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Research

Rapid diversification of the Australian *Amitermes* group during late Cenozoic climate change

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Late Cenozoic climate change led to the progressive aridification of Australia over the past 15 million years. This gradual biome turnover fundamentally changed Australia's ecosystems, opening new niches and prompting diversification of plants and animals. One example are termites of the Australian *Amitermes* group (AAG), consisting of the Australian *Amitermes* and affiliated genera. Although the most speciose and diverse higher termite group in Australia, little is known about its evolutionary history. We used ancestral range reconstruction and diversification analyses to illuminate 1) phylogenetic relationships of the AAG, 2) biogeographical processes leading to the current continent-wide distribution and 3) timing and pattern of diversification in the context of late Cenozoic climate change. By estimating the largest time-calibrated phylogeny for this group to date, we demonstrate monophyly of the AAG and confirm that their ancestor arrived in Australia ~11–10 million years ago (Mya) from Southeast Asia. Ancestral range reconstruction indicates that Australia's monsoon region was the launching point for a continental radiation shaped by dispersal and within-biome speciation rather than vicariance. We found that multiple arid-zone species diversified from mesic and tropical ancestors in the Plio-Pleistocene, but also observed diversification in the opposite direction. Finally, we show that diversification steadily increased from ~8 to 9 Mya during the 'Hill Gap' and accelerated from ~4 Mya in concert with major ecological change during the Pliocene. Consistent with rapid diversification, species accumulation then slowed down into the present, likely caused by progressive niche saturation. This study provides a stepping stone for predicting future responses of Australia's termite fauna in the face of human-mediated climate change.

Keywords: *Amitermes* group, Australia, historical biogeography, rapid diversification, past climate change

Introduction

Australia exemplifies evolutionary challenges that changing climate can pose to organisms and ecosystems. Starting in the late Miocene roughly 10 million years ago (Mya), Australia's previously warm and wet climate became cool and dry, a period of regional



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climatic instability known as the ‘Hill Gap’ (10–6 Mya, Hill 1994). Rainforests retreated to local refugia (Yeates et al. 2002, Cassis et al. 2017), while climatic oscillations of the Pliocene and Pleistocene further shaped the present-day arid and semi-arid zones (Byrne et al. 2008). Despite its relatively young age, the Australian arid biome has a rich and unique flora and fauna (Raven and Yeates 2007, Powney et al. 2010, Guzik et al. 2011, Ladiges et al. 2011, Andersen 2016), suggesting either the persistence of ancient lineages or (rapid) radiations in parallel with the increasing aridification of the continent (Crisp et al. 2004, Byrne et al. 2008). Thus, Australia’s extraordinary biodiversity has not only been shaped by relictualism stemming from the breakup of Gondwana (Barrett and Williams 1998, Barden and Ware 2017), but also by vicariance, in situ speciation and phylogeographic structuring of populations in response to local environmental conditions (reviewed in Cassis et al. 2017). Vicariance, particularly, has been shown to be important in the evolutionary trajectory of many arid zone taxa (Cracraft 1982, Crisp and Cook 2007, Rabosky et al. 2007).

Today, Australia’s arid zone covers roughly 70% of the continent and separates the once predominant mesic biome into eastern and south-western mesic zones (Byrne et al. 2008). The mesic biome includes the last remnants of rainforest in Australia and is characterized by rainfall during winter (Byrne et al. 2011). Despite receiving similar total rainfall, the monsoonal tropics in northern Australia are distinguished by summer rainfall, cyclones and a dry winter season (Bowman et al. 2010). While the flora and fauna of each major biome has been extensively studied (Pepper et al. 2011, Cardillo et al. 2017, Harms et al. 2019, reviewed in Byrne et al. 2008, 2011, Bowman et al. 2010, Rix et al. 2015), only a handful of studies have addressed patterns of diversification between Australian biomes at a continental scale (Fujita et al. 2010, Owen et al. 2017, Brennan and Keogh 2018), and none so far on Australia’s rich termite fauna (Calaby and Gay 1959).

Here, we examine the diversification of *Amitermes* Silvestri and allied genera (*Ahamitermes*, *Drepanotermes*, *Incolitermes* and *Invasitermes*), which we refer to as the Australian *Amitermes* group (AAG). The AAG forms the most diverse and speciose group of higher termites (Termitidae) in Australia, including about 100 described species (Krishna et al. 2013), many of which are important to ecosystem functioning across the continent (Coventry et al. 1988, Noble et al. 2009, Evans et al. 2011). The AAG and other termite lineages arrived in Australia relatively recently, 11–13 Mya (Bourguignon et al. 2017), suggesting that they initially diversified as more or less warm/wet conditions of the late Miocene were coming to an end, before facing rapidly intensifying aridification in the Plio-Pleistocene. Indeed, diversification in other Australian animal and plant groups coincides with the increase in aridity and the expansion of the arid zone in the last 10 million years (Byrne et al. 2008, 2018), including Australian *Coptotermes* and Nasutitermitinae (Lee et al. 2015, Arab et al. 2017).

Under niche conservatism theory, we would expect that early lineages of the AAG were limited by the environmental conditions of their native tropical ranges in Southeast Asia (Bourguignon et al. 2017) and that diversification into other

Australian biomes was rare. Instead, AAG species occur across the continent, are adapted to temperate, (sub)tropical and arid climates, and have persisted through periods of severe climate change (Abensperg-Traun and Steven 1997). We hypothesise that aridification forced frequent biome shifts (i.e. dispersal events) and promoted radiations within biomes, as in other Australian continental radiations (Catullo and Keogh 2014, Toon et al. 2015, Brennan and Oliver 2017). Because termites are poor dispersers (Eggleton 2000), we expect that biogeographic patterns have been largely shaped by within-biome speciation. To quantify biome shifts and other biological processes (e.g. within-biome speciation, vicariance), we first test the monophyly of the AAG, which would indicate a single introduction event on the Australian continent, then infer ancestral biomes under different biogeographic models. Finally, we test whether diversification rates have changed over time. Recent studies have shown that the aridification of Australia acted as a driver of diversification, resulting in species accumulation over short evolutionary time frames (McLeish et al. 2007, Rabosky et al. 2017, reviewed in Byrne et al. 2018). Since the AAG is highly diverse but relatively young, we hypothesise that diversification accelerated during periods of late Cenozoic climate change (e.g. during the ‘Hill Gap’ and Plio-Pleistocene).

Material and methods

Mitochondrial genome sequencing

The final data set comprised 135 mitochondrial genomes (Supporting information): 87 *Amitermes* and *Drepanotermes* mitochondrial genomes sequenced in this study and 48 sequences from NCBI, including 15 *Amitermes* and *Drepanotermes* and 33 outgroup taxa to root the phylogenetic inferences. Two different sequencing and assembly strategies were used: 1) long-range PCR followed by deep-amplicon sequencing and 2) ultra-low coverage (1X) whole-genome sequencing (WGS). Due to heterogeneity at third codon positions, we excluded them from downstream analyses, resulting in a final concatenated sequence alignment partitioned into four subsets: a) first, and b) second codon positions of protein-coding genes, c) 12S and 16S rRNA genes, and d) tRNA genes. For details see Supporting information.

Genetic distances and phylogenetic relationships

To visualize genetic (dis)similarity among AAG sequences, we performed principal coordinates analysis (PCoA) on just the AAG sequences from the final concatenated sequence alignment. Phylogenetic relationships were inferred by maximum likelihood analysis using IQ-TREE ver. 2.0.6 (Minh et al. 2020). To date our phylogeny, we used four termite fossils as internal calibrations (Supporting information) implemented as exponential priors. Divergence dating was performed with BEAST ver. 2.6.1 (Bouckaert et al. 2019) and a maximum-clade-credibility (MCC) tree was obtained using TreeAnnotator implemented in BEAST ver. 2.6.1. For details see Supporting information.

Biogeographic history

We used our best time-calibrated MCC tree to compare biogeographic models and estimate ancestral ranges using the maximum-likelihood approach implemented in BioGeoBEARS ver. 1.1.2 (Matzke 2013). We compared three different biogeographic models, which include different cladogenetic processes: 1) DEC (dispersal-extinction-cladogenesis) includes subset sympatry, 2) DIVALIKE (likelihood interpretation of DIVA) includes widespread vicariance and 3) BAYAREALIKE (likelihood interpretation of BayArea) includes widespread sympatry. The best-fitting model was assessed with the Akaike information criterion (AIC, Akaike 1974).

Prior to analysis, we excluded all outgroup taxa and non-Australian *Amitermes*. We pruned splits younger than 1.5 million years, retaining a single representative of each species/independent evolutionary unit to avoid spurious 'speciation' events, as recommended on the BioGeoBEARS website (<<http://phylo.wikidot.com/biogeobears-mistakes-to-avoid#toc6>>). This resulted in a tree with 72 terminal tips, which were assigned to the four major biomes in Australia (modified from Fujita et al. 2010: S, mesic south-western zone; A, arid zone; M, monsoonal tropics; and E, mesic eastern zone) by collection site (Fig. 1c and Supporting information). Where tips could be unambiguously attributed to a described species, occurrence records from the Atlas of Living Australia (<www.ala.org.au>, accessed 10 July 2020) were used to assist biome assignment. We allowed a maximum of two biomes to form a species range, while excluding all combinations of non-adjacent biomes (i.e. 'monsoonal tropics + mesic south-western zone' and 'mesic eastern zone + mesic south-western zone'), resulting in 9 ranges.

We used 100 biogeographical stochastic mappings (BSMs) to obtain overall probabilities of anagenetic and cladogenetic events (Matzke 2016, Dupin et al. 2017), which depend on geographic distributions, the time-calibrated phylogeny and the best-fitting model. This quantified the relative roles of dispersal and vicariance in cladogenesis during the diversification of the AAG.

To assess the effect of topological uncertainty during model selection, we randomly sampled 100 pruned trees from the posterior distribution of the Bayesian analysis, summarized their ancestral range estimates, and compared AICc values of the estimates for DEC, DIVALIKE and BAYAREALIKE models using a custom R script modified from Magalhaes et al. (2021).

Model and rates of diversification

The temporal pattern of lineage diversification was visually assessed with a semi log-scaled lineage-through-time (LTT) plot in the R package 'phytools' (Revell 2012) using the pruned time-calibrated MCC tree, as well as 500 simulated LTTs assuming a pure-birth process of the same duration and resulting in the same total number of species. To account for phylogenetic uncertainty regarding divergence estimates and topology, we created LTTs for each of 100 pruned posterior trees. The γ statistic, which can detect whether the net diversification rate deviated over time from a pure birth model (standard normal distribution with a mean of 0; Pybus and Harvey 2000), was simultaneously calculated for the MCC tree and the 100 pruned posterior trees. We conducted a Monte Carlo constant rates test (MCCR test, Pybus and Harvey 2000) implemented in the R package 'LASER' (Rabosky 2006), to account for incomplete sampling (Fordyce 2010). The test

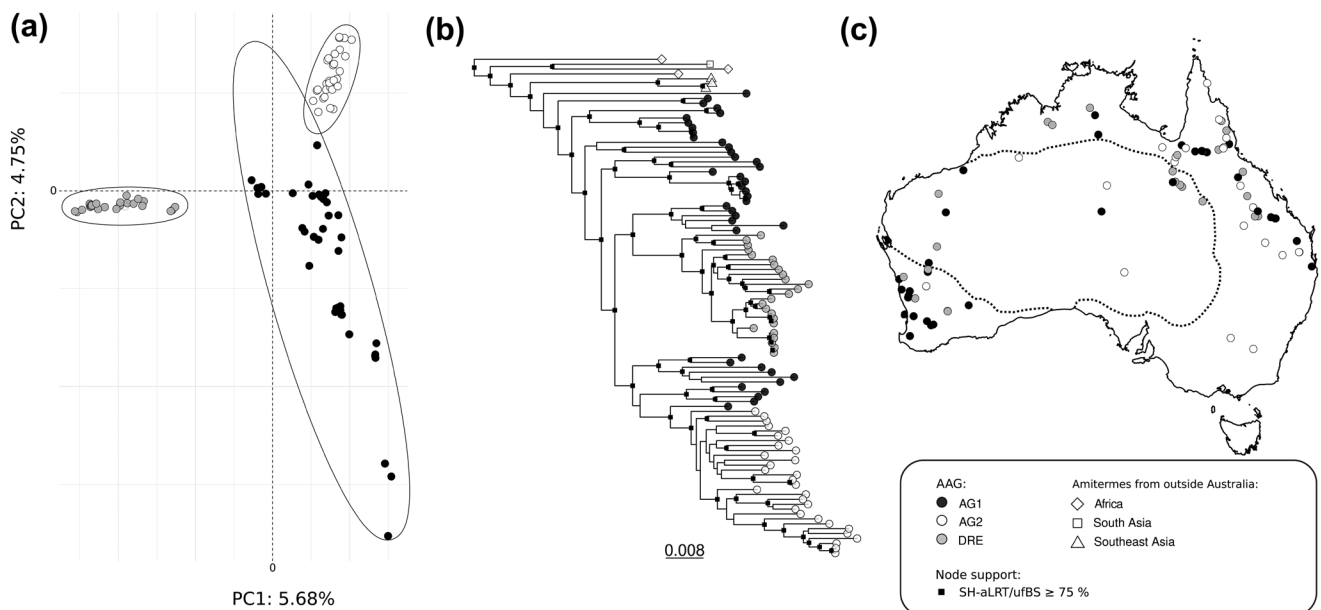


Figure 1. (a) The PCoA showed three distinct genetic clusters within the Australian *Amitermes* group (AAG), (b) two of which (*Drepanotermes* (DRE) and *Amitermes* group 2 (AG2)) are recovered as monophyletic by the maximum likelihood analysis. (c) Map shows sampling locations of AAG taxa included in this study in relation to the arid zone (dashed line, modified from Fujita et al. 2010).

mimicked incomplete sampling by randomly pruning taxa from phylogenies, which were simulated to the full size of the group (about 100 described species per Krishna et al. 2013). We used 10 000 replicates under the null hypothesis of a constant rate pure-birth diversification process.

In addition, we compared the fit of alternative evolutionary models with respect to our multi-LTT plot using the ‘run_diversification_analyses.R’ script (Condamine et al. 2018). This analytical pipeline includes the R packages ‘RPANDA’ (Morlon et al. 2016) and ‘DDD’ (Etienne et al. 2012). Both approaches account for the absence of species (both extinct and missing from the phylogeny) and how this may affect historical diversification rates. We used four different models, of which two assume constant diversification rates including the pure-birth (or Yule) model assuming no extinction, and the constant rate birth–death model (CR) with extinction but constant rates of speciation and extinction over time and among lineages. The other two models assume diversity-dependence, namely the density-dependent linear (DDL+E) and the density-dependent exponential (DDX+E) models. Both models quantify diversification rates as functions of changes in species accumulation over time. The DDL+E model assumes a linear dependence of speciation rate with extinction (E), while the DDX+E model assumes an exponential dependence of speciation rate with extinction.

We fitted all models under three alternative scenarios to account for different proportions of missing species in our phylogeny. Similar to other termite taxa (Watson and Abbey 1993), the ‘true’ diversity of the AAG is likely much higher than currently described. Hence, we assumed that the group a) consists of the currently reported 100 species, b) includes more species than known today (150) or c) is actually much larger than currently described (250). In other words, we assumed that the sampling fractions in our phylogeny were 72, 48 and 29%, respectively. The AIC approach was used to evaluate the best-fitting model, reported as the bias-corrected AIC version (AIC_c, Burnham and Anderson 2002, Posada and Buckley 2004). To determine the goodness of fit of candidate evolutionary models, we used the lowest AIC_c score and Δ AIC_c scores, where the differences between the lowest (or best) AIC_c and the AIC_c of each alternative model are calculated, and thus, the best model has Δ AIC_c=0. All analyses were run on the MCC tree and the 100 pruned posterior trees.

To complement the model-fitting approach, we employed BAMM ver. 2.5.0 (Bayesian analysis of macroevolutionary mixtures, Rabosky 2013, 2014, bamm-project.org), which can automatically detect diversity-dependence on phylogenetic trees, shifts in diversification rate through time and key innovations. We ran BAMM for 100 million generations with default parameters and a burn-in of 25% using the same pruned time-calibrated MCC tree as above. To account for incomplete taxon sampling, we implemented 0.72 as sampling fraction (72 taxa/independent evolutionary units in our phylogeny relative to the ~100 described AAG species). Since prior settings can have a substantial impact on BAMM analyses (Moore et al. 2016), we used a gradient of values

for the prior on the number of shifts in diversification (compound Poisson process), ranging from the default value of 1.0 (higher probability of no rate shift) to 0.1 (higher probability of multiple rate shifts), with a step of 0.1. The best-fitting run (i.e. highest posterior probability for the number of shifts) was selected for downstream analyses. The R-package ‘BAMMtools 2.1’ (Rabosky 2014) was used to check for convergence (ESS > 200) and mixing of the MCMC chain in each analysis. To incorporate phylogenetic uncertainty in the BAMM analysis, we used the best-fitting Poisson rate prior (0.1, Supporting information) and computed the best shift configuration for the 100 pruned posterior trees.

Results

Genetic distances and phylogenetic relationships

Phylogenetic reconstructions based on Bayesian and ML inferences consistently recovered a monophyletic AAG (> 85% SH-aLRT/ufBS values and posterior probabilities), which is sister to *A. dentatus* from Southeast Asia (Fig. 1b and Supporting information). The PCoA indicated three major groups within the AAG (Fig. 1a): *Amitermes* group 1 (AG1), *Amitermes* group 2 (AG2) and *Drepanotermes* (DRE). The latter two formed independent monophyletic crown groups nested within the paraphyletic group AG1, which were well-supported in all phylogenetic analyses (> 95% SH-aLRT/ufBS values and posterior probabilities, Fig. 1 and Supporting information).

Divergence estimates, based on the model-averaging approach (bmodeltest) without third codon positions, dated the split between the AAG and the Southeast Asian species at 10.99 Mya (95% HDP: 9.52–12.81 Mya) (Supporting information). Two major divergence events, *Drepanotermes* at 6.5 Mya (95% HDP: 5.6–7.67 Mya) and AG2 at 5.55 Mya (95% HDP: 4.77–6.45 Mya), correspond roughly to the end of the paleoclimatic ‘Hill Gap’ (10–6 Mya) in the late Miocene (Supporting information). An estimated 12% of DRE and 53% of AG2 lineages diverged during the Pliocene (~5.3–2.6 Mya) compared to 33% of AG1 lineages, while recovered divergence time for 35 out of 95 lineages within the AAG were < 1.5 Mya (Supporting information).

Biogeographic history

AIC model selection favored the DIVALIKE model for the evolution of the phylogenetic relationships shown in the MCC tree. DIVALIKE was 1.8 AIC units lower than DEC and 29.1 AIC units lower than BAYAREALIKE (Table 1). Models that included vicariant processes (DEC and DIVALIKE) gave very similar histories compared to the BAYAREALIKE model (results under DEC and BAYAREALIKE are available in Supporting information). The impact of topological uncertainty on the model selection process was examined by combining the AIC_c values of the ancestral range estimates for each of the 100 posterior trees and for each of three models (Supporting information). DEC and DIVALIKE explain the

data equally well, so we chose DIVALIKE for downstream analysis, as it allows for widespread vicariance, a process important in the evolutionary trajectory of many arid zone taxa (Cracraft 1982, Crisp and Cook 2007, Rabosky et al. 2007).

Ancestral range reconstruction based on the DIVALIKE model estimated that the most probable ancestral range for the AAG is a combination of the monsoonal tropics+arid zone ($p=0.49$) followed by the monsoonal tropics (0.29), and other state combinations (0.32) (Fig. 2). The two monophyletic crown groups AG2 and DRE were inferred to have different ancestral ranges. DRE most likely originated in the mesic south-western zone + arid zone (0.46) followed by the arid zone (0.39), while the former probably arose in north-northeastern Australia (monsoonal tropics + arid zone, 0.61) (Fig. 2).

The BSM results indicate a complex biogeographical history, driven largely by within-biome speciation and dispersal events (46.2% and 34.6% of the total number of events) rather than vicariance events (19.2%, Table 2). The highest number of dispersals occurred from the arid zone to the mesic south-western zone (~9 of 38 total estimated events), followed by movements from the arid zone to the monsoonal tropics (~7 of 38) and from the monsoonal tropics to the arid zone (~6 of 38) (Supporting information). More than half of all estimated dispersal events (52.1%) started in the arid zone, with the next common source being the monsoonal tropics (28.5%) (Fig. 2 and Supporting information). Most of these movements were directed towards the arid zone (28.1%), followed closely by the monsoonal tropics and the mesic south-western zone (26.6% and 24.6%, respectively) (Fig. 2 and Supporting information).

Model and rates of diversification

The multi-LTT plot suggests a rather continuous trend of increasing diversification from ~8 to 9 Mya with a sudden, abrupt incline from ~4 Mya, which exceeds the 95% confidence interval followed by a slowdown to the present day. MCCr tests yielded significantly negative γ statistics for the MCC tree (-2.36 , $p < 0.0001$) and the 100 posterior trees (-2.38 ± 0.02 , $p < 0.0001$), respectively, indicating non-constant species accumulation over time, as shown by the multi-LTT plot (Fig. 3).

The diversity-dependent linear model (DDL+E) was the best-fitting estimate of evolutionary diversification within the AAG (Table 3), based on four candidate models used in the maximum-likelihood diversification analyses. This further supports the idea that a non-constant mode of diversification shaped the evolutionary trajectory of the AAG. The same holds true when we assume that only 48% or 29% of the 'true' diversity of the group was sampled in the MCC tree and in the

100 posterior trees, respectively (Table 3). This indicates that the results are robust against potential missing species.

BAMM analyses based on the MCC tree detected no major shifts in the rate of diversification within the AAG (Supporting information), irrespective of the prior value that governs the number of rate shifts. The best-fitting run with the highest probability was fixed at 0.1 (Supporting information). For the 100 pruned posterior trees, no shift was detected for 98 trees, and only two trees showed one rate shift that occurred at the same location (Supporting information). Consistent with a pattern of rapid diversification, the rate of diversification decreased markedly over time (Supporting information), while the extinction rate remained near zero (mean extinction rate of ~0.05, Supporting information).

Discussion

Phylogenetic relationships

The AAG is monophyletic and sister to *A. dentatus* from Southeast Asia, in agreement with previous results based on a very restricted selection of AAG taxa (Bourguignon et al. 2017). Our phylogeny indicates a single arrival event of the ancestor to the AAG on the Australian continent through the Southeast Asian Archipelago about 11–10 Mya. This northern route is thought to have facilitated the dispersal of many insect species (Condamine et al. 2013, Matos-Maraví et al. 2018), after the Southeast Asian and Australian Plates collided 25–20 Mya (Hall 2002).

Lineages not included in the current work, *Ahamitermes*, *Incolitermes* and *Invasitermes*, are endemic inquilines in the nests of other termites (six species in total, Gay 1955, Calaby 1956, Abensperg-Traun and Perry 1998) and share derived traits such as the near or complete loss of soldiers (Gay 1968) and highly specialised mandibles (Miller 1984). *Ahamitermes* and *Incolitermes* are exclusively found in *Coptotermes* mounds in the southwest and north-northeast of Australia (Hill 1942, Gay 1956, 1966). Mound-building in their hosts, *C. acinaciformis* and *C. brunneus*, evolved ~2.5 Mya (Lee et al. 2015), suggesting that both genera are young evolutionary lineages. *Invasitermes* are usually found in mounds of *Amitermes laurensis*, but also in other *Amitermes* mounds in northern Australia (Miller 1984, Watson and Abbey 1993). This close relationship suggests that the two species of *Invasitermes* arose after AG2. It is unclear whether these three genera are also nested within AG1 or represent divergent lineages of AG2, however, it is very likely that the missing genera diversified recently in situ on the continent. Thus, we are confident that

Table 1. Summary statistics of three biogeographic models estimated using BioGeoBEARS and the maximum-clade-credibility (MCC) tree. The DIVALIKE model (in bold) was selected for downstream analyses based on Δ AIC scores. d – dispersal parameter; e – extinction parameter.

Model	LnL	Number of parameters	d	e	AIC	Δ AIC
DEC	-143.8	2	0.06	0.04	291.8	1.8
DIVALIKE	-142.9	2	0.07	0.03	290	0
BAYAREALIKE	-157.4	2	0.07	0.13	319.1	29.1

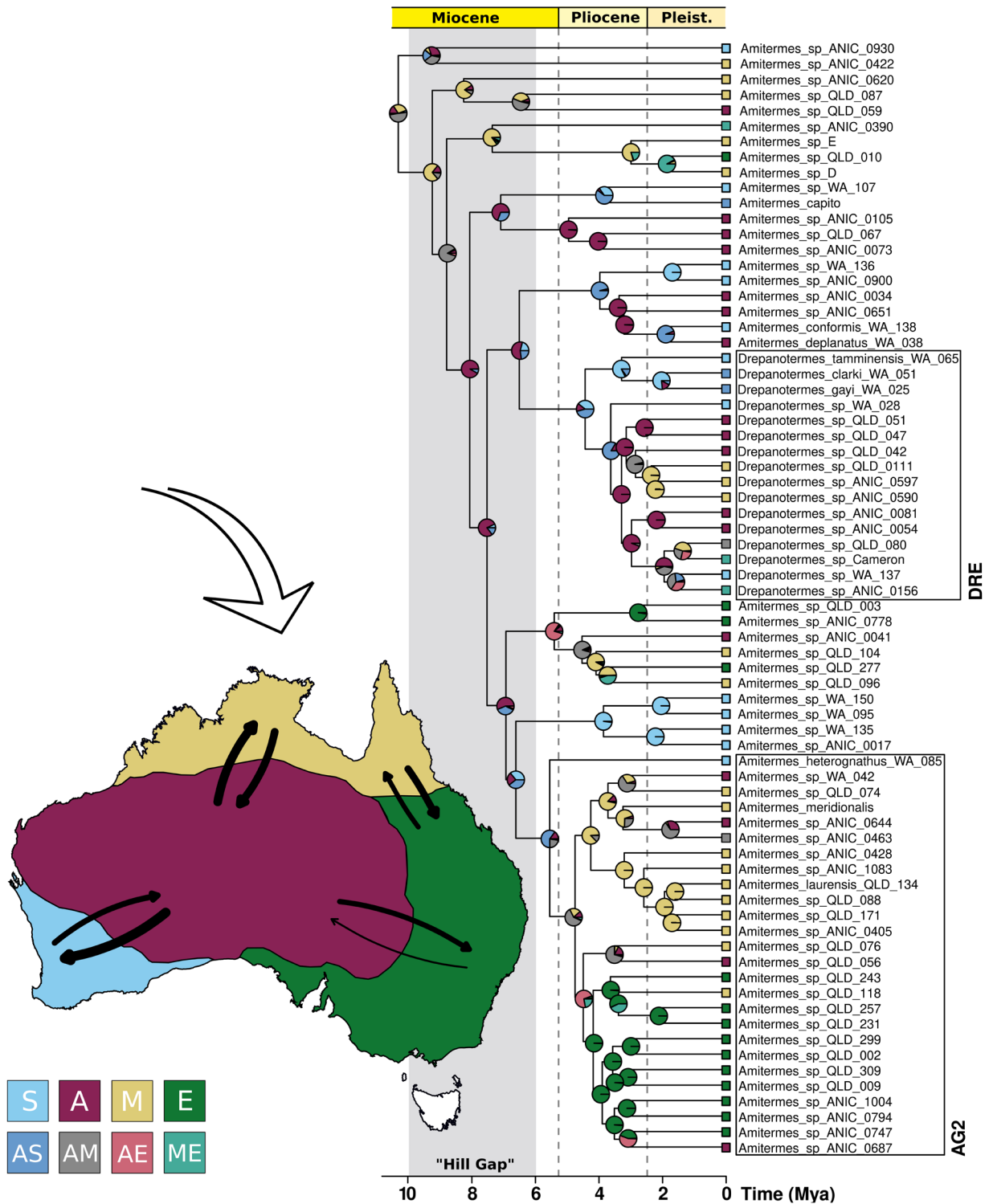


Figure 2. Ancestral range reconstruction of the Australian *Amitermes* group (AAG) based on the DIVALIKE model. Relative probabilities of ancestral areas are shown in pie charts at nodes. Colored squares identify biomes: S, mesic south-western zone, A, arid zone, M, monsoonal tropics, E, mesic eastern zone. Combinations of biomes (e.g. AS, arid zone+mesic south-western zone) are also indicated in colored squares, but not shown on the map. The 'Hill Gap' is shaded in grey. Black arrows indicate direction and frequency of dispersal events between biomes and line thickness indicates the number of event counts summarized with biogeographical stochastic mapping (BSM) (Supporting information). The white arrow indicates the putative arrival direction of the ancestor of the AAG (Discussion).

Table 2. Summary counts of 100 biogeographical stochastic mappings (BSMs) based on the DIVALIKE model using BioGeoBEARS. The estimated number of events for the different types are given in mean numbers with standard deviations (SD) and percentages.

	Dispersal	Within-biome speciation	Vicariance	Total number of events
Mean	37.51	50.15	20.85	108.5
SD	± 1.7	± 1.91	± 1.91	± 1.7
% of total events	34.6	46.2	19.2	100

including these genera would not change our overall findings on the biogeography and diversification of the AAG.

In our PCoA (Fig. 1a), AG2 and *Drepanotermes* were clearly separated from AG1 and recovered in all phylogenetic analyses with high nodal support (Fig. 1b and Supporting information). They are nested among lineages of AG1, rendering *Amitermes*, as currently described, paraphyletic. This confirms the long-standing notion that *Drepanotermes* and the minor inquiline genera are derived from *Amitermes* (Hill 1942, Watson 1982, Miller 1984).

Historical biogeography of the AAG

Our reconstruction of their biogeographical history indicates that the ancestral range of the AAG is a combination of the

monsoonal tropics + (present-day) arid zone (Fig. 2). This does not necessarily conflict with our phylogenetic reconstructions, but simply reflects the likely geographic distribution of the most recent common ancestor of extant AAG species. Irrespective of where the group originated, the available evidence, (including deep nodes in our phylogeny,) indicates that Australia’s monsoon region was the starting point for the radiation of the AAG across the continent. Accordingly, early lineages that speciated in situ may have been preadapted to seasonal climates, as their Southeast Asian ancestor evolved under similar climatic conditions (Bowman et al. 2010), allowing them to quickly expand their distributions in the monsoonal tropics.

Our estimate of ancestral ranges using the best-fitting model DIVALIKE suggests around 37 dispersal events during

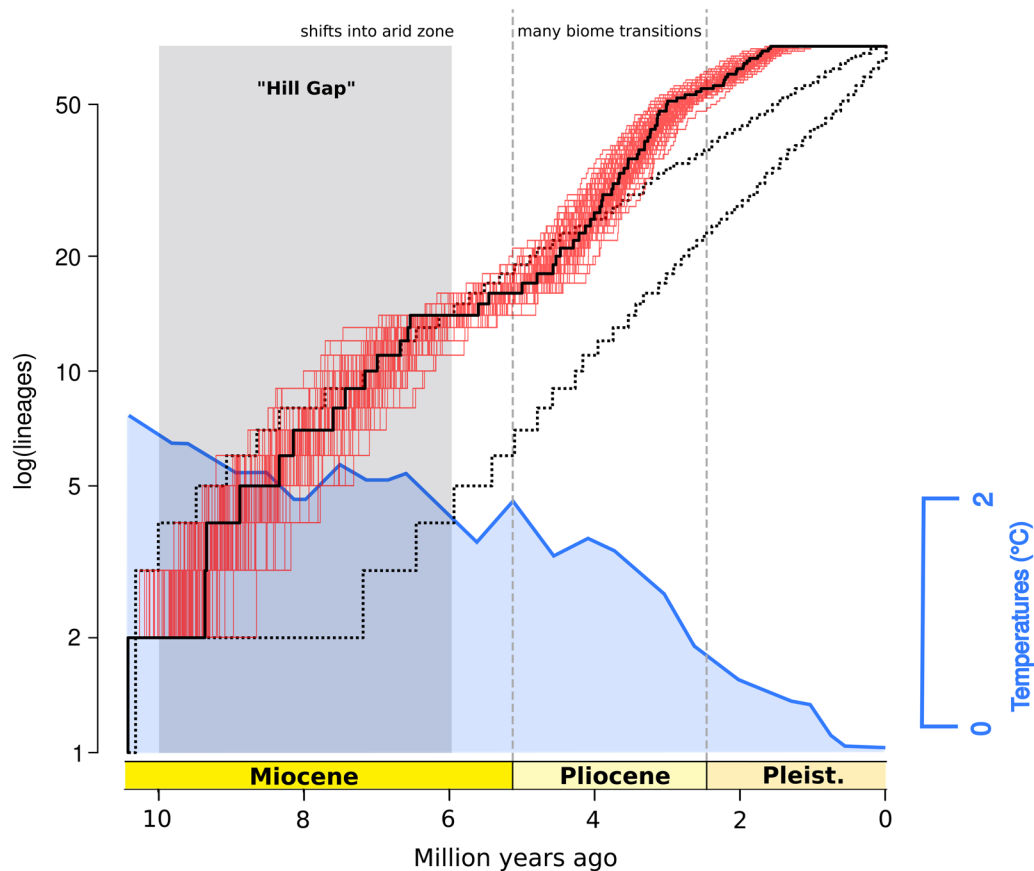


Figure 3. Lineage-through-time (LTT) curves of the maximum-clade-credibility (MCC) tree (black) and variation in relative branching times represented in the posterior sample, as generated from 100 posterior trees (red), show a sudden incline in diversification from ~4 Mya (exceeding the 95% confidence interval generated by simulated LTTs (dashed lines)), preceded by a period of continuously increasing diversification from 8 Mya. Periods of increased diversification correlate with major biome transitions. Deep ocean temperatures through time are given in blue (modified from Zachos et al. 2001) and the ‘Hill Gap’ is shaded in grey.

Table 3. Comparison of alternative evolutionary models fitted to the diversification history of the Australian *Amitermes* group (AAG). Included models are Yule (pure-birth model), CR (constant-rate birth death model), DDL+E (density-dependent linear diversification model) and DDX+E (density-dependent exponential diversification mode). The best-fit of models are based on ΔAICc scores. AICc values for the 100 pruned posterior trees are given in parentheses. λ – speciation rate; μ – extinction rate.

Model	logL	λ	μ	AICc	ΔAICc
72/100					
Yule	-167.0	0.29	0	336.0 (337.2)	27.7 (25.6)
CR	-167.0	0.29	0	338.1 (339.3)	29.8 (27.7)
DDL+E	-151.0	0.74	< 0.01	308.3 (311.6)	0
DDX+E	-179.5	0.57	0.35	365.3 (368.2)	57.0 (56.6)
72/150					
Yule	-162.8	0.36	0	327.6 (328.7)	17.5 (15.4)
CR	-162.8	0.36	0	329.7 (330.9)	19.6 (17.6)
DDL+E	-151.9	0.74	< 0.01	310.1 (313.3)	0
DDX+E	-161.9	1.52	0.12	330.1 (330.5)	20.0 (17.2)
72/250					
Yule	-158.4	0.45	0	318.8 (320)	1.0 (2)
CR	-158.4	0.45	0	320.9 (322.1)	3.1 (2.1)
DDL+E	-155.7	1.01	0.16	317.8 (318)	0
DDX+E	-158.6	1.15	0.04	323.5 (325.9)	5.7 (7.9)

the radiation of the AAG, with 31 events occurring from or to the arid zone. Compared to other continental radiations, this number is not particularly high. For example, Smitsen and Rowe (2018) reported 12 transitions between biomes for 31 extant species of Australian rodents (*Pseudomys* division) in the last 5 Mya. In the highly diverse endemic radiation of Australian pygopodoid geckos, a study of 155 taxa detected over 100 biome shifts over a period of 50–64 million years (Brennan and Oliver 2017). Thus 37 dispersal events might even be considered relatively low, which may be related to termites' generally poor dispersal abilities (Eggleton 2000). It is therefore important to consider our reconstructions of ancestral ranges and inference of biological processes (i.e. within-biome speciation, range expansion and vicariance) in the context of gradual biome turnover during the last 15 million years in Australia. Early in the AAG radiation, environmental and climatic conditions were much different than today. For example, the arid zone as we know it, with iconic sand desert landscapes, is no older than one million years (Fujioka and Chappell 2010) and formed in response to increasing aridification in the Miocene and Pleistocene (Byrne et al. 2008, 2018). Even today's stony deserts did not develop until the end of the Pliocene (~3–2 Mya, Fujioka et al. 2005), while central Australia seems to have been covered by open woodlands and gallery forests at least since the late Miocene (Mao and Retallack 2019, but see also Travouillon et al. 2009). This means that the initial radiation of the AAG during the late Miocene occurred before major biogeographical barriers, e.g. the Great Sandy Desert in Western Australia, developed, although they have apparently driven recent phylogeographic structuring in *Amitermes laurensis* (Ozeki et al. 2007) and we would expect to see similar structuring in other species occurring on either side of the Carpentarian Gap in northern Australia (e.g. *Amitermes subtilis*, *A. vitiosus*, *Drepanotermes rubriceps*, *D. diversicolor*). Such a relatively benign habitat likely fostered successful expansion into or through the evolving arid zone. Open sclerophyllous forests, including *Acacia* and *Eucalyptus*, have been widespread since the Paleogene

(summarized in Crisp and Cook 2013); these plants are primary food sources of AAG taxa in semi-arid and arid regions of Australia (Andersen and Jacklyn 1993, Abensperg-Traun et al. 1995) and their widespread distribution certainly also contributed to successful range expansion of these termites.

As expected, within-biome speciation is the most frequent type of event recovered in the BSM analysis. This reflects the large size of the regions and the associated predominance of lineages endemic to individual biomes. Such geographic restriction is in contrast to species occurrence records for some AAG taxa in our study, however high inter- and intraspecific variability made taxonomic reconciliation with historical morphology-based records impracticable. Nonetheless, shallow Plio-Pleistocene divergences in our phylogeny, particularly seen in AG2, tend to occur in close geographic proximity, likely reflecting phylogeographic structuring of species in response to habitat heterogeneity caused by intensifying aridification (Fujioka and Chappell 2010).

The present-day distributions of many plant and animal species on the continent have been related to the formation of biogeographic barriers (Crisp and Cook 2007, Owen et al. 2017, Harms et al. 2019), which formed in response to increasing aridity over the last 20 million years, particularly in central Australia (Cracraft 1982), and to dramatic sea level fluctuations during Pleistocene interglacial periods (Zachos et al. 2001). The lowest number of events in our study was inferred for vicariance, occurring about half as often as dispersal events. We observed a strong correspondence between the frequency of vicariance events in the Plio-Pleistocene and the diversification of arid lineages from mesic and tropical ancestors, suggesting that the formation of potential vicariance barriers resulted in repeated allopatric speciation (Cracraft 1982). This is consistent with complex diversification dynamics shown in other organisms (summarized in Byrne et al. 2018). However, we also observed diversification in the opposite direction, in which mesic and tropical species diverged from arid ancestors, for example in *Drepanotermes*. Such a pattern has been recently shown in rodents (Smitsen and Rowe 2018), geckoes (Brennan

and Oliver 2017) and spinifex grasses (Toon et al. 2015). Spinifex grasses of the family Triodiinae are commonly harvested by *Drepanotermes* spp. (Watson and Perry 1981), which might indicate that the latter co-diversified with the former.

Rapid diversification during late Cenozoic climate change

Multiple lines of evidence suggest that the AAG diversified rapidly in times of major environmental and climatic change in the late Cenozoic. Our multi-LTT plot and MCCR tests suggest that species accumulation over time deviated from a pure-birth model of constant diversification (Fig. 3). This is supported by the DDL+E model, the best-fitting estimate of evolutionary diversification within the AAG, which suggests that the rate of diversification decreases over time due to species accumulation and niche saturation. The diversification curve showed a rather continuous trend of increasing diversification during the ‘Hill Gap’ and latest Miocene followed by an abrupt rise in the Pliocene that slows down to the present day (Fig. 3). This curve shape is not consistent with an early burst model of evolution (Yoder et al. 2010), in which the available niche space is filled rapidly in the early history of a newly arriving group. Although the large-scale expansion of open woodland, xerophytic shrubland and C₃ grasslands at the expense of rainforest ecosystems on a continental scale during the ‘Hill Gap’ (Hill 1994, Martin 2006, Cassis et al. 2017) may have promoted diversification in early lineages of the AAG, the increase was rather steady and speciation mainly occurred in ranges similar to their natives ones in Southeast Asia, indicating niche conservatism in early lineages. For the AAG as a whole, early invasion of the arid zone resulted not in rapid diversification, as was found for pygopodoid geckos (Brennan and Oliver 2017), agamid lizards (Rabosky et al. 2007) and grasses (Crisp et al. 2004), but a slower expansion, has been shown for cicadas (Owen et al. 2017).

During the Pliocene, the diversification rate accelerated and frequent biome transitions can be observed (Fig. 3). This burst of speciation, notably in AG2 and *Drepanotermes*, correlates with major ecological change on the continent caused by regional tectonic forcings (Byrne et al. 2008). Australia’s drift to the north and the progressive constriction of the Indonesian Throughflow changed Pacific and Indian Ocean circulations (Christensen et al. 2017), leading to the expansion of C₄ grasslands in response to the establishment of the modern-like Australian monsoon regime ~3.5 Mya (Andrae et al. 2018). At the Pliocene–Pleistocene boundary, climatic conditions changed abruptly from humid to arid, and the arid zone expanded in the following million years (Pepper and Keogh 2021). Thus climatic instability and the emergence of novel habitats arising from the intensifying aridification of the Australian continent may have provided opportunities for the AAG to diversify rapidly during the Plio–Pleistocene, similar to gall thrips (McLeish et al. 2007).

Biome transitions were much more common in the Pliocene than in the late Miocene or Pleistocene suggesting that species diversification was driven by ecological divergence. In

particular, the crown groups AG2 and *Drepanotermes*, which include the majority of mound-building AAG, diversified rapidly during this time. Mound-building species (e.g. *A. meridionalis*, *A. laurensis*) have become ecologically dominant in mesic and tropical regions (Andersen and Jacklyn 1993, Abensperg-Traun and Perry 1998), suggesting an important role in the rapid diversification of AG2 and *Drepanotermes*. However, BAMM inferences found no rate shift(s) associated with the acquisition of this trait; indeed, in nearly all cases no rate shifts were detected by BAMM (Supporting information).

Another reason for ecological divergence might be the increasing predation pressure by many different animals, including mammals, ants and lizards (Holt 1990, Abensperg-Traun and de Boer 1992, dos Reis et al. 2012), particularly within the arid zone. Most termite-eating animals are found in the semi-arid and arid regions of Australia, where termites make up the greatest proportions of their diets (Abensperg-Traun 1994, Palmer 2010). Termite-eating lizards, in particular, are abundant in the arid zone (Morton and James 1988), and there seems to be a positive link between lizard and termite richness in central Australia (Pianka 1981, Colli et al. 2006). While *Amitermes* soldiers have been described as generally ‘the embodiment of cowardice and uselessness’ (Hill 1922), *Drepanotermes* soldiers are moderately large, produce copious amounts of defensive secretions, and have long sickle-shaped mandibles. They are numerous and can be highly effective against predatory ants (e.g. *Iridomyrmex*: Greenslade 1970, for discussion of temporary nest occupation see Holt 1990), as well as other insects and spiders (Hill 1922), and vertebrates (echidnas: Abensperg-Traun and de Boer 1992, lizards: Hill 1922). Nonetheless, predator–prey relationships are poorly understood (Noirot and Darlington 2000) and it appears to be unlikely that predation alone can explain the macroevolutionary dynamics within the AAG.

A sudden decrease in the diversification rate, such as that shown in our multi-LTT plot, has been attributed to mass extinction events (Crisp and Cook 2009). However, the AAG seems to have diversified in the near absence of extinction; compared to other dictyoptera, extinction rates in termites are generally exceptionally low (Legendre and Condamine 2018). Nonetheless, there are long naked branches in our phylogeny suggestive of extinction events, and the current distribution of sister species in opposite corners of Australia suggests the occurrence of repeated range expansions and contractions coupled with extinction in the past (Fig. 2), a pattern also observed in *Banksia* (Cardillo and Pratt 2013) and *Pseudotyrannochthonius* pseudoscorpions (Harms et al. 2019). In the absence of a fossil record, extinction events are difficult to identify (Rabosky 2010, Louca and Pennell 2021), and to our knowledge no mass extinction in Australian insects is known from the Plio–Pleistocene.

Patterns of decreasing diversification are sometimes attributable to incomplete taxon sampling (Cusimano and Renner 2010). In the present study, our conservative approach to young lineages may actually underestimate the number of species emerging in the past 1.5 million years, exaggerating the Pleistocene plateau in the multi-LTT plot (Fig. 3). In addition, we would expect this apparent rate change to be less abrupt

with greater representation from the central deserts and NW Western Australia. Further, *Amitermes* includes many soil-dwelling (and possibly soil-feeding) species, which are more often under-sampled in phylogenetic studies (Chouvenec et al. 2021). Despite these limitations, the large number of recent (< 2 Mya) splits reflect ongoing diversification. This can also be observed in the closely related species and species complexes of the AAG (e.g. *Drepanotermes perniger*, Watson and Perry 1981), often in sympatric associations, and the high degree of endemism (Gay 1968, Watson and Perry 1981, Watson and Perry 1991, Abensperg-Traun and Perry 1998).

Correlations between increasing rates of diversification and past climate events in the ‘Hill Gap’ and the Plio-Pleistocene have been documented before. For example, Braby and Pierce (2007) showed that butterflies of the genus *Delias* diversified rapidly coincident with major ecological change in the ‘Hill Gap’ and Plio-Pleistocene, and suggested that ecological opportunity may have driven rapid speciation in this species-rich genus of butterflies. In allodapine bees, the rate of diversification accelerated during the ‘Hill Gap’, however only in temperate-adapted lineages (Chenoweth and Schwarz 2011), while xeric-adapted lineages radiated constantly over time. Chenoweth and Schwarz (2011) related this to allopatric speciation promoted by habitat fragmentation in mesic regions. During the Plio-Pleistocene, gall thrips (McLeish et al. 2007) experienced increasing rates of diversification coincident with the intensifying aridity in Australia.

To our knowledge, this is the first study addressing diversification rates in Australian termites. Interestingly, a worldwide survey of all termite families recovered increased speciation rates in fungus-growing Macrotermitinae over the last 10 Mya, which the authors attributed to the expansion of C₄ grasslands in Africa (Pie et al. 2021). Similar expansions of C₄ grasslands occurred several million years later in Australia (Andrae et al. 2018), and may be an interesting factor for a more detailed exploration of AG2 or *Drepanotermes* evolution. We expect future studies on termites will show correlations of changes in diversification rates with past periods of climate and ecological change.

Our results indicate that the AAG has an immense potential to adapt to changing climatic conditions. Because the activity of termites is thought to increase the resistance of semi-/arid environments to prospective future climate change (Bonachela et al. 2015), the AAG could play an important role in maintaining Australian ecosystems in the face of human-mediated climate change. Current climate models predict a change over the next 50 years in Australia nearly as great as that of the last 10 million years (Hughes 2003); it remains to be seen whether the AAG can adapt even more quickly than it has in the past to keep up with the current pace of global climate change.

Conclusion

This study illuminates the evolutionary history of the most speciose termite group in Australia and is one of the few biogeographical studies with a continent-wide focus. Consistent

with dispersal patterns in other insects (Yeates and Cassis 2017), the group’s ancestor arrived in Australia via a northern route from Southeast Asia. Despite being poor dispersers, early lineages were apparently able to expand their range quickly under favorable conditions in the late Miocene. The progressive aridification of the Australian continent and expansion of the arid zone, especially in the last 4 million years, has shaped the evolutionary trajectory of many, if not all, of the AAG lineages and continues to shape them. Multiple lines of evidence suggest that the AAG diversified rapidly in the context of late Cenozoic climate change. Many studies show that the intensifying aridification of the Australian continent triggered rapid diversification (summarized in Byrne et al. 2018), and this is the first study to do so for Australian termites. Congruent with diversity-dependent patterns, species accumulation declined likely due to progressive niche saturation. However, other factors such as key innovations or predation certainly play(ed) an important role in the rapid diversification of the AAG, however it remains to be seen to what extent.

Additional taxon sampling in underrepresented semi-/arid regions is necessary to answer open questions related to migration patterns during initial expansion across Australia and later diversification within the arid zone. This and other studies of the Australian fauna demonstrate the resilience of termites against naturally occurring environmental change. In this case, the aridification of the Australian continent was not an evolutionary dead end for the AAG but rather the impetus for adaptation and diversification.

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Bastian Heimburger: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Leonie Schardt:** Data curation (supporting); Formal analysis (supporting); Resources (supporting). **Alexander Brandt:** Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting). **Stefan Scheu:** Conceptualization (supporting); Methodology (supporting); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Tamara R. Hartke:** Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Project administration (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.sn02v6x6m>> (Heimbürger et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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