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Mass turnover and recovery dynamics of a diverse Australian continental radiation

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Trends in global and local climate history have been linked to observed macroevolutionary patterns across a variety of organisms. These climatic pressures may unilaterally or asymmetrically influence the evolutionary trajectory of clades. To test and compare signatures of changing global (Eocene-Oligocene boundary cooling) and continental (Miocene aridification) environments on a continental fauna, we investigated the macroevolutionary dynamics of one of Australia's most diverse endemic radiations, pygopodoid geckos. We generated a time-calibrated phylogeny (>90% taxon coverage) to test whether (i) asymmetrical pygopodoid tree shape may be the result of mass turnover deep in the group's history, and (ii) how Miocene aridification shaped trends in biome assemblages. We find evidence of mass turnover in pygopodoids following the isolation of the Australian continental plate ∼30 million years ago, and in contrast, gradual aridification is linked to elevated speciation rates in the young arid zone. Surprisingly, our results suggest that invasion of arid habitats was not an evolutionary end point. Instead, arid Australia has acted as a source for diversity, with repeated outward dispersals having facilitated diversification of this group. This pattern contrasts trends in richness and distribution of other Australian vertebrates, illustrating the profound effects historical biome changes have on macroevolutionary patterns.

KEY WORDS: Aridification, Australia, geckos, extinction, macroevolution.

The field of macroevolutionary study has grown tremendously as novel analytical methods and ever-larger phylogenies help to reveal patterns of diversity through space and time. Similarly, our rapidly improving understanding of climate history provides the opportunity to link together climatic and evolutionary histories, to directly test the impact of paleoclimate regimes on trends in diversification. The ability to investigate more sophisticated questions across groups of varied species richness, age, and distribution, has revealed consistent macroevolutionary patterns in response to climatic change, including the influence of the tempo and intensity of climatic change (Stadler 2011a; Crottini et al. 2012). Additionally, we can now more accurately test how macroevolutionary mechanisms affect diversification, and compare similar and asymmetrical trajectories of clades under shared climatic histories (Hunter 1998). The accumulating body of evidence suggests that heterogeneity is ubiquitous in phylogenetic, spatial, and temporal diversity. Realizing this, goals have shifted to identifying and testing for the causes of such heterogeneity.

Phylogenetic tree building methods have revealed heterogeneity as imbalance among (phylogenetic) or along (temporal) branches of the tree, initiating questions regarding the intrinsic and extrinsic drivers of such disparity. Imbalance in clade richness is often attributed to intrinsic organismal influences such as ecological differentiation and key innovation (Phillimore and Price 2008; Rabosky 2013; Scantlebury 2013). Conversely, temporal and distributional heterogeneity is frequently explained by extrinsic factors such as geographic and climatic change (Moen and Morlon 2014). Macroevolutionary signature of climatic change however, is highly dependent upon their relative rate and intensity of the variation. For example, rapid perturbation at the K-Pg boundary resulted in global mass extinction of vertebrate groups and unilaterally changed terrestrial assemblages (Halliday et al. 2016). In contrast, protracted environmental changes of the Late Jurassic and Early Cretaceous caused heterogeneous turnover and replacement (Tennant et al. 2016). Together, historical processes of differing scales help explain patterns seen in contemporary diversity.

Rapid cooling and glaciation at the Eocene-Oligocene boundary (EOb, ∼34 Ma) has been implicated in considerable biotic turnover globally (Zanazzi et al. 2007; Stadler 2011a; Sun et al. 2014). In Australia, this period demarcates a split from Antarctica and the opening of the circumpolar current, initiating a new period of in-situ diversification (Williams 1984). However, no empirical studies have investigated the impact of rapid (duration <100,000 years) EOb global cooling on the macroevolution of Australian taxa, perhaps due to the paucity of extant radiations that predate the EOb, and limitations of a poor fossil record. Instead, patterns of spatial and phylogenetic richness are more often associated with mid-Miocene continental expansion of arid habitats (Byrne et al. 2008) and contraction of forested systems (Byrne et al. 2011). In contrast to the dramatic cooling of the EOb, the better documented decline of Australian mesic biomes was a more gradual aridification following the Middle Miocene Climatic Optimum ∼15 Ma (Martin 2006).

Among biome types, arid climes have traditionally been considered harsh, physiologically exclusive habitats (Axelrod 1967). This has led to the belief that arid regions are species depauperate sinks of diversity (Crisp et al. 2009). Miocene aridification of Australia has been implicated in fracturing and extinction of mesic-adapted terrestrial and aquatic vertebrates (Potter et al. 2012; Unmack et al. 2013; Catullo and Keogh 2014). In contrast, arid biome expansion has been identified as integral in the rapid proliferation of arid-tolerant squamate reptiles (Jennings et al. 2003; Rabosky et al. 2007; Shoo et al. 2008). The variable response of Australian biota to aridification draws attention to the importance of investigating the influence of changing climate on contrasting geographic (global vs continental) and temporal (ancient vs contemporary; rapid vs gradual) scales.

Squamate reptiles represent Australia's most species-rich vertebrate assemblage, comprising more than 1000 species. The varied ages of Australian squamate radiations make them valuable for investigating patterns of continental and island biogeography, invasion, and diversification. Here, we focus on the oldest near-endemic Australian squamate group, pygopodoid geckos, a Gondwanan (crown: 50–70 Ma) suprafamily (families: Carphodactylidae, Diplodactylidae, Pygopodidae) of morphologically and ecologically diverse lizards. Pygopodoids present an ancient set of codistributed sister clades and an ideal system for investigating the variables influencing macroevolutionary trends across closely related radiations.

To address the impact of historical climate change, we have assembled the most complete (>150 Australian spp.; >90% species richness) fossil-calibrated phylogeny of the Pygopodoidea to date. We first investigate the macroevolutionary trajectory of these geckos in the context of global climate change using Bayesian methods to determine if (i) temporal asymmetry in the pygopodoid tree identified by Oliver and Sanders (2009) provides evidence of mass turnover at the EOb, and if so, was (ii) postextinction recovery consistent among families? Second, we question if regional trends in (iii) habitat transitions and (iv) biome-specific diversification rates have been influenced by continental aridification. Our analyses of rates and timing of pygopodoid gecko diversification support a signature of profound turnover near the EOb. Subsequent expansion of arid habitats coincides with elevated diversification in and transition out of this biome, highlighting the influence of continental aridification on Australian macroevolution and contemporary diversity.

Materials and Methods

PHYLOGENETIC AND DISTRIBUTIONAL DATA

We compiled a multilocus dataset of mtDNA (ND2) and nDNA (RAG1, RAG2, C-mos, PDC, ACM4, DYNLL1) markers for 155 ingroup Australian pygopodoid taxa, and 36 outgroup taxa stretching out to *Gallus gallus* (Table S1). Sequences were compiled largely from prior phylogenetic study of Australian geckos (Jennings et al. 2003; Oliver et al. 2007, 2009; Doughty et al. 2010; Oliver et al. 2010; Oliver and Bauer 2011; Pepper et al. 2011; Oliver et al. 2012, 2014; Brennan et al. 2016), and broad-scale investigations into Gekkotan systematics (Gamble et al. 2012, 2015). Taxon coverage among loci varies (Table S1), but is greatest for the mitochondrial locus ND2 (95%), and generally lower for nDNA loci (RAG1–68%, RAG2–65%, PDC–50%, DYNLL1–10%, C-mos–44%, ACM4–42%). Ingroup sampling represents the most inclusive Australian pygopodoid dataset to date (155 spp.; 90.5%), including recognized, molecularly divergent, cryptic lineages, that are likely to be elevated to species level (Doughty et al. 2016; Oliver and Doughty 2016).

For analyses of biome-associated diversification, we partitioned Australia into five discrete biomes that capture both accepted definitions (observed patterns of biological differentiation) and a widely used objective climate classification scheme (modified Köppen-Geiger climate classification; Stern et al. (2000)). Five-region classification is as follows: (i) Savannah—(Equatorial and Tropical in Stern et al. (2000)) and largely corresponding to savannah biome in northern Australia; (ii) Temperate—largely corresponding to the temperate biomes of previous analyses and covering broad areas in south-eastern and south-western Australia; (iii) Subtropical—corresponding to widely isolated areas on the east and west coast of Australia; (iv) Arid—consisting of both arid and surrounding semi-arid regions and "grassland" regions of Stern et al. (2000) and covering the vast majority of Australia (77.8%); (v) Wet forest—highly relictual pockets of generally fire sensitive forest dotted along Australia's east coast (Byrne et al. 2008; Byrne et al. 2011). This fifth category was not captured by Stern et al. (2000), but reflects both present day and historical data that indicate regions of permanently wet

forest have a phylogenetically and ecologically distinctive endemic biota, widely considered to represent the vestiges of a formerly much more widespread mesic adapted biota (e.g., Byrne et al. (2011)). Distributions of all taxa were mapped out against the simplified climate classification using the spatial portal of the Atlas of Living Australia (http://spatial.ala.org.au) and taxa occurring in more than one biome were coded as such. Several genera (*Aprasia*, *Crenadactylus*, arid zone *Oedura*) have members that outwardly code to the arid zone, but likely persist in refugial pockets of mesic habitat (Oliver et al. 2010). To account for the potential for this to bias analyses toward arid biomes, we established a second biome scoring, which incorporates mesic distribution of these taxa, and refer to it as the "mesic refugial" model in downstream biogeographic analyses.

DIVERGENCE TIME ESTIMATION

Divergence dates were estimated in a two-step process using an uncorrelated relaxed molecular clock and birth-death tree prior as implemented in BEAST v.1.8.3 (Drummond et al. 2006; Drummond and Rambaut 2007; Gernhard 2008). An initial BEAST analysis was run on the multilocus nuclear dataset alone, and was constrained by a number of fossil and secondary calibrations (Table S2). We ran two independent analyses for 300 million generations, sampling every 100,000 generations, and upon completion, inspected, and combined the log files using Tracer (Rambaut et al. 2014) and LogCombiner (Rambaut and Drummond 2007) to ascertain that the posterior, likelihood, and all priors reached convergence (ESS>200). Investigations into phylogenetic rate heterogeneity, including mass extinction, are directly linked to divergence-time estimates. Temporal bias in dated trees caused by poorly specified fossil calibrations may be passed on to bias in inference and timing of diversification heterogeneity, so to investigate the robustness of our divergence time estimates to our fossil calibrations, we iteratively removed each calibration and reran the dating analysis. Upon completion, we created a maximum clade credibility (MCC) tree from a set of post burn-in trees for each new dating scheme, and compared key nodes against the nuclear only MCC tree and a set of 100 trees randomly pulled from the posterior using paleotree (function "compareNodeAges") (Bapst 2012).

Exclusion of mtDNA from our initial dating analysis aimed to alleviate the potential for the combination of saturated mtDNA data and old outgroup calibrations to inflate divergence date estimates (Dornburg et al. 2012). From the nuclear only analysis, we extracted the range of generic, intergeneric, and family-level divergence events as 95% CIs from 100 random post burn-in trees via TreeAnnotator. These CIs were applied as secondary calibrations (Table S2) to the combined-locus mtDNA/nDNA analysis, and used in combination with the same fossil calibrations applied previously. Presence and implementation of secondary calibrations were largely dependent upon nuclear sampling, and applied to provide consistent constraint across the pygopodoid tree. All secondary calibrations, with exception of the Archosauria + Lepidosauria split, were implemented with uniform distributions to allow for the high degree of uncertainty of estimates within the 95% CI.

TEMPORAL RATE HETEROGENEITY AND MASS TURNOVER

To test for temporal variation in diversification rates, including Oligocene mass turnover, we used CoMET (May et al. 2015), as implemented in TESS (Höhna et al. 2016). CoMET is a Bayesian statistical method capable of identifying rate heterogeneity along the branches of a phylogeny. We used alternate methods of estimating diversification rates (TreePar, LASER, BAMM) to investigate the robustness of temporal diversification trends across methods, and results are included in Table 1 and Supplemental Materials (Table S4, Supplemental Methods). However, we rely largely upon our TESS results, because this framework is the only currently available method for jointly estimating diversifying rate shifts (λ, μ), and mass extinction (but see Laurent et al. 2015). TESS simultaneously runs simulations across multiple episodically varying birth-death models, and estimates the joint posterior distribution of shifts in rate of speciation (lambda—λ), extinction (mu—μ), and mass extinction events. In the episodic birth-death framework implemented by TESS, rates may change temporally along the tree allowing the timed placement of rate shifts and mass extinction events; however, rates among subclades at any given time remain fixed. Because all phylogenetic diversification analyses are sensitive to the estimated timing of divergence events, we implemented a sequential Bayesian approach to estimating diversification rates and mass extinction, by integrating over 100 trees randomly sampled from the post burn-in posterior distribution of our combined mito-nuclear BEAST analysis.

In TESS, occurrence of mass turnover is estimated as a function of magnitude (probability of survival), and like λ and μ, comparisons between the empirical tree and plausible models are evaluated by simulated reproducibility (Bayes factors and Posterior Probabilities). TESS additionally allows likelihood estimations (functions "tess.likelihood" and "tess.steppingStoneSampling"), to provide comparison across models and analytical programs (results: Table S4). To first investigate if there is phylogenetic support for mass turnover in our set of empirical trees, we constructed two pairs of competing models: (1) a constant-rate birth-death null model ($null_1$), and a constant-rate birth-death model (crbdME) that incorporates mass extinction (see: TESS package vignettes), and (2) a variable-rate birth-death (speciation rate shift < 10 mya) null model ($null_2$), and a variable-rate birth-death (identical speciation rate shift) model with mass extinction (vrbdME). Using the same diversification and turnover parameters, we then estimated

Table 1. Summary of results of diversification and morphological rate analyses.

Macroevolutionary question	Method (function)	References	Settings	Results by taxonomic clade			
				Pygopodoidea	Carphodactylidae	core Diplodactylidae	Pygopodidae
Temporal heterogeneity in diversification (heterotachy)	TreePar (bd.shifts.optim)	(Stadler 2011a)	6 BD nested models, testing 0–5 rate shifts episodically	3 shifts located at 30 (↑), 8 (↓), and 4 (↓) Ma	1 shift (↓) in speciation at 3 Ma	2 shifts in speciation at 16 (↓) and 4 (↓) Ma	1 shift (↓) in speciation at 5 Ma
	TESS (tess.mcmc; tess.likelihood; tess.likelihood. rateshift)	(Höhna et al. 2016)	3 models (constant BD, episodically varying BD, exponentially decreasing BD) implemented with function tess.likelihood	Episodically varying BD, with 2 shifts, located at 7 (↓), and 4 (↓) Ma	Constant rate BD	Constant rate BD	Constant rate BD
	CoMET (tess.analysis)	(May et al. 2015)	rjMCC across episodically varying BD with mass extinction	Mass extinction at 30 Ma, and shifts in speciation rate at 8 (↓) and 4 (↓) Ma	1 shift (↓) in speciation at 3 Ma	2 shifts in speciation at 7 (↓) and 4 (↓) Ma	1 shift (↓) in speciation at 5 Ma
	Gamma statistic: APE (gammaStat)	(Pybus and Harvey 2000; Paradis et al. 2004)	Gamma statistic and two-tailed T test for significance	Diversification has significantly decreased through time	Diversification has significantly decreased through time	Diversification has significantly decreased through time	Diversification has significantly decreased through time
	LASER (pbtree; ltt95)	(Rabosky 2006)	95% CIs of 1000 trees modeled under PB and constant rate BD models	LTT falls below 95CI at 30 Ma for both PB and BD	3 shifts in speciation at 8 (↑), 5 (↓), and 3.3 (↓) Ma	2 shifts in speciation at 9.7 (↓), and 3 (↓) Ma	1 shift (↓) in speciation at 2 Ma
Among clade heterogeneity in diversification	BAMM and BAMMtools (speciation.extinction)	(Rabosky et al. 2014b)	1 model estimating diversification rate heterogeneity	Diversification rates do not differ significantly among subclades	Diversification rates do not differ significantly among subclades	Diversification rates do not differ significantly among subclades	Diversification rates do not differ significantly among subclades
Trait-dependent (biome) heterogeneity in diversification	GeoSSE in diversiTree (find.mle; mcmc; constrain)	(Maddison et al. 2007; FitzJohn et al. 2009; Goldberg et al. 2011)	5 sets (each biome) of 5 nested models testing: equal speciation (eq.div) equal extinction (eq.ext) equal dispersal (eq.disp) no speciation between biomes (no.sAB)	Elevated speciation rate in arid zone	Not tested	Not tested	Not tested

PB, pure birth; BD, birth death; LTT, lineage through time; CI, confidence interval; ↑ increase in rate; ↓ decrease in rate; Ma, million years ago. Table is organized by the macroevolutionary question investigated, the method (R package or C++ program) and functions used (references included), settings applied or models compared, and results by clade.

the marginal likelihoods of the two models sets via stepping-stone-sampling (function "tess.steppingStoneSampling," each run for 10,000 iterations, 1000 discarded as burn-in, 100 stepping stones). After looping through all posterior trees, we compared models via Bayes factors (2 ln Bf). To determine significant difference between focal and null models, we followed Kass and Raftery (1995) and identified BF = 0 to 2 as "not worth more than a bare mention," BF = 2 to 6 as "positive" support, BF = 6 to 10 as "strong" support, and BF > 10 as "very strong" support.

After initial model comparisons, we estimated the timing and intensity of mass extinction with TESS (function "tess.analysis"). The power of methods that use molecular phylogenies to infer mass extinctions (such as TESS/CoMET) is sensitive to the timing of such an event, relative to the total tree depth. Events that occur deep in a group's history are confidently discovered less frequently (see May et al. (2015) for discussion) than those occurring more recently, however, false discovery rates (inferring a mass extinction event when one has not occurred) remain consistently low (8.1–9.9%). As a result, these methods are indirectly restricted to a conservative estimate of the occurrence of mass turnover. We ran the analyses (iterated over 100 post burn-in trees) with the hyper-priors including the time of a mass extinction event ("estimateMassExtinctionTimes") to be estimated empirically from the data, an MCMC length of 200,000 generations, with the first 10% discarded as burnin, a minimum ESS requirement of 500 to determine convergence, and four independent runs each conditioned on taxa and survival. We applied the same Bayes factor significance thresholds as above and as have been used previously (May et al. 2015).

PHYLOGENETIC RATE HETEROGENEITY

To determine if pygopodoid clades have diversified at a similar pace, we used BAMM (Rabosky et al. 2014a), which also estimates λ and μ dynamically, but allows rates among lineages to vary at any given time. This cross-clade comparison results in the ability of contemporary clades to decouple diversification (λ and μ) values among groups. BAMM highlights clades that diverge significantly from background rates of diversification, placing a credible set of shift placements along branches or at nodes. We executed three independent "speciationextinction" analysis runs with BAMM specified priors for 100,000,000 generations, sampling each 100,000 generations, and discarded the first 20% as burn-in. We used BAMMtools (Rabosky et al. 2014b) for postrun statistics and visualization of results, and to compare across runs for convergence. To provide another comparison of diversification rates across groups we also ran clade-specific (Carphodactylidae, Pygopodidae, Diplodactylidae, core Diplodactylidae) TESS analyses, and pairwise chi-square tests to determine significant differences. All methods allowed us to correct for incomplete taxon sampling via clade-specific sampling frequencies.

BIOGEOGRAPHY, AND BIOME TRANSITION AND SPECIATION RATES

Changing global and local climate, particularly aridification, have been implicated in influencing the diversification of most major Australian terrestrial radiations (see Byrne et al. 2011; Table 1). To investigate the evolution of biome distribution in the Pygopodoidea, we used BioGeoBEARS (Matzke 2013) to simultaneously reconstruct ancestral biome states and model biome shifts across the tree. Species were assigned to one or more biomes as outlined in the Materials and Methods. We ran an additional 50 biogeographic stochastic maps to provide a confident estimate of the frequency and directionality of across biome dispersal events, and account for uncertainty in ancestral biome reconstruction and state transitions (Matzke 2016). Transition frequencies and directionality were plotted in ggplot2 (Wickham 2009).

To determine rates of biome-specific diversification and habitat transitions, we applied the geographic extension of the state speciation and extinction model GeoSSE (Goldberg et al. 2011). Inputs were accompanied by phylogenetic sampling corrections to account for our taxonomically incomplete phylogeny (FitzJohn et al. 2009). We used the incorporated maximum likelihood search algorithm to estimate the model parameters and provide a starting point for our Markov Chain Monte Carlo (MCMC) sampling, which was run for two independent chains of 10,000 generations each. To determine best fitting models, we used analysis of variance (ANOVA) and likelihood ratio tests (LRT) to reject poorly supported diversification models, and ANOVA and two-tailed *t*-tests to compare differences in diversification rates among biomes. To check for vulnerability to Type I error in our phylogeny, and reduce the possibility of potentially misleading results from SSE methods (Maddison and FitzJohn 2015), we followed Rabosky and Goldberg (2015) and established a relative significance criterion for neutral traits across our tree. Using phytools (function "sim.char") we executed 100 simulations of a binary, neutral, discrete trait across our phylogeny, as GeoSSE is limited to analyzing binary-only data (Revell 2012). We then estimated the parameter (speciation, extinction, dispersal) rates using the maximum likelihood function ("find.mle") in GeoSSE, and summarized the rates across the 100 independent binary trait simulations. We used this distribution of trait likelihood ratios, as well as the upper and lower means of simulated traits to determine a 95% CI specific to our tree. This simultaneously tested for tendency of null traits to be associated with significant diversification rates, as well as giving us a confidence metric tailored to this dataset.

DATA ACCESSIBILITY

All alignments, divergence dating operator files, biome codings, and analysis scripts have been archived at Data Dryad: http://dx.doi.org/10.5061/dryad.991p6.

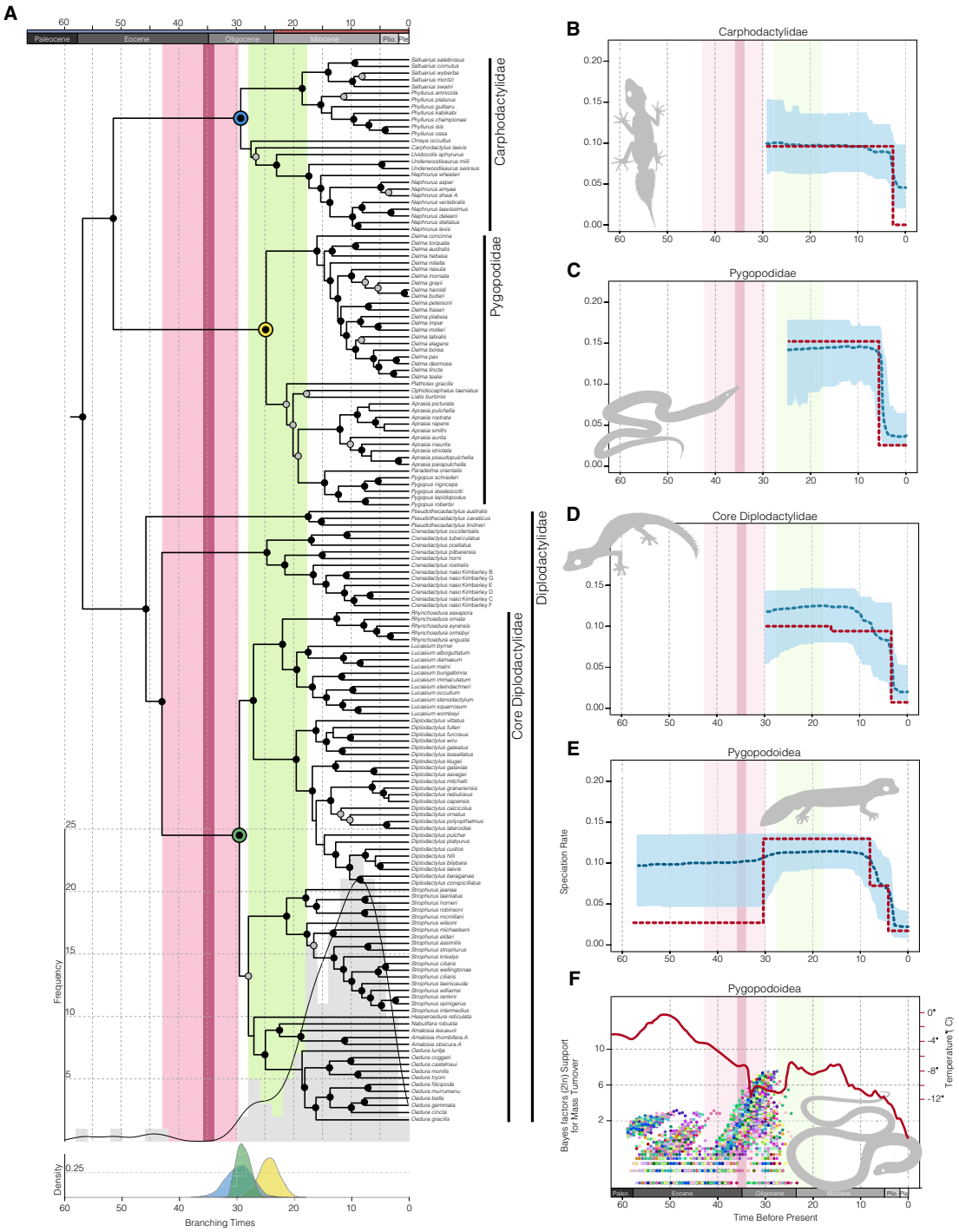

Figure 1. (A) Fossil calibrated phylogeny of the Pygopodoidea, nodes with >95 posterior probabilities are indicated by black circles, gray circles indicate posterior probabilities >80. Vertical pink bar highlights naked stem lineages likely the result of mass turnover at the Eocene-Oligocene boundary, indicated by vertical red bar. Green bar and node age density plots (bottom) draw attention to temporal congruence in crown divergences across all three families, including the diversification of all extant genera save *Crenadactylus* and *Pseudothecadactylus*. Histogram at bottom of tree shows frequency of branching events, which are clustered in the mid and late Miocene. Speciation rate estimates of (B) Carphodactylidae, (C) Pygopodidae, (D) core Diplodactylidae, (E) Pygopodoidea, are shown at right. Rate estimates were determined by TESS (blue dotted line, light blue 95% CI), and TreePar (red dotted line). (F) Shows CoMET results of analysis of mass turnover, across 100 trees as colored circles and support evaluated using Bayes Factors (BF (2ln) ≥ 6 is significant). Red line traces the change in mean sea surface temperature, adapted from Zachos et al. (2001). This is used to illustrate coincidence of mass turnover in the Pygopodoidea and dramatic drop in global temperature at the Eocene-Oligocene transition.

Results

DIVERGENCE TIME ESTIMATION

Results of the six locus nuclear BEAST analysis support ($PP \geq 0.98$) the monophyly of all Australian pygopodoid genera and families (Fig. 1). Short internode distances among some genera are associated with phylogenetic uncertainty (Fig. 1, highlighted in green vertical bar), consistent with previous studies (Nielsen et al. 2016; Skipwith et al. 2016; Brennan et al. 2016). Our mean estimate of the crown divergence of Pygopodoidea (57 Mya; 50–64) is slightly younger than previous results, but the 95% CI overlaps with most estimates (56–74 Ma—Skipwith et al. 2016; 65–75 Ma—Gamble et al. 2015; 60–85 Ma—Garcia-Porta and Ord 2013). Investigation of key node ages from alternative fossil calibration schemes yielded dates that did not fall outside confidence intervals of ages estimated from 100 posterior trees of the fully calibrated nuclear BEAST analysis (Fig. S3), and were also consistent with dates from our combined mito-nuclear divergence estimates, indicated no conflict across calibrations and datasets.

DIVERSIFICATION AND RATES, TEMPORAL HETEROGENEITY, AND MASS TURNOVER

Pygopodoid diversification rates reveal a general trend of rate decay consistent with results of Garcia-Porta and Ord (2013). Variable rate models (LASER, TreePar, TESS) applied to the combined MCC tree commonly indicate speciation rate declines occurring within the most recent 10 million years (Table 1; Table S3; Fig. S2). To investigate evidence of, timing, and consistency of support for a mass extinction event, we iterated analyses over 100 trees sampled from the BEAST posterior. TESS model comparison of marginal likelihoods always positively (2ln BF > 3) preferred models including mass extinction (vrbdME, crbdME) to the null ($null_1$, $null_2$) models. However, support for a vrbdME over crbdME model was generally negligible (2ln BF < 3) (Fig. S4). Model support for mass extinction encouraged our investigation into the timing of such an event. Ninety-five percent of trees provide positive (2ln BF > 3) support, and 58% of trees provide strong (2ln BF > 6) support for a mass extinction event occurring between 27 and 32 million years ago, prior to the crown radiations of pygopodids, carphodactylids, and "core" diplodactylids (Fig. 1, Table S3).

AMONG-CLADE DIVERSIFICATION RATE COMPARISONS

BAMM "speciationextinction" analysis does not identify significant heterogeneity in diversification rates among pygopodoid clades, despite similar crown ages, and disparate species richness (Carphodactylidae ~30 Ma, 30 spp.; Diplodactylidae ~30 Ma, 100+ spp.; Pygopodidae ~25 Ma, 46 spp.). Results of clade-specific CoMET analyses identify diversification rates that do not differ significantly among groups (Table S4).

BIOGEOGRAPHY AND TRAIT-ASSOCIATED SPECIATION

BioGeoBEARS analysis identified DEC+j and DIVAlike+j as equally most preferred (Δ-ln$L$ = –0.1, ΔAIC = 0.3) models of historical biogeography. Inclusion of the jump parameter "j," is favored considerably over the simpler DEC and DIVA like models (Δ-ln$L$ = 51.2), signifying the influence of between-biome founder-event speciation. DEC+j and DIVAlike+j ancestral biome reconstructions are concordant across all nodes with the exception of greater ambiguity in DIVAlike+j results of the interfamilial divergences. Results support a forest origin of the Carphodactylidae, and an arid origin of the Diplodactylidae (Fig. 2). It is necessary to note that biome reconstruction of deep nodes near the crown of Carphodactylidae and Pygopodidae may be confounded by poorly supported intergeneric relationships.

The frequency of outward dispersal events from the arid zone exceeds that of all other biomes combined (mean = 55; 51% of total events), suggesting elevated transition out of arid regions, into more mesic surrounds ("mesic" = savannah, subtropical, temperate, forest; Fig. 3). Outward transitions (source; 55) from the arid zone also double that of incoming events (sink; 22).

GeoSSE was used to test if major Australian biomes show evidence of differing diversification (λ, μ) and transition (q) rates by constraining rates of these three parameters (Table S5). Our analyses established that best-fit models varied across biomes: arid—eq.μ (equal extinction, speciation, and transition rates vary); temperate and savannah—eq.μq (equal extinction and transition rates, speciation may vary), subtropical and forest— eq.$\lambda\mu q$ (all rates equal). When state rates were compared against background rates (all other states combined), we found significant trends in arid (higher), and temperate and savannah (lower) diversification rates. Arid and subtropical zones display a significant elevation in transition rates. Trends identified as significant do not differ between our initial biome scoring and the "mesic refugial" alternative model.

Neutral trait simulations developed a CI for diversification and transition rates in and between two regions ("A" and "B"), giving maximum and minimum mean values built from our phylogeny. After comparison against our summary statistics, estimation of rates of arid zone speciation, and outward dispersal of arid and subtropical taxa remain significantly greater than simulations ($P < 0.05$).

Discussion

Analysis of pygopodoid gecko diversification reveals early Oligocene mass turnover, consistent with fossil and phylogenetic

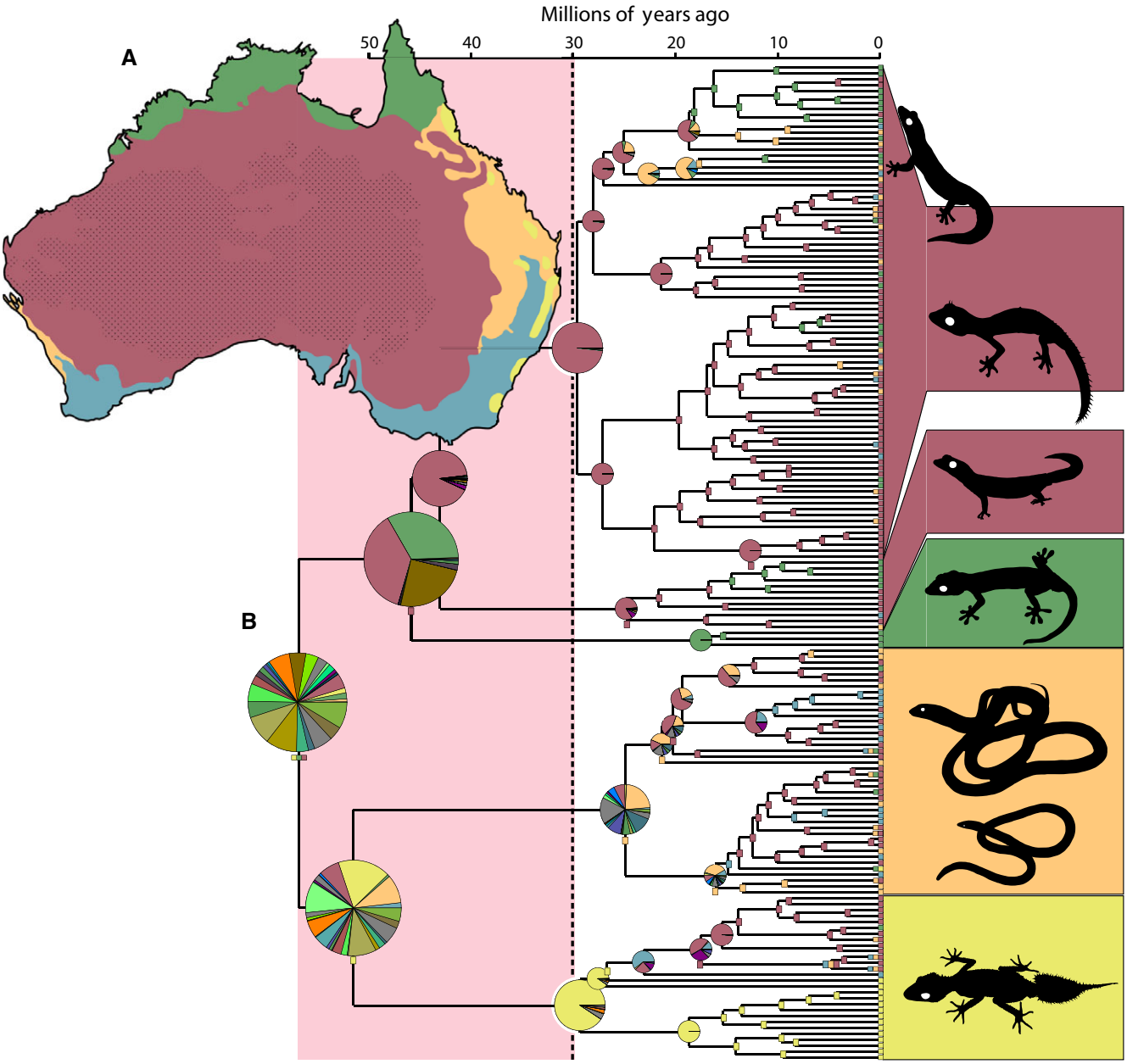

Figure 2. (A) Map of continental Australia as divided by our biome classifications: savannah (green), temperate (blue), subtropical (orange), forest (yellow), arid (red). (B) BioGeoBEARS ancestral state reconstruction under the DEC+j model of biogeographic dispersal. Colors of pie charts correspond to biome types previously mentioned. Pie charts indicate ancestral biome reconstructions of given nodes. Colored boxes below pie charts indicate majority reconstruction of visually ambiguous nodes. Colors present in pie charts but not on the inset Australian biome map indicate shared occurrence in more than one biome. Pink vertical bar indicates period impacted by Eocene-Oligocene turnover, and equivocal reconstructions. Shaded boxes to the right of the tree highlight ancestral biome reconstructions of major clades, from top to bottom: core Diplodactylidae, *Crenadactylus*, *Pseudothecadactylus*, Pygopodidae, Carphodactylidae. Extant pygopodoid diversity is greatest in arid biomes: more than 53% (91 spp.) include arid regions in part of their range, and more than 44% (75 spp.) exist exclusively in the arid zone.

signature of Australian and global contemporaries (Antonelli and Sanmartín 2011; Sun et al. 2014). This period of elevated extinction following dramatic climatic change at the Eocene Oligocene transition, illustrates visible signature of global events on broad phylogenetic groups. Contemporary patterns in species distributions are however, more accurately explained by recent continental, gradual processes, particularly continental aridification. Combining these concepts, the Australian Pygopodoidea likely originated in the Cretaceous and has largely diversified via postextinction response in the Oligocene,

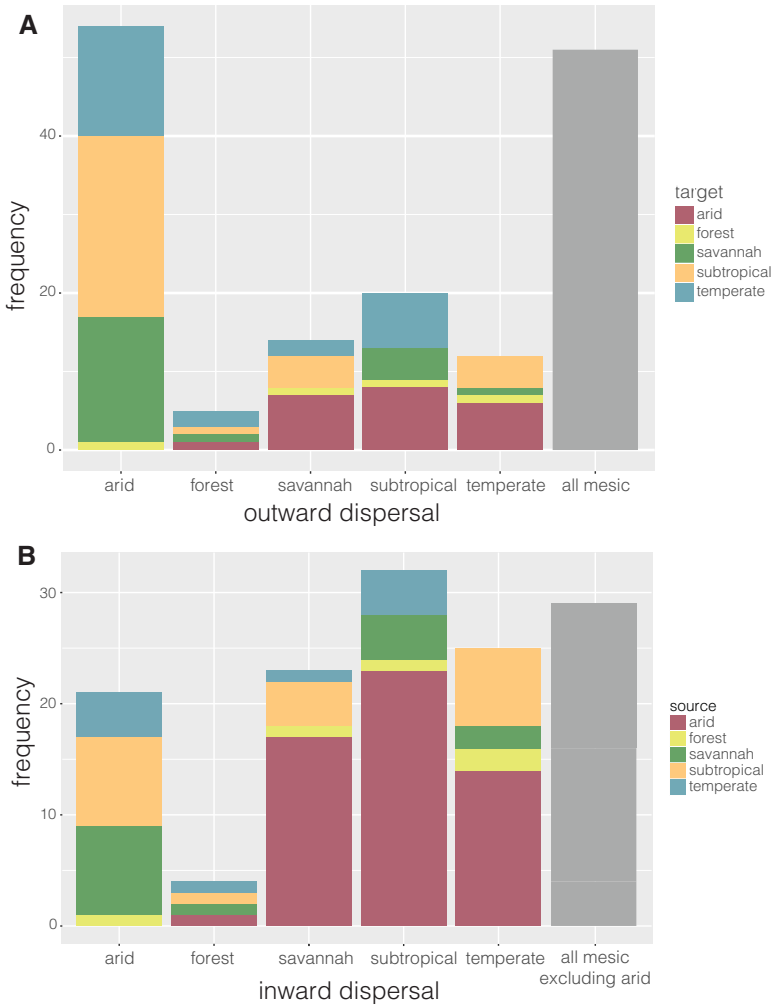

Figure 3. Directional biome transition frequencies. (A) Histogram showing frequency and composition of outward transitions from five biome types and gray composite bar showing combined outward frequencies from four mesic biomes. Frequency of dispersal out of the arid zone is greater than out of all four mesic biomes combined. (B) Histogram showing frequency and composition of incoming transitions into five biome types, and gray composite bar showing combined incoming frequencies from four mesic biomes, excluding transitions from the arid zone. Dispersal from the arid zone makes up the majority of inward transitions into three of four mesic biomes. All transitions into mesic biomes narrowly exceed that of dispersals into the arid zone.

flourishing during the protracted Miocene aridification of Australia.

EXTINCTION AND GLOBAL CLIMATE CHANGE

Mass turnover of pygopodoid geckos in the early Oligocene provides an explanation for previously noted (Oliver and Sanders 2009) temporal heterogeneity in the diversification of this group, and homogeneity in crown family divergence ages (Fig. 1). However, molecular phylogenetic signature of such turnover is difficult to reliably identify in the absence of appropriate fossil material (Quental and Marshall 2010). To rely on molecular data alone requires that the group in question both significantly predate and survive a period of mass turnover. Signal of such an event may be further confounded by asymmetrical effects of elevated extinction on different groups (Wilson et al. 2012). To be detectable, signal must generally be consistent among clades, else conflicting trends may smother signature of turnover. Furthermore, without a fossil record, those groups that go completely extinct or survive as relics and fail to subsequently rebound, provide either no molecular signature, or signature largely indistinguishable from long-term low-cladogenic persistence. We provide evidence of just such an exceptional occurrence in Australian pygopodoid geckos.

Diversification dynamics of the Pygopodoidea add to a growing body of evidence supporting mass turnover across broad phylogenetic groups of the late Eocene and early Oligocene (Hooker et al. 2004; Pearson et al. 2008; Sun et al. 2014; Cantalapiedra et al. 2015). The EOb is marked by a period of global climatic

turbulence, including rapid cooling (>5°C in <100,000 years) and aridification (Zachos et al. 2001; Liu et al. 2009). Throughout Southeast Asia and Australia, floristic history provides evidence of contracting rainforest and mesic sclerophyllous habitats (Byrne et al. 2011; Buerki et al. 2013). We suggest that a rapid drop in temperature and contraction of suitable habitat likely outpaced the adaptability of ancestrally mesic pygopodoid geckos. Especially given that most extant taxa are characterized by low vagility and fecundity (Read 1999). This trend in assemblage turnover between the Eocene and Oligocene is potentially also reflected in the radiation and invasion of a number of other Australian squamate lineages, and indicates that climatic change at the EOb ushered in a new era for accumulating Australian diversity.

Congruent crown divergences of Australian pygopodoid families (~25–30 Ma) (Fig. 1), typified by short internode distances and poor resolution of basal intergeneric relationships, is consistent with the theory that, following periods of mass turnover surviving lineages often undergo rapid adaptive radiation. Accelerated postextinction diversification is suggested to be the result of open niche space provided by dramatic loss of standing diversity and opportunity in new or changing habitats (Erwin 2001; Chen and Benton 2012). Here, we suggest similar responses by pygopodoid geckos to the climate and biome turnover of Oligocene Australia. Cooling of the early Oligocene gave way to warming in the late Oligocene, which has been implicated as an important driver of diversity in mammals (Stadler 2011a) and other terrestrial flora and fauna (Sun et al. 2014). This warming trend encapsulates a period of ecological diversification marked by arboreal and terrestrial divergences in carphodactylids and diplodactylids, and diurnal, nocturnal, fossorial, and arboreal clades of pygopodids. Consistent rates of cladogenesis among families indicate a common postextinction response of pygopodoid families following perturbation in the early Oligocene.

DIVERSIFYING DURING CONTINENTAL BIOME CHANGE

In contrast to the relatively rapid climatic change and ensuing turnover of the Oligocene, protracted Miocene aridification of the Australian continent coincides with signal of phylogenetic expansion in pygopodoids. Current understanding of the Australian arid zone has suggested a gradual trend toward aridification throughout the latter half of the Miocene, transitioning from drought-sensitive wet forests to drought-tolerant eucalypts and acacias (Crisp and Cook 2013). Aridification was punctuated by marked mesic pulses in the Pliocene (Sniderman et al. 2016), and Pleistocene (Martin 2006), however the overall trend has continued with the arid zone extending to encompass more than 70% of the continent. The slower tempo of Miocene biome rearrangement suggests that instead of immediate unilateral losses in diversity, there was opportunity for lineages pruned from the phylogeny to be gradually replaced by the proliferation of taxa capable of making the shift to arid biomes (Byrne et al. 2008, 2011). This more recent trend in continental aridification better explains contemporary patterns in distribution and the diversification of extant pygopodoids.

Globally, desert ecosystems have been considered net sinks for diversity (Crisp et al. 2009). Despite the difficulties of persisting in arid biomes, arid climes have had a profound influence on the evolution of plants and animals (Stebbins 1952). In Australia, exceptionally diverse communities of squamate species may be found in sympatry, including closely related lineages (Pianka 1969; Jennings et al. 2003; Goodyear and Pianka 2008). However, the drivers of this arid zone squamate richness have been difficult to pinpoint (Pianka 1989; Powney et al. 2010). The young age of this biome paired with our findings of accelerated rates of arid pygopodoid speciation lend support to the theory that invasion of a novel geographic region or biome is associated with relative rapid diversification (Yoder et al. 2010). Although few other studies have explicitly investigated the speciation dynamics of Australian radiations, predominantly arid zone clades of Australian skinks (*Ctenotus*, *Lerista*) (Rabosky et al. 2014a), *Hylaeus* bees (Kayaalp et al. 2013), and *Triodia* and *Acacia* plants (Crisp and Cook 2013) show elevated rates of speciation, suggesting that this pattern may be widespread.

Elevated arid zone diversification may be attributable to varied intrinsic, extrinsic, and artefactual causes, some of which are likely unique to the Australian continent and focal group. Firstly, the geographic area of the Australian arid zone exceeds that of all other Australian biomes combined, creating a greater platform for speciation and divergence. While primary productivity is low compared to more mesic neighboring biomes, space, and habitat heterogeneity are high. Alternatively, higher arid zone richness may be a consequence of nonrandom extinction. Shrinking mesic biomes have undoubtedly been associated with range restriction and likely elevated extinction of their inhabitants, and so signal from extant taxa may provide an inaccurate representation of historic mesic richness (Bryant and Krosch 2016). Finally, as a group, squamate reptiles are physiologically predisposed to handle heat-stress and evaporative water-loss (Pough 1980; Cox and Cox 2015). In geckos, this preadaptation to arid climes is extended by an ancestral transition to nocturnality, and avoidance of dangerous heat and radiation (Gamble et al. 2015).

Our investigation of biome transitions suggests that arid habitats are a considerable source of Australian continental diversity. Arid zone pygopodoid richness is not trapped exclusively within the arid zone, and elevated diversification rates have resulted in frequent dispersal into peripheral mesic biomes. Though geographic size and perimeter undoubtedly contribute to this, intrinsic factors of ecology may explain elevated transition rates as well. Frequent sympatry of closely related species, and higher local

(alpha) species diversity of squamates in the arid zone (James and Shine 2000; Powney et al. 2010), is likely a result of greater niche differentiation. In this vein, ecological diversity cultivated in the arid zone of Australia may have provided successful transitions back into mesic biomes (Nielsen et al. 2016).

Conclusions

Macroevolutionary studies focusing on broad patterns in diversification may be strengthened by incorporating local (here, continental) mechanisms that may better explain patterns in extant diversity (Vermeij and Leighton 2003). Our investigation of a diverse continental vertebrate radiation is consistent with the understanding that global changes may profoundly and unilaterally impact disparate phylogenetic groups, however subsequent biome assemblages may respond dissimilarly. In these instances, studies of sister-clade dynamics provide valuable insight into such patterns of diversity as they undergo pressure from congruent and contrasting diversifying influences. We provide new evidence of the dramatic impact that rapid (Eocene-Oligocene cooling) climatic change has had on the Australian biotic assemblage. Protracted aridification has also been instrumental in shaping trends in Australian biodiversity (Barker and Greenslade 1982; Cracraft 1986). However, contrary to patterns seen in other Australian radiations, the arid zone has facilitated the diversification of pygopodoid geckos, acting as a source for neighboring habitats. Contrasting signature in response to rapid and gradual climate regimes draw attention to their varied influences on macroevolution, and highlights the necessity of further investigation of historical biogeography among Australian clades. Understanding the importance of the Australian arid zone as a source for continental diversity is paramount to developing a clearer picture of how Australia's regional fauna have been assembled.

AUTHOR CONTRIBUTIONS

I.G.B. conceived and designed the study, and analyzed the data; I.G.B. and P.M.O. collected the data and wrote the article.

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Supporting Information

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

Table S1. Molecular sampling used in this paper. Data includes the name binomials used in this study, and museum identification numbers.
Table S2. Fossil calibrations collected for this study.
Table S3. Results of temporal and among clade estimates of diversification rate heterogeneity, grouped by analytical program.
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Figure S4. Bayes factor comparisons among constant rate (crbd = ConstBD, crbdme = ConstBDME) and variable rate (vrbd = shiftBD, vrbdme = shiftBDME) TESS models investigating support for a mass extinction event.