyses were bound geographically to the AMT. Based on these findings, we adopted the Kimberley – Northern Province boundary presented in Shelley et al. (2019). However, given that the southern province boundary on the east coast has not been defined and only one endemic terapontid is found in that region, we maintained the Northern – Eastern Province boundary defined in Unmack (2001, 2013) (Figure 3). Species distributions used in our ancestral range reconstruction analysis are presented in Appendix S1.

Although 51 of the 53 species included in our analysis are restricted to less than two Australian freshwater biogeographical provinces, *Amniataba percoides* 1 and *Leiopotherapon unicolor* (Australia's most widespread freshwater fish) are found across four and six of the provinces respectively. By setting the maximum number of possibly occupied freshwater biogeographical provinces per lineage to six, the program could not identify the highest likelihood biogeographical province for any nodes internal to the *L. unicolor* lineage, rather it determined that all provinces were equally likely for all nodes. Given that

this finding does not make intuitive sense and that they were clearly influenced by the anomalous widespread *L. unicolor*, we addressed the issue by removing records of *L. unicolor* from the most geographically marginal biogeographical regions within the range of Terapontidae (Pilbara Province and Murray-Darling Province; Figure 3), setting the maximum number of occupied regions per lineage to four. This significantly improved the ability of "BioGeoBEARS" to resolve the likely ancestral ranges at the internal nodes.

We compared three biogeographical models to help determine the main factors influencing the evolution of the biogeography of Terapontids in the AMT (e.g. dispersal, vicariance, founder event speciation): (a) dispersal-extinction-cladogenesis model DEC (DEC; Ree & Smith, 2008); (b) dispersal-vicariance analysis DIVALIKE (DIVA; Ronquist, 1997); and (c) BayArea model BAYESLIKE (Landis, Matzke, Moore, & Huelsenbeck, 2013). Each model included three free parameters: d = dispersion or range extension; e = extinction or range contraction; and $+J$ = rate of founder event speciation. The $+J$ parameter represents the rate of founder event speciation during cladogenesis where one of the daughter species occupies an area that is unoccupied by the other daughter species. We compared the model fit of each of the six available models DEC, DEC + J, DIVALIKE, DIVALIKE + J, BAYESLIKE and BAYESLIKE + J using the bias-corrected Akaike information criterion (AICc) test in "BioGeoBEARS" (see Appendix S2 for model results). The results indicated that the DEC + J model was optimal, followed by the DEC model ($\Delta AICc = 5.83$). However, the DEC + J model has been criticized on conceptual grounds, and the use of AIC to compare its fit to other DEC-based models was also questioned (Ree & Sanmartín, 2018). For these reasons, we use the biogeographical inferences from the DEC model in "BioGeoBEARS" to determine the most probable ancestral freshwater biogeographical regions occupied by the members of Terapontidae at each of the internal nodes on our *BEAST phylogeny. We note that both the DEC and DEC + J models presented similar results and our interpretation of both, regarding our hypotheses, was the same.

2.4 | Diversification analysis

To identify which diversification scenario, cradle or museum, is more likely (Figure 1), we investigated the tempo and mode of species diversification in terapontids using the "APE 5.3" (Paradis, Claude, & Strimmer, 2004) and "TREEPAR 3.3" (Stadler, 2011) packages for R and the *BEAST TREE.

We used the approach developed by Stadler (2011) to estimate discrete shifts in speciation and extinction rates, together with rate shift times, in potentially incomplete phylogenies. We used the function "bd.shifts.optim" in "TREEPAR" to estimate the maximum-likelihood speciation and extinction rates along with the possible shift times in the terapontid radiation. The analysis was run with the following settings: start = 0, end = crown age, grid = 0.1 million years (to allow for fine-scale estimation of rate shifts), sampling fraction (ρ) = 53/67 (we have sampled 79% of known terapontid species), four possible shifts in speciation and extinction rates were tested

(the maximum for the program), and `posdiv = FALSE` to allow the diversification rate to be negative (i.e. allows for periods of declining diversity). To determine the best-fit model, we calculated and compared AICc scores for each.

We also tested if diversity-dependence diversification may better explain the diversity dynamics of the group than the discrete shifts hypothesis. This is important as while species accumulate within a group, they fill geographical and niche space, potentially reducing the opportunities for further speciation and increasing extinction risk as they reach saturation point towards the present (Pigot, Phillimore, Owens, & Orme, 2010). We used the method developed by Etienne and Haegeman (2012) for estimating speciation and extinction rates as a function of the number of species, implemented in "TREEPAR". We used the function "bd.densdep.optim" with the following settings: `discrete = TRUE`, the missing species were taken into account (`rho = 53/67`), an initial carrying capacity (`minK`) set at 67 (current diversity estimates including candidate new species), whereas the maximum carrying capacity (`maxK`) was fixed at $1.5 \times$ extant diversity. The best likelihood score indicates whether the group is at equilibrium or not.

Finally, to visualize lineage accumulation through time and any deviations in lineage accumulation from our null hypothesis (constant diversification through time), we constructed Lineage-through-time (LTT) plots in "APE". We plotted null distributions under Yule and birth-death processes, using the branching times and lambda (k) from our maximum clade credibility *BEAST TREE. Significant deviations from the null distribution indicate changes in the rate of diversification and/or extinction through time. We evaluated the LTT plot by running 1,000 simulations under varying diversification models (e.g. pure birth vs. birth = 0.3 and death = 0.1) and plotting Terapontidae LTT against those results.

3 | RESULTS

3.1 | Diversification analysis

We reconstructed an LTT plot for the phylogeny of Terapontidae using the time-calibrated phylogeny from the *BEAST analysis presented in Shelley, Swearer, et al. (2018). Based on AICc values, the "TREEPAR" analysis supported a varying rate model of diversification with a shift occurring in the Pleistocene (mean = 1.4 Ma; Table 1). This shift represented a sharp increase to 0.39 from a mean diversification rate of 0.15. The turnover rate (extinction/speciation) increased from 0.00 to 0.09. These findings are consistent with the prediction of the cradle hypothesis that recent diversification rates will be higher than background rates. The models that tested for more than one shift time were not supported by AICc values.

Diversity-dependence analyses indicated that current terapontid diversity is not saturated as the ML estimate is obtained for the maximum carrying capacity at 101 species ($\log L = -150.183$) compared to the 55 current sampled species. Therefore, the discrete shift model better explains diversification patterns than the

TABLE 1 Results from the TREEPAR analyses conducted on the Terapontidae time-calibrated *BEAST tree

Model	Pm	-logL	AICc	Δ AICc	AICc weight	r1	τ 1	st1	r2	τ 2	st2	r3	τ 3	st3	r4	τ 4	st4	r5	τ 5
BD constant	2	153.40	311.04	4.74	0.06	0.88	0.04	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
BD 1 shift	5	147.51	306.30	0	0.64	0.15	0.00	1.4	0.39	0.09	NA	NA	NA	NA	NA	NA	NA	NA	NA
BD 2 shifts	8	144.72	308.79	2.49	0.19	0.18	<0.00	1.4	1.5	0.36	24.6	0.08	-0.4	NA	NA	NA	NA	NA	NA
BD 3 shifts	11	140.85	310.13	3.83	0.09	0.00	0.51	1.4	2.31	1.01	24.6	0.48	0.05	26.3	-1.61	-1.2	NA	NA	NA
BD 4 shifts	14	137.15	313.34	7.04	0.02	0.27	0.42	1.4	1.45	4.57	24.6	1.09	0.36	25	0.06	-0.95	26.3	-0.53	-6.91

Note: Pm, number of parameters in the model; -logL, the log-likelihood of the model; AICc, bias-corrected Akaike information criterion scores of the model; Δ AICc, the difference of the AICc scores between the null hypothesis (BD constant) and models that include shifts in diversification rate; AICc weight, conditional probabilities for each model; r1, diversification rate at present; t1, turnover rate at present; st1, most recent shift time. Other diversification and turnover rates, as well as shift times, going deeper in the past are denoted with numbers (for example, r2, t2 and st2). The model of best fit (BD 1 shift) is given in bold. A likelihood ratio test between the incrementally more complex models found that this model was statistically supported ($p = .008$).

diversity-dependent processes. These analyses estimated the mean speciation rate at 0.836 and mean extinction rate at 0.306.

The LTT plots (inset in Figure 4) depicted a clear deviation from the null distribution at the transition between the Pliocene and Pleistocene, followed by a distinct increase in lineage formation during the later half of the Pleistocene, further supporting the findings of our “TREEPAR” analysis.

3.2 | Divergence dating and ancestral range reconstruction

Dates derived from the *BEAST analysis and marginal probability (MP) scores from our ancestral area reconstructions produced in “BioGeoBEARS” for nodes discussed herein are presented in Table 2. All *BEAST estimates had effective sample sizes >200. Ancestral area MP scores were also visualized on the *BEAST phylogeny (Figure 4). The complete results are summarized in Appendix S3. Ignoring the DEC + J model (see Methods), the AICc analysis indicated that the DEC model was the best fit for the data (AICc = 245.097) and was >5 AICc units higher than the next best model (BAYAREALIKE + J, AICc = 245.097). The parameters estimated for the DEC model were as follows: $d = 0.005$, $e = <0.000$, and $j = 0$.

The ancestral range estimations received high probabilities at most nodes, although the states attributed to nodes between the tree root and the deeper nodes within lineage B were far more ambiguous, largely due to the influence of the two widespread taxa *L. unicolor* and *A. percoides* that are nested within that lineage, and the relatively large number of ancestral ranges.

We estimated the earliest divergence within Terapontidae, between the marine/euryhaline and freshwater lineages (node A), to be in the early Oligocene (c. 31.0 Ma). The divergence between the freshwater lineages occurred c. 24.8 Ma with the highest support being for a transition into the Northern Province (MP = 0.10; node B). While the probability of this range estimate was low, it is further supported by higher probabilities of Northern Province distributions at the two following nodes (MP = 0.28, node C; MP = 0.21, node D). All Kimberley Province taxa were nested within nodes with inferred ranges within Northern Province, indicating early transitions occurred from Northern Province into Kimberley Province. Three possible transitions were inferred between the two regions, occurring during the late-Miocene around 8.8 Ma (node E) and 6.9 Ma (node F) and the Pliocene around 4.0 Ma (node G). In each of these cases the ancestor is predicted to have been widespread across the multiple provinces. However, these were preceded by two notable Kimberley Province endemic radiations including *Syncomistes* (starting at node G, MP = 1.00) and *Amniataba* (starting at node H, MP = 1.00), and several current Kimberley Province endemic lineages in *Hephaestus*, *Hannia* and *Leiopotherapon*.

In summary, all divergence events (13) with inferred ranges in the Kimberley Province only occurred <3 Ma ago during the Pliocene-Pleistocene glacial cycles, with the overall median divergence time being 0.89 Ma (± 0.71). This further implies that 80% of Kimberley Province terapontids diversified within the province in the last

3 Ma. An additional three divergence events in widespread ancestors with inferred ranges that included the Kimberley Province and neighbouring Northern Province, respectively, gave rise to a Kimberley Province endemic species (nodes I, J and K; median divergence time 1.3 ± 0.61 Ma). Taken as a whole, 16 out of the 24 divergence events (67%) that occurred within Terapontidae within the last 3 Ma either occurred within the Kimberley Province or due to vicariance separating a widespread ancestor in the Kimberley Province from the neighbouring Northern Province and elsewhere. These results are consistent with the predicted time frame of increased diversification stated in the cradle hypothesis. Conversely, no divergence events with inferred ranges in the Northern Province only occurred <3 Ma ago and the mean age of divergence was 10.8 Ma (± 6.5).

4 | DISCUSSION

The origin and diversification of the Kimberley's diverse endemic fauna has been widely researched (see Pepper & Keogh, 2014), yet never explicitly investigated using a diverse and widespread group with a complete regional phylogeny. Accumulating phylogenetic evidence has prompted two prominent competing hypotheses: (a) the “museum” mode of diversification, in which lineages accumulate steadily through time due to constant speciation rate and/or low extinction rate; and (b) the “cradle” mode in which lineages are generated recently and rapidly. Here, we provide the first explicit test of these hypotheses.

4.1 | Patterns of diversification across the AMT

Terapontid diversification rates did not remain constant through time but underwent a significant positive shift during the Pleistocene (c. 1.4 Ma; Table 2). This shift corresponded with a significant change in global climate as glacial cycles transitioned from high-frequency, low-amplitude glaciations (every 20–40 kyr) during the change between the Pliocene and Pleistocene epochs, to low-frequency, high-amplitude glaciations (every 100 kyr) that became established midway through the Pleistocene (Huybers, 2007). This diversification rate shift was largely due to speciation in the Kimberley Province and rates have continued to increase since then due to ongoing speciation within the region (Figure 4). These results provide the first empirical evidence for the cradle hypothesis, with the Kimberley acting as a source of neoendemism, rather than a stable accumulator of endemics over time.

This finding raises the question of why there is such a bias towards endemic speciation in the Kimberley Province when the entire AMT was shaped by the same climatic events. The answer could lie in the unique interaction between the climate and geology of the region. The AMT is a geologically old, largely flat landscape that has remained relatively unchanged for millions of years; most major tectonic action (e.g. mountain building) occurred >30 Ma (White, 1994). The landscape is punctuated by three high-elevation sandstone

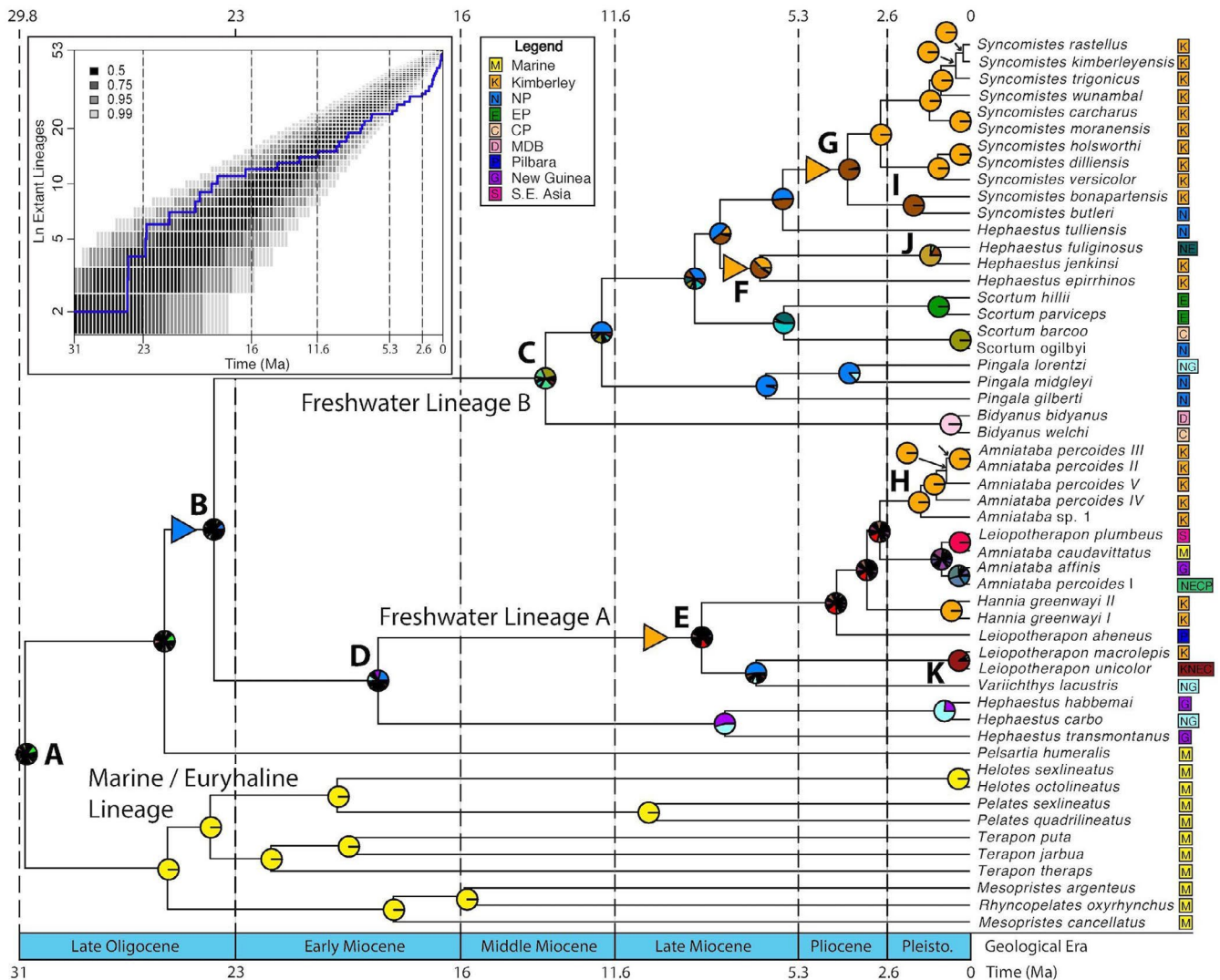


FIGURE 4 Maximum clade credibility tree and historical biogeography of the family Terapontidae. A geological timescale is placed at the bottom of the chronogram spanning the epochs since 29.8 Ma. Present-day distribution of each species is informed at the tips by coloured squares with an alphabetic character code. For each node, the BioGeoBEARS ancestral range reconstruction is indicated by a coloured pie graph (representing the most likely ancestral area as a marginal probability score). For a description of nodes discussed in the text see Table 2. For a description of all nodes see Appendix S2. The colour codes for nodes with multiple ancestral regions predicted are denoted by composites of the primary range colours (e.g. Northern Province (green) + Kimberley Province (orange) = Northern Province/Kimberley Province (yellow)). Coloured triangles on branches indicate transitions between biogeographical ranges. The three major lineages are also labelled. Inset: lineages-through-time (LTT) plot. The null distribution under a Yule process is depicted, using the branching times and lambda (k) from our dated tree, with coloured shading representing the confidence intervals. LTT plots represent the number of lineages with living descendants against time. If $l = 0$ and k are constant, LTT plots will show exponential growth. Significant deviations from this expectation indicate that diversification is changing with time

formations including the Kimberley and Arnhem Land plateaus and the ranges of Cape York Peninsula, that each represent focal points of freshwater fish endemism in the region (Kennard et al., 2010).

Topographically complex regions are drivers and maintainers of species diversification through the provision of refugia (Bowman et al., 2010; Fjeldsaå & Lovett, 1997; Woinarski, Mackey, Nix, & Traill, 2007). Compared to the surrounding lowland areas in the AMT, these rugged upland regions limit the migration between catchments, provide a more thermally buffered environment, offer moister habitats by generating orographical rainfall

and limiting the evaporation by providing the shade, and the sandstone-based gorges have more permanent water present due to hyporheic water being forced to the surface (Bowman et al., 2010; Fjeldsaå & Lovett, 1997; Pepper & Keogh, 2014). In the context of the AMT, the Kimberley Plateau provides an extreme example of this geological complexity. The catchments running off the plateau are short and highly confined by the rugged surface topography. Many run through deeply dissected gorges from their headwaters to the coast, severely limiting the potential for lateral movement of the aquatic fauna between rivers. Furthermore, the

TABLE 2 Combined results of phylogeny, estimates of divergence times and biogeography of Terapontidae for nodes discussed in the text

Node		Chronogram			BioGeoBEARS		
		PP	95% HDP	Mean Age	Range	MP	L
A	<i>M. cancellatus</i> – <i>T. theraps</i>	0.50	20.3–32.7	26.3	M	1.00	0.69
B	<i>H. transmontanus</i> – <i>B. welchi</i>	0.73	19.5–31.6	24.8	N	0.10	<0.00
C	<i>B. welchi</i> – <i>P. gilberti</i>	0.98	10.7–17.8	13.9	NC	0.28	0.01
D	<i>H. transmontanus</i> – <i>V. lacustris</i>	0.99	14.2–26.3	19.4	N	0.21	0.01
E	<i>V. lacustris</i> – <i>L. aheneus</i>	0.99	6.6–11.3	8.8	KNPG	0.14	<0.00
F	<i>H. epirrhinos</i> – <i>H. jenkinsi</i>	0.74	4.1–9.6	6.9	KN	0.53	0.05
G	<i>S. butleri</i> – <i>S. versicolor</i>	0.99	2.5–5.6	4.0	KN	0.97	0.15
H	<i>Amniataba</i> sp.1– <i>A. percoides</i> IV	0.93	0.8–2.6	1.6	K	1.00	0.92
I	<i>S. butleri</i> – <i>S. bonapartensis</i>	0.37	0.1–4.0	1.9	KN	1.00	0.14
J	<i>H. jenkinsi</i> – <i>H. fuliginosus</i>	1.00	0.2–2.7	1.3	KNE	0.76	0.07
K	<i>Leiopotherapon unicolor</i> – <i>L. macrolepis</i>	1.00	0.0–1.0	0.4	KNEC	0.90	0.06

Note: This table refers to Figure 4, organized by species pairs, showing the (i) posterior probability (PP) values obtained from our Bayesian analysis, (ii) estimated median age with the 95% HPD for the chronograms and (iii) highest probability ancestral range obtained from the BioGeoBEARS analyses with the likelihood score (L) and the marginal probability (MP). For geographical analysis, only the first split at a node is given and can be non-significant.

plateau extends out to the coastline, so lowland floodplain and estuarine habitats are largely absent (see Kennard et al., 2010). Opportunities for inter-catchment connection at current sea levels would thus be largely limited to dispersal across marine environments. Molecular evidence indicates that dispersal of the highly vagile and widespread rainbowfish *Melanotaenia australis* is greatly limited between rivers on the Kimberley Plateau, so it is expected that other species would be similarly constrained (Phillips, Storey, & Johnson, 2009). Further evidence can be taken from their narrow ranges; 57% of terapontids (40% of the entire fish community) are restricted to a single river system or tributary (Morgan, Allen, Pusey, & Burrows, 2011; Shelley, Morgan, et al., 2018). This lies in stark contrast to the neighbouring Northern Province, which has only one narrow-range endemic terapontid (3% of the entire fish community; Unmack et al., 2013). However, this may not have always been the case. During Quaternary glacial cycles, sea levels ranged from –120 to –140 m below current levels during glacial maxima to +5 to +8 m during the warm interglacial periods, periodically exposing and covering lowland areas of the wide continental shelf every 20–100 kyr (Hope et al., 2004). A recent analysis aimed at determining past and present environmental variables that have the strongest influence on freshwater fish species turnover in the AMT found that in the Kimberley Province,

both current stream confinement and past connectivity between rivers during low sea level events were the key variables influencing the dissimilarity of fish communities between rivers (Shelley et al., 2019). In terms of freshwater dependent species, it seems likely that these climate cycles would have represented alternating periods of between catchment connection and isolation and furthermore, they occurred at timescales long enough to facilitate vicariant speciation (Hewitt, 2000).

4.2 | Biogeographical history of Terapontidae

Our molecular dating analysis and ancestral range reconstructions suggest the freshwater terapontid lineages diverged from an ancestral marine/euryhaline ancestor in the early Oligocene c. 31.0 Ma (Figure 4, Table 1), diversifying into freshwater habitats in the Northern Province of the AMT. This timing coincides with establishment of monsoonal conditions in northern Australia that marked the origin of the AMT (c. 40–30 Ma; Greenwood, 1996; Macphail & Stone, 2004; Pole & Bowman, 1996), and greater separation of the Australian continent from Antarctica (c. 45–32 Ma; Talent, 1984). Conditions in the AMT at the time of the freshwater invasion would have been warm and wet, but becoming increasingly cooler and drier over time as Australia drifted north to its current position (Martin,

2006; McGowran, Holdgate, Li, & Gallagher, 2004). Widespread aridification of the Australian continent, in particular desertification of the continental interior, was reached in the middle Miocene c. 10–15 Ma (Fujioka & Chappell, 2010; McGowran et al., 2004).

Three possible transitions into Kimberley Province occurred from Northern Province between late-Miocene c. 8.8 Ma and Pliocene c. 4.0 Ma (Figure 4, Table 1). It is clear that terapontids have not had a long history in Kimberley Province, and a particularly short history relative to the neighbouring Northern Province. Deeper divergences across a number of Australian freshwater fishes and other freshwater groups centre around this period (fishes: Page, Sharma, & Hughes, 2004; Unmack & Dowling, 2010; Unmack et al., 2013; crustaceans: Chenoweth & M. Hughes, 2003; Cook et al., 2006; Munasinghe, Burridge, & Austin, 2004; Ponniah & Hughes, 2004; Murphy & Austin, 2005; mussels: Baker et al., 2003). A likely explanation is that increasing aridification led to the isolation of many freshwater populations, thus promoting allopatric speciation (Munasinghe et al., 2004; Unmack, 2013; Williams & Allen, 1987). Our analysis suggests the arid region of the Victoria River Valley became a major barrier to terapontid range expansion from the Northern Province towards the end of the Pliocene. The final step in the formation of the Kimberley Province, as it exists today, was the creation of the Great Sandy Desert dune fields that isolate the region from the Pilbara Province to the south. These dune fields formed in response to a Pleistocene climatic shift c. 1 Ma, although gradual aridification would have begun earlier (Fujioka, Chappell, Fifield, & Rhodes, 2009). Molecular evidence from the rainbowfish *M. australis* suggest a divergence between the Pilbara and Kimberley populations around 0.8–1.7 Ma, supporting the hypothesis that some degree of freshwater connection existed up until the dune systems were formed (Unmack et al., 2013; Young, Evans, & Simmons, 2011). Due to the formation of these barriers, there have been no transitions back out of Kimberley Province via a freshwater pathway indicating these have been significant long-term barriers.

4.3 | Evidence of adaptive radiation

Once in Kimberley Province, the terapontids diversified rapidly, predominantly through lineages containing *Amniataba* (5 species) and *Syncomistes* (11 species). While these lineages diverged at roughly the same time (Table 1), *Amniataba* remains relatively morphologically conserved, whereas *Syncomistes* displays an impressive degree of morphological variability in body size, tooth shape/number and jaw structure (Shelley et al., 2017). Davis, Unmack, Vari, and Betancur-R (2016) concluded that following the transition of Terapontidae into freshwater habitats, diversification among the freshwater lineage has been largely driven by evolution towards morphologies best suited for the exploitation of various food types, particularly non-animal prey. *Syncomistes* is unique among the Kimberley Province fish community as the genus has a detritivorous/ algivorous feeding mode, while the rest are predominantly predatory feeders (insectivores/ generalized carnivores; Davis et al., 2012). The *Syncomistes* feeding mode represents a major

shift from the ancestral carnivorous mode and would have made available trophic resources largely unutilized by other fish groups in the region (Davis et al., 2012). The clear water, sandstone-based rivers of the Kimberley Plateau promote abundant filamentous algal growth, and the region provides more of this habitat than any other in the AMT. We hypothesize that Kimberley Province presented empty niche space for large bodied detritivorous/ algivorous feeders and thus contributed to a rapid radiation within that lineage.

5 | CONCLUSIONS

Our study used a model group to examine the biogeographical and diversification processes that governed the origin and evolution of Kimberley freshwater biodiversity. The weight of evidence suggests that the Kimberley Province has been a “cradle” of evolution for Terapontidae, rather than a “museum”. Our analysis provides strong evidence for a geologically recent transition from Northern Province into Kimberley Province during the late-Miocene followed by a significant increase in terapontid speciation rates during the Pleistocene, driven by speciation in Kimberley Province. Given the majority of these freshwater obligate taxa diversified in-situ, it can be inferred that Kimberley Province provided significant refuge during the hyper-arid glacial maximum periods of the Pleistocene. This would have implications for all species that are not well adapted to arid conditions and is likely relevant over longer time-scales than is evidenced in this study, as the AMT would have been influenced by increasing aridity from the middle Miocene, long before the estimated transition of terapontids into Kimberley Province (McGowran et al., 2004). While Kimberley Province may be a cradle of biodiversity, it has not been a source of biodiversity to surrounding regions as no evidence of a transition from Kimberley Province to surrounding biogeographical provinces. The arid zones that define the region's boundaries appear to have provided highly effective barriers to freshwater fish movement, further facilitating the development of what is arguably the most unique freshwater fish fauna on the continent.

While there is mounting evidence that the Kimberley is an ancient centre of diversity for a number of terrestrial taxa (Pepper & Keogh, 2014) our results highlight the importance of more recent processes in generating the great endemic diversity of freshwater fish. Future research should focus on whether this pattern is congruent across other freshwater fishes and other freshwater taxa, and whether it holds across groups with varying dispersal potential. Understanding current patterns in aquatic biodiversity and the evolutionary and ecological processes that have shaped them is of particular importance for developing broad-scale conservation management strategies for one of the Australia's most unique bioregions (Pepper & Keogh, 2014).

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COMPETING INTERESTS

The authors declare that they have no competing interests.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All work had animal ethics approval from the Research Ethics and Integrity office at the University of Melbourne, ID 1212470.1. All collections by the authors were made under Government of Western Australia, Department of Fisheries permit, Ref. 220/12. Collections by the authors in National Parks were made under Department of Parks and Wildlife Permit SF008685 (2012–2013) and SF009877 (2014–2015).

DATA AVAILABILITY STATEMENT

All gene sequences used in this analysis are available from GenBank. Full details of the accession numbers are presented in Appendix S4. A posterior distribution of trees from the *BEAST analysis can be found in the Dryad database (<https://doi.org/10.5061/dryad.95qd72v>).

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BIOSKETCH

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Authors' contributions: J.J.S., S.E.S and M.C.L. conceived the ideas; J.J.S., M.C.L, P.J.U., S.E.S and T.D. collected the data; J.J.S. analysed the data under the supervision of P.J.U.; J.J.S. led the writing and all the authors contributed through editing.

SUPPORTING INFORMATION

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

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