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The Evolution of the Australian *Amitermes* group

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Bastian Heimburger

from Magdeburg

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Thesis Committee

Prof. Dr. Stefan Scheu, Animal Ecology, JF Blumenbach Institute

Prof. Dr. Christian Roos, Primate Genetics Laboratory at the German Primate Center

Dr. Tamara R. Hartke, Animal Ecology, JF Blumenbach Institute

Members of the Examination Board

First Reviewer: **Prof. Dr. Stefan Scheu**, Animal Ecology, JF Blumenbach Institute

Second Reviewer: **Prof. Dr. Christian Roos**, Primate Genetics Laboratory at the German Primate Center

Further Members of the Examination Board

Prof. Dr. Mark Maraun, Animal Ecology, JF Blumenbach Institute

PD. Dr. Sven Bradler, Animal Evolution and Biodiversity, JF Blumenbach Institute

Prof. Dr. Christoph Bleidorn, Animal Evolution and Biodiversity, JF Blumenbach Institute

Dr. Nico Posnien, Developmental Biology, JF Blumenbach Institute

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"Nothing in Biology Makes Sense Except in the Light of Evolution"

Theodosius Dobzhansky, 1973

Contents

Summary

Although the Australian *Amitermes* Group (AAG) is the most diverse and speciose group of higher termites (Termitidae) in Australia, relatively little is known about the origin and evolution of the group. Recent phylogenetic studies of the major termite groups suggest that the AAG and other derived subfamilies arrived in Australia from Southeast Asia in the mid-to-late Miocene (Bourguignon *et al.* 2017), after the Australian and Southeast Asian plates collided (Zachos *et al.* 2001). Today, the group is distributed across the continent (Watson and Abbey 1993) and has an unparalleled rate of endemism (Calaby and Gay 1959): only two Australian taxa (*A. arboreus* and *A. laurensis*) are known to also occur in Papua New Guinea (Miller 1994, see also Krishna *et al.* 2013). Currently, the group is split into five genera broadly based on nesting/feeding habits: subterranean or protected foraging (*Amitermes*), foraging in the open (*Drepanotermes*), or living exclusively within the nests of other termite species (*Ahamitermes*, *Incolitermes*, and *Invasitermes*) (Krishna *et al.* 2013).

In this thesis, I reconstructed a robust "backbone" phylogeny to recapitulate the diversification and biogeographical history of the AAG, which coincides with the aridification of the continent over the last 15 million years (Byrne *et al.* 2008, 2018). The results are consistent with migratory patterns in other insects that followed a northern route from Southeast Asia (Yeates and Cassis 2017), suggesting that the ancestor of the AAG likely arrived in Australia by rafting in logs. The favorable conditions in the late Miocene, with extensive woodlands and open forests, presumably facilitated the rapid range expansion of early lineages across Australia. The evolutionary trajectory of the AAG shows a diversity-dependent pattern in which a steady increase in the diversification rate from the late Miocene onwards is followed by a period of accelerated diversification in the Pliocene. At the boundary of the Plio-Pleistocene, the diversification rate decelerated. Diversification analyses showed that declining species accumulation is likely due to progressive niche saturation.

Finally, by combining both barcoding sequences and whole mitochondrial genomes, I reconstructed the ancestral nesting habit of *Drepanotermes*, related nesting habits to past climatic conditions, and predicted current and future habitat suitability of selected taxa. It is the first time that

both abiotic and biotic factors were used to predict habitat suitability in Australian termites. Results show that mound-building evolved multiple times within *Drepanotermes* and likely facilitated its spread into regions characterized by high temperature and precipitation. Indeed, mound-builders are more common in hot and wet regions of Australia, in contrast to subterranean species, which are generally found in more arid conditions. Generally, mound-building appears to be an adaptation to extreme weather events (*e.g.* floods and bushfires). Evidence of strong phylogenetic signal of bioclimatic variables linked to seasonality (*e.g.* precipitation of warmest quarter) supports my hypothesis that mounds are selectively favored over subterranean nests in habitats experiencing occasional, unpredictable extreme events.

Zusammenfassung

Obwohl die australische *Amitermes*-Gruppe (AAG) die diverseste und artenreichste Gruppe der höheren Termiten (Termitidae) in Australien ist, ist relativ wenig über ihren Ursprung und ihre Evolution bekannt. Neuere phylogenetische Studien der wichtigsten Termitengruppen legen nahe, dass die AAG und andere abgeleitete Unterfamilien im mittleren bis späten Miozän aus Südostasien nach Australien gelangten (Bourguignon *et al.* 2017), nachdem die australische Platte mit der südostasiatischen Platte kollidierte (Zachos *et al.* 2001). Heute ist die Gruppe auf dem Kontinent allgegenwärtig (Watson and Abbey 1993), und der Grad an Endemismus beispiellos auf dem Kontinent (Calaby and Gay 1959): Es sind nur zwei australische Taxa (*A. arboreus* und *A. laurensis*) in Papua-Neuguinea bekannt (Miller 1994, siehe auch Krishna *et al.* 2013). Derzeit wird die Gruppe in fünf Gattungen eingeteilt, die grob auf ihren Nistformen/Ernährungsweisen basieren: unterirdische oder geschützte Nahrungssuche (*Amitermes*), Nahrungssuche im Freien (*Drepanotermes*) oder ausschließliches Leben in den Nestern anderer Termitenarten (*Ahamitermes*, *Incolitermes* und *Invasitermes*) (Krishna *et al.* 2013).

In dieser Dissertation erstellte ich eine robuste „Rückgrat"-Phylogenie, um die Diversifizierung und biografische Geschichte der AAG zu rekonstruieren, die mit der Trockenheit des Kontinents während der letzten 15 Millionen Jahre zusammenfällt (Byrne *et al.* 2008, 2018). Die Ergebnisse stimmen mit Wanderungsbewegungen anderer Insekten überein, die aus Südostasien über eine nördliche Route nach Australien gelangten (Yeates and Cassis 2017). Dies deutet daraufhin, dass der Vorfahre der AAG wahrscheinlich durch Rafting in Baumstämmen nach Australien gelangte. Die günstigen Bedingungen im späten Miozän, mit ausgedehnten und offenen Wäldern, erleichterten vermutlich die schnelle Verbreitung der frühen Abstammungslinien in ganz Australien. Der evolutionäre Verlauf der AAG zeigt ein diversitätsabhängiges Muster, bei dem einem stetigen Anstieg der Diversifizierungsrate ab dem späten Miozän eine Phase beschleunigter Diversifizierung im Pliozän folgte. An der Grenze des Plio-Pleistozäns verlangsamte sich der Verlauf der Diverfizierung. Analysen zeigten, dass die abnehmende Artenakkumulation wahrscheinlich auf eine fortschreitende Nischensättigung zurückzuführen ist.

Darüber hinaus rekonstruierte ich mittels Barcoding-Sequenzen und mitochondrialen Genomen die ursprünglichen Nistgewohnheiten von *Drepanotermes*, sowie in Bezug auf vergangene klimatische Bedingungen. Ich untersuchte außerdem die aktuelle und zukünftige Habitateignung für ausgewählte Taxa. Dies ist die erste Studie ihrer Art in der für australische Termiten sowohl abiotische als auch biotische Faktoren verwendet wurden, um die Eignung eines Habitats vorherzusagen. Meine Ergebnisse weisen daraufhin, dass der Bau von Hügeln innerhalb von *Drepanotermes* mehrmals evolviert ist, was wahrscheinlich die Ausbreitung in Regionen erleichtert hat, die durch hohe Niederschläge und Temperaturen gekennzeichnet sind. Tatsächlich sind Hügel-bauende Arten häufiger in heißen und feuchten Regionen Australiens anzutreffen, im Gegensatz zu unterirdischen Arten, die zumeist trockene Bedingungen bevorzugen. Das Bauen von Hügeln scheint ebenso eine Anpassung an extreme Wetterereignisse (z.B. Überschwemmungen und Buschbrände) zu sein: Hinweise auf ein starkes phylogenetisches Signal im Zusammenhang mit saisonalen bioklimatischen Faktoren (z.B. Niederschlag in den drei wärmsten Monaten des Jahres) unterstützen meine Annahme, dass Hügel in bestimmten Extremereignissen selektive Vorteile gegenüber unterirdischen Nestern besitzen.

Contributions to the chapters of this thesis

Chapter 1

Rapid Diversification of the Australian *Amitermes* group during late Cenozoic Climate Change

Conception and design of the study, data analysis, data interpretation, writing and figures

Chapter 2

Historical and future climate change fosters expansion of Australian harvester termites, *Drepanotermes*

Conception and design of the study, data analysis, data interpretation, writing and figures

I General Introduction

Termites: Eusocial ecological engineers

Termites (Blattodea: Isoptera) are eusocial insects which diverged from cockroach-like ancestors around 150 million years ago (Mya) (Lo *et al.* 2000, Inward *et al.* 2007, Bourguignon *et al.* 2018). They are characterized by an obligate gut symbiosis (Bignell *et al.* 2011) and eusociality, which includes the reproductive division of labor with overlapping generations and cooperative brood care (Batra 1966) by sterile neuter soldier and worker castes (Batra 1966, Noirot 1985, Roisin and Korb 2011). Co-evolution with symbionts allowed termites to degrade lignocellulose from wood with unparalleled efficiency (Hooper *et al.* 2000, Ohkuma and Brune 2011, Dietrich *et al.* 2014), and subsequent dietary diversification (Klass *et al.* 2008, Brune and Dietrich 2015), together with the development of large and complex eusocial systems, propelled termites to ecological dominance in tropical and subtropical regions. As ecosystem engineers, termites modify topography, chemical properties, and the growth rate of plants in their environment (Lobry de Bruyn and Cononacher 1990, 1995, Jouquet *et al.* 2016, Walsh *et al.* 2016). In some habitats, termites may serve as keystone species providing nutrition and shelter for other arthropods, small vertebrates, and plants (Bignell and Eggleton 2000). Today, there are over 3000 described termite species around the world (Krishna *et al.* 2013), of which 300 are native to Australia.

The "dead heart" of Australia: The arid zone

Australia changed dramatically in the last 35 million years, after the continent separated from Antarctica (Crisp *et al.* 2004, Rhodes *et al.* 2005, Hall 2011). The Australian plate drifted over 3,000 km northeast (Sandiford 2007, Quigley *et al.* 2010) and made contact with the Southeast Asian Plate about 25 to 20 Mya (Hall and Sevastjanova 2012). Gradual biome turnover began in the early and mid Miocene (~23-11 Mya), as subtropical and mesic regions shrank while the arid zone developed (Byrne *et al.* 2008, 2011). With the end of the Miocene (~10-6 Mya), generally wet and warm climatic conditions finally ended for most of the continent (Hill 1994).
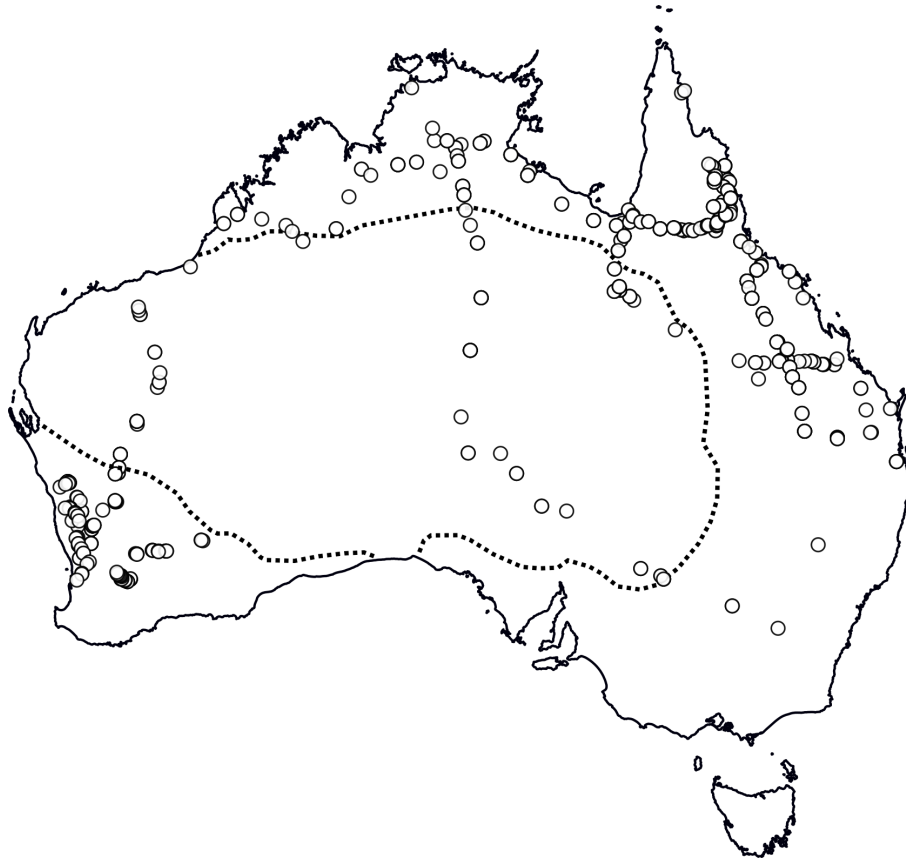
Figure 1   Sampling locations of AAG colonies (arid zone indicated by dashed line).

Increasing aridification led to a widespread contraction of rainforest elements to small remnants on Australia's north and east coasts (Martin 2006, Byrne *et al.* 2011). This massive loss of stabilizing vegetation cover caused unprecedented erosion and opened niches which were eventually filled by sclerophyllous and xeric vegetation (Martin 2006, Byrne *et al.* 2008). After a short period of recurring warm and wet conditions at the Miocene-Pliocene boundary (~6 Mya), fully arid landscapes, including sand and stony deserts with annual precipitation levels well below 250 mm, emerged in the Plio-Pleistocene (~4-1 Mya, Fujioka *et al.* 2005; Fig. 1). As such, Australia's arid biome is relatively young compared to other biomes on the continent (Fujioka *et al.* 2005).

The arid zone, once considered the "dead heart" of Australia (Gregory 1906), is anything but dead: it is home to an astonishing variety of arid-adapted animals and plants (reviewed in Crisp *et al.* 2004, Byrne *et al.* 2008, 2018). A rich literature shows that this tremendous diversity can be traced to the persistence of ancient lineages stemming from the breakup of Gondwana (Barrett and Williams

1998, Barden and Ware 2017), but also to more recent explosive radiations in concert with Australia's desertification (Rabosky *et al.* 2007, Guzik *et al.* 2011).

In addition to the practical ecological value an increased understanding of the arid biome would bring, it is also an ideal system to study speciation and species radiation. The harsh environmental conditions that developed over a relatively short period of time provided unavoidable selection pressure on organisms and communities. The success of arid-adapted species within the AAG can help us to understand how termites have adapted to semi-arid and arid environments worldwide and may continue to do so under future climate-change scenarios.

Nesting habits of termites

Termites can be classified broadly into two life types, which are related to nesting and feeding habits (Abe 1987). First, the one-piece nesting termites including Kalotermitidae, Termopsidae and a small number of Rhinotermitidae (Korb 2007). These wood-dwelling species live exclusively inside a single piece of wood, only leaving the nest for mating and subsequent colony foundation (Abe 1987). In these species, food source and shelter are one and the same, circumventing the need for foraging but inevitably limiting the size and longevity of a colony.

The second life type includes separate-piece nesting termites, in which the nest exists separately from the food source (Korb 2007). Colony size and maximum colony age are not as limited by food availability as in wood-dwelling termites, because they may forage on a variety of food sources. For this reason, they are also called foraging termites. The evolution of separate-piece nesting is thought to have contributed significantly to the radiation of termites, particularly of the most specialized termite group Termitidae (Inward *et al.* 2007). Foraging termites can live in a diverse range of nest structures, for example in underground galleries, arboreal nests, or mounds (Fig. 2).

Phylogenetic studies show that mound-building has evolved multiple times in parallel worldwide, including in Australia (Lo *et al.* 2004, Inward *et al.* 2007). However, in spite of an increasing number of studies (Lee *et al.* 2015, Arab *et al.* 2017, Beasley-Hall *et al.* 2018, Wijas *et al.* 2022), the evolutionary transition from non-mound-building (*e.g.* arboreal/subterranean nesting) to

mound-building is not well understood. Davies *et al.* (2014) reported that topology, geology, and climatic variables can influence the distribution of mound-building taxa and the density of mounds, yet it is not known whether these abiotic factors played a role in the acquisition of mound-building, representing a classic chicken-and-egg conundrum. Regardless of the factors involved, the adaptive benefits are evident, including food storage, defense from predators, and environmental homeostasis (Noirot and Darlington 2000, Korb 2003, 2011).

A deeper understanding of this variation in nesting habits from both an ecological and evolutionary perspective will help us understand whether mound-building AAG taxa can cope with the dramatic changes our planet is facing in the light of human-mediated climate change and answer open questions related to the acquisition of mound-building.
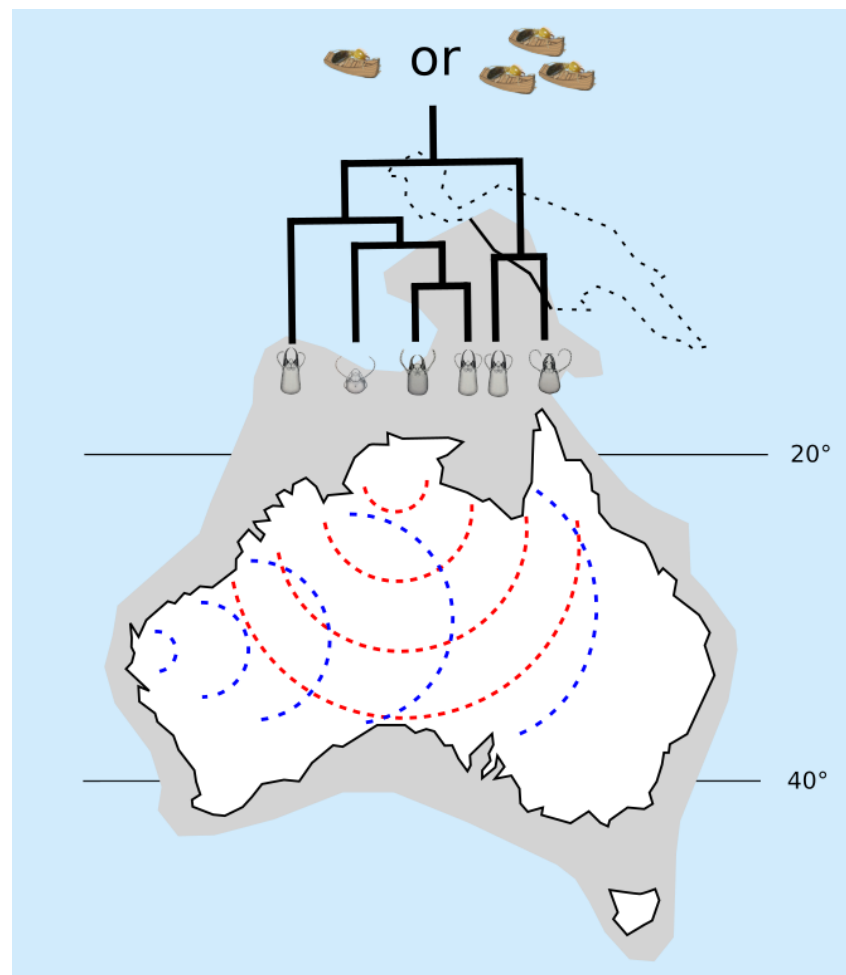
The Australian Amitermes *group*

The phylogenetic relationships of the AAG have never been satisfactorily addressed, as the only higher-level phylogenies containing AAG taxa place them as sister group to an unresolved polytomy of Asian and African *Amitermes* (three molecular markers, Inward *et al.* 2007) or to the Asian *Amitermes* (mitochondrial genomes, Bourguignon *et al.* 2017). The larger number of species and genes included in the latter study, combined with biogeographic patterns of other "young" Australian taxa (Cassis *et al.* 2017), suggest that the ancestors of the AAG most likely originated from Southeast Asia and may have arrived on the Australian continent *via* floating logs in the Miocene (Bourguignon *et al.* 2017) (Fig. 2). It is not yet known whether the AAG resulted from a single arrival (*e.g.* Australian *Coptotermes* (Lee *et al.* 2015)) or multiple arrivals (*e.g.* Australian Nasutitermitinae (Arab *et al.* 2017)). This thesis will provide a definitive conclusion for these open questions regarding the origin of the AAG.

The hypothesized arrival period in Australia is characterized by shrinking mesic habitats and expansion of the arid biome and its xeric vegetation (Byrne *et al.* 2008, 2011), which shifted ecological niches toward drier conditions subsequently occupied by new groups of organisms (Crisp and Cook 2013). Thus, Australia's extraordinary biodiversity has not only been shaped by relictualism (*e.g.* the damselfly *Hemiphlebia* (Trueman 1996), the dragonfly Petaluridae (Barrett and Williams

1998), and the lower termite *Mastotermes* (Barden and Ware 2017)), but also by vicariance, *in situ* speciation, and subdivision of recent populations (reviewed in Rix *et al.* 2015). Today, the AAG plays a dominant role in ecosystems from tropical to temperate latitudes with the highest number of species in southwestern Western Australia (Abensperg-Traun and Steven 1997), a region known as a global hotspot of relictualism (Yeates *et al.* 2002, Cassis *et al.* 2017). The proposed Western Australian origin of the Australian harvester termites *Drepanotermes,* based on the gradient of species numbers from the Northwest Cape eastward (Watson and Perry 1981), also supports the idea of continental colonization by early AAG ancestors followed by recolonization of aridified areas by derived species (Fig. 2).

Figure 2 Map of Australia and the continental shelf (highlighted in gray) during the presumed arrival of the AAG in the late Miocene (~10 Mya); the developing New Guinea land mass is indicated by the black dashed line (modified from Norman *et al.* 2018). Boats depict the hypothesized introduction event (or events) of AAG ancestors from Southeast Asia to Australia *via* transoceanic dispersal. Relationships among affiliated genera are depicted by a hypothetical phylogenetic tree with typical head morphology (modified from Hill 1942) of soldiers of AAG genera

(except soldierless *Invasitermes*, head of winged adult instead, second from left) shown at tips. The potential direction of the initial continental colonization by AAG ancestors is highlighted by red dashed lines. Re-colonisation of aridified areas by derived lineages, exemplified by the radiation of *Drepanotermes* (Watson and Perry 1981), is depicted with blue dashed lines.

Foundational work on the AAG (Hill 1942, Gay 1968, Watson and Perry 1981) was unable to resolve the relationships between the genera and species based on their morphology. The morphological distinctions characterizing the derived groups *Drepanotermes, Ahamitermes*, *Incolitermes*, and *Invasitermes* correspond to ecological traits such as nesting and feeding habits, in contrast to the variability within the Australian *Amitermes*. This may be due to parallel evolution during recolonization, which is difficult to disentangle without molecular tools (see Lo *et al.* (2016) on Australian roaches). Single or multiple molecular marker studies of families, genera, or species groups (*e.g.* Inward *et al.* 2007, Legendre *et al.* 2008, Dedeine *et al.* 2016) and mitogenomes for higher level phylogenies (Cameron *et al.* 2012, Bourguignon *et al.* 2015, 2017), have proven the viability of these techniques in termites generally while all but ignoring the AAG.

In this thesis, I use robust phylogenetic trees to elucidate how AAG taxa have shaped and been shaped by the development of the Australian arid zone in the context of past global climate change. Their continent-wide distribution, spanning temperate to (sub)tropical and arid conditions, makes them an ideal system to study the influence of Australia's aridification on biogeographical patterns.

The Australian harvester termites, Drepanotermes

The genus *Drepanotermes* Silvestri is endemic to Australia and can be found across the continent (Watson and Perry 1981, Watson 1982). The greatest number of species occurs in the northwestern corner of Australia near the North-West Cape, the proposed origin of the genus (Watson and Perry 1981). To date, 23 species have been described, some of which exhibit very extensive ranges in semi-arid and arid regions of Australia (see ala.org.au for occurrence records).

Drepanotermes, also called Australian harvester termites, have evolved unusual traits for termites such as grazing in the open by day and night (Watson and Perry 1981). Foraging parties, groups of mostly older workers that cut and transport food material, are protected from a wide range of predators (Holt 1990, Abensperg-Traun and De Boer 1992, dos Reis *et al.* 2012) by large, heavily sclerotized soldiers. The gathered food material is stored in dedicated chambers in their nests, which can be broadly classified into two types: (1) subterranean, with exclusively belowground galleries, or (2) mounds, ranging from more or less flat pavement nests to mounds nearly two meters in height (Fig. 3; Watson and Perry 1981).
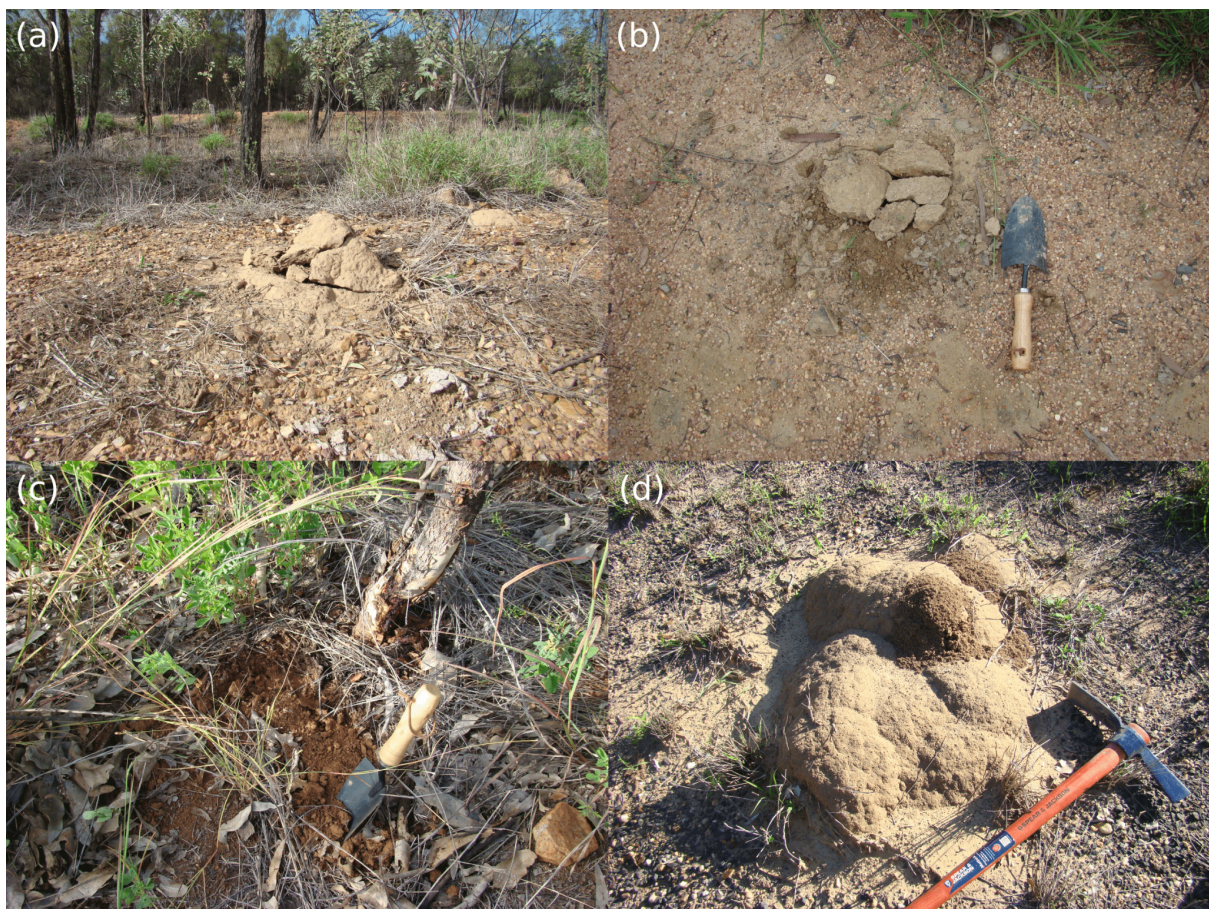

Figure 3 Variation of nesting habits including: (a) mound of *Drepanotermes perniger* (~30 cm high), (b) pavement nest of *Drepanotermes rubriceps*, (c) undefined subterranean nest of *Drepanotermes* sp., and (d) mound complex of *Drepanotermes perniger*. In (d), dark brown portions of the mound have been newly constructed.

Most *Drepanotermes* species live in subterranean gallery systems (Watson and Perry 1981) which are often hard to detect, presenting only small chimney-like tubes used for nest ventilation or release of winged dispersers and foraging holes above ground. On the other hand, in the hummock grasslands spanning from Western Australia to the Northern Territory, bare circular areas known as "fairy circles", are very common and a defining feature of the landscape. Despite competing hypotheses about their origin (Walsh *et al.* 2016, Getzin *et al.* 2016), they are clearly related to pavement nests of *Drepanotermes* spp (Fig. 3). Interestingly, Aboriginal people recognized long ago that such bare patches are made by termites and generations of indigenous Australians have used them as resting areas and walking paths (Walsh *et al.* 2016).

Reported densities of hundreds of active mounds per hectare are not uncommon (Watson *et al.* 1973, Holt and Easey 1993, Abensperg-Traun and Perry 1998), and may be inhabited by tens of thousands of individuals each. Mounds are often found in aggregations, and may or may not be connected by tunnels. In most cases, it is impossible to tell whether clustered nests (mounds) are unrelated, form a single colony (polycalism, see Holt and Easey 1985) or represent daughter nests which have become independent from the parent colony (colony budding, see Vargo and Husseneder 2011). Mounds are also frequently taken over or co-inhabited by non-mound-building termites (Watson and Perry 1981), so it is sometimes difficult to determine the original nest-builder.

Mound-building species can also be divided into obligate and facultative species, with the former always building mounds and the latter living either in mounds or subterranean nests (Watson and Perry 1981). Regardless of the nesting strategy, all *Drepanotermes* are responsible for crucial amounts of carbon mineralisation in the habitats in which they occur (Holt 1987) and can be considered keystone species (Whitford 1991). They not only influence the identity and productivity of plants around their nests through their activity in the soil (Coventry *et al.* 1988, Spain and McIvor 1988, Congdon *et al.* 1993, Park *et al.* 1994, Lobry de Bruyn and Conacher 1995), but also provide vital living space and food resources for ants (Holt and Greenslade 1980, Holt 1990, Yamada 2007), reptiles (Morton and James 1988, Abensperg-Traun 1994), and small mammals (Moro *et al.* 2014). The occurrence of *Drepanotermes* species has also been shown to influence local species richness of lizards in the arid zone (Colli *et al.* 2006).

Illuminating their evolutionary history will help to understand how *Drepanotermes* became ecologically dominant on the continent. Ancestral state reconstruction of a key life-history trait, namely nesting type, will show whether mound-building was acquired once or multiple times independently, and whether it is correlated with paleoclimatic events. Additionally, environmental niche modeling will be used to infer range limits of species and habitat suitability under current and projected future environmental conditions. The periods of severe drought and intense cyclones predicted for Australia in the future (IPCC 2019), may affect individual species differently depending on their nesting preferences.

Outline of this thesis

In this thesis, I examine the evolutionary history of the Australian *Amitermes* group and test the idea that radiation of this group coincided with the aridification of the Australian continent over the past 15 million years. To do this, I generated the largest molecular data set of the group to date, including over 680 colonies from across Australia, and utilized barcoding and whole mitochondrial genome sequences to reconstruct robust phylogenetic trees. These phylogenies were used to infer biogeographical patterns that shaped the evolutionary trajectory of the group. In addition, I reconstructed the ancestral nesting habit of *Drepanotermes* and predicted potential species ranges under current conditions and projected climate-change scenarios.

In **Chapter 1**, I investigate phylogenetic relationships, biogeographical history, and diversification patterns in the AAG. I reconstruct a robust "backbone" phylogeny based on mitogenomes, resulting in the first time-dated phylogeny explicitly focused on the most diverse and speciose group of higher termites in Australia (Watson and Abbey 1993). The results show that the AAG is a monophyletic group which arrived via a single introduction event in the late Miocene. Originating in Southeast Asia, early lineages expanded their range quickly in the northern monsoonal tropics and later into other regions of Australia. The diversification rate increased steadily from the late Miocene onwards and accelerated during the Pliocene in concert with the intensifying aridification and major ecological change on the continent. Diversification analysis show that progressive niche saturation led to a slowdown in species accumulation.

In **Chapter 2**, I focus on the Australian endemic genus *Drepanotermes*, which diverged from *Amitermes* in the late Miocene and diversified during Plio-Pleistocene times, to elucidate the evolutionary history of Australian harvester termites in the face of past, present, and future climate change. I use the largest molecular data set to date to delineate species within *Drepanotermes*, reconstruct their ancestral nesting habits, and predict present and future habitat suitability under the prospect of global climate change. I investigate whether distributional patterns are related to rainfall variability, temperature, and predation pressure, among other factors. Under different impact levels of climate scenarios (Dunlop *et al.* 2012), I test whether arid-adapted *Drepanotermes* species will become more widespread as Australia faces further aridification in the years to come, expanding the potential habitat space for arid-adapted *Drepanotermes*.

Results suggest that *Drepanotermes* includes far more species than currently described and that their ancestor most likely constructed subterranean nests. Mound-building evolved several times independently and likely facilitated repeated diversification into more humid and hot regions of Australia. Today, most mound-builders are distributed along an increasing temperature and rainfall gradient, as reflected in strong phylogenetic signals of limiting environmental factors. Habitat suitability modeling showed that species ranges are mainly shaped by abiotic factors like annual temperature, rather than biotic factors like vegetation cover or predation pressure. In most cases, current species ranges will probably remain habitable in the near future, independent of nesting preferences. While areas of suitable habitat are expected to increase substantially over the next 50 years, limited dispersal capabilities of winged reproductives preclude extensive range expansion in such a short period of time.

In *III General Discussion*, I place my results in the wider context of evolutionary diversification in Australia during late Cenozoic climate change. I demonstrate how biogeographical and diversification patterns in the AAG have been shaped by the development and expansion of the arid zone from the mid to late Miocene onwards, similar to other organisms such as lizards or spinifex grasses. I discuss possible evolutionary processes that may have led to the observed patterns of rapid diversification in concert with the aridification of Australia. Finally, I illustrate the role of evolutionary adaptations,

such as mound-building, that enabled members of the AAG to become ecologically dominant in the

arid zone and beyond .

II Research Chapters

Chapter 1

Rapid Diversification of the Australian *Amitermes* group during late Cenozoic Climate Change

Bastian Heimburger, Leonie Schardt, Alexander Brandt, Stefan Scheu, Tamara R. Hartke

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 from Southeast Asia. Ancestral range reconstruction indicates that Australia's monsoon region was the launching point for a continental radiation shaped by range expansions 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 ~8-9 Ma during the "Hill Gap" and accelerated from ~4 Ma in concert with major ecological change during the Pliocene. Consistent with rapid diversification, species accumulation slowed down to the present-day, likely caused by progressive niche saturation. This study provides a stepping stone for predicting the future response of Australia's termite fauna in the face of human-mediated 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 (Ma), Australia's previously warm and wet climate became cool and dry, a period of regional climatic instability known as the "Hill Gap" (10-6 Ma, Hill 1994). The widespread 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, Guzik *et al.* 2011, Powney *et al.* 2010, 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). In particular, vicariance 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 *i.a.* the last remnants of rainforest in Australia and is characterized by high levels of rainfall during the winter season (Byrne *et al.* 2011). Despite receiving similar total amounts of 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 continent-wide 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 play important roles in ecosystem functioning across the continent (Coventry *et al.* 1988, Noble *et al.* 2009, Evans *et al.* 2011). The AAG and other termite lineages are thought to have arrived in Australia relatively recently, 11 to 13 Ma (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 the challenge of 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 have been 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). Hence, we hypothesise that Australia's aridification facilitated frequent biome shifts (*i.e.* dispersal events) and promoted radiations within biomes as shown 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, vicarance), we first test the monophyly of this group of higher termites, 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 rates accelerated during periods of late Cenozoic climate change (*e.g.* during the "Hill Gap" and Plio-Pleistocene).

MATERIALS AND METHODS

Mitochondrial Genome Sequencing

The final data set comprised 135 mitochondrial genomes (see Supporting information, Table S1): 87 *Amitermes* and *Drepanotermes* mitochondrial genomes sequenced in this study and 48 sequences from NCBI, including 15 *Amitermes* and *Drepanotermes* sequences and 33 sequences of 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 the positions 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 further 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 (see Table S2) implemented as exponential priors. Divergence dating was performed with BEAST 2.6.1 (Bouckaert *et al.* 2019) and a maximum-clade-credibility (MCC) tree was obtained using TreeAnnotator implemented in BEAST 2.6.1. For further details about phylogenetic inferences and divergence dating 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 the R package BioGeoBEARS v.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*. Additionally, we pruned the tree of splits younger than 1.5 million years, retaining only 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, abbreviated as: S, mesic south-western zone, A, arid zone, M, monsoonal tropics, and E, mesic eastern zone) depending on the collection site (Fig. 1c and Table S3). Where tips could be unambiguously attributed to a described species, occurrence records from the Atlas of Living Australia (http://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'), which resulted in 9 possible ranges in total.

We used 100 Biogeographical Stochastic Mappings (BSMs) to obtain the overall probabilities of the anagenetic and cladogenetic events (Matzke 2016, Dupin *et al.* 2017), which depend on the geographic distributions, the time-calibrated phylogeny, and the best-fitting model. This allowed us to quantify the relative role of dispersal and vicariance at cladogenesis in the diversification of the AAG.

To assess the effect of topological uncertainty during the model selection process, we randomly sampled 100 pruned trees from the posterior distribution of the Bayesian analysis, summarized the ancestral range estimates, and compared the AICc values of the estimates for the

models DEC, DIVALIKE, and BAYAREALIKE, 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 (see above), 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 used 100 pruned posterior trees (see above) and created LTTs for each of them. The γ statistic (Pybus and Harvey 2000) was simultaneously calculated for the MCC tree and the 100 pruned posterior trees, which can detect whether the net diversification rate deviated over time from a pure birth model (standard normal distribution with a mean of 0). 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 mimicked incomplete sampling by randomly pruning taxa from phylogenies, which were simulated to the full size of the group (*i.e.,* about 100 described species in Krishna *et al.* (2013)). We used 10,000 replicates under the null hypothesis of a constant rate pure-birth diversification process.

In addition to the MCCR test, we compared the fitting 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 take into account the absence of species (both extinct and missing from the phylogeny) and how this is likely to 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 (AICc, Burnham and Anderson 2002, Posada and Buckley 2004). To determine the goodness of fit of candidate evolutionary models, we used the lowest AICc score and ΔAICc scores, where the differences between the lowest (or best) AICc and the AICc of each alternative model are calculated, and thus, the best model has ΔAICc = 0. All analyses were run on the MCC tree and the 100 pruned posterior trees.

To complement the model-fitting approach, we employed BAMM 2.5.0 (Bayesian Analysis of Macroevolutionary Mixtures, Rabosky *et al.* 2013, 2014, Rabosky 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 *et*

al. 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, Tab. S5) 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 Figs. S1-2). 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 Figs. S1-2).

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 Ma (95% HDP: 9.52-12.81 Ma) (Fig. S2). Two major divergence events, *Drepanotermes* at 6.5 Ma (95% HDP: 5.6-7.67 Ma) and AG2 at 5.55 Ma (95% HDP: 4.77-6.45 Ma), correspond roughly to the end of the paleoclimatic „Hill Gap" (10-6 Ma) in the late Miocene (Fig. S2). An estimated 12% of DRE and 53% of AG2 lineages diverged during the Pliocene (~5.3-2.6 Ma) compared to 33% of AG1 lineages, while recovered divergence time for 35 out of 95 lineages within the AAG were < 1.5 Ma (Fig. S2).
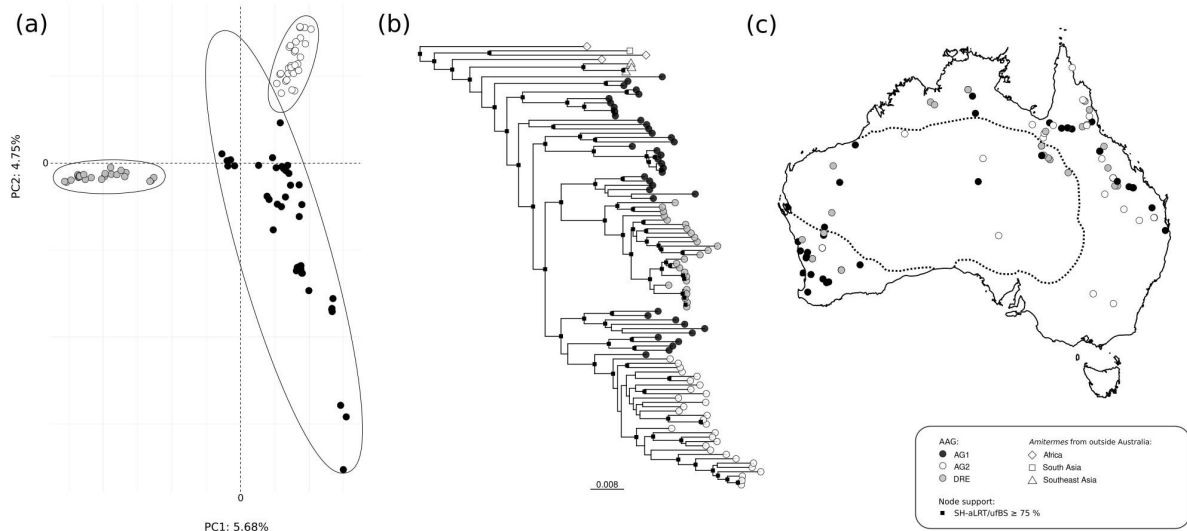
Figure 1. (a) The PCoA showed three distinct genetic clusters within the AAG, (b) two of which (DRE and AG2) are recovered as monophyletic by the maximum likelihood analysis. (c) Map shows sampling locations of AAG taxa included in this study in relation to the arid zone (dashed line, modified from Fujita *et al.* 2010).

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 Fig. S3). The impact of topological uncertainty on the model selection process was examined by combining the AICc values of the ancestral range estimates for each of the 100 posterior trees and for each of three models (Fig. S4). 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).

Table 1 Summary statistics of three biogeographic models estimated using BioGeoBEARS and the MCC tree. The DIVALIKE model (in bold) was selected for downstream analyses based on ΔAIC scores.

Model	LnL	Number of parameters	d	e	AIC	ΔAIC
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

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) (Table S4). 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 Table S4). 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 Table S4).
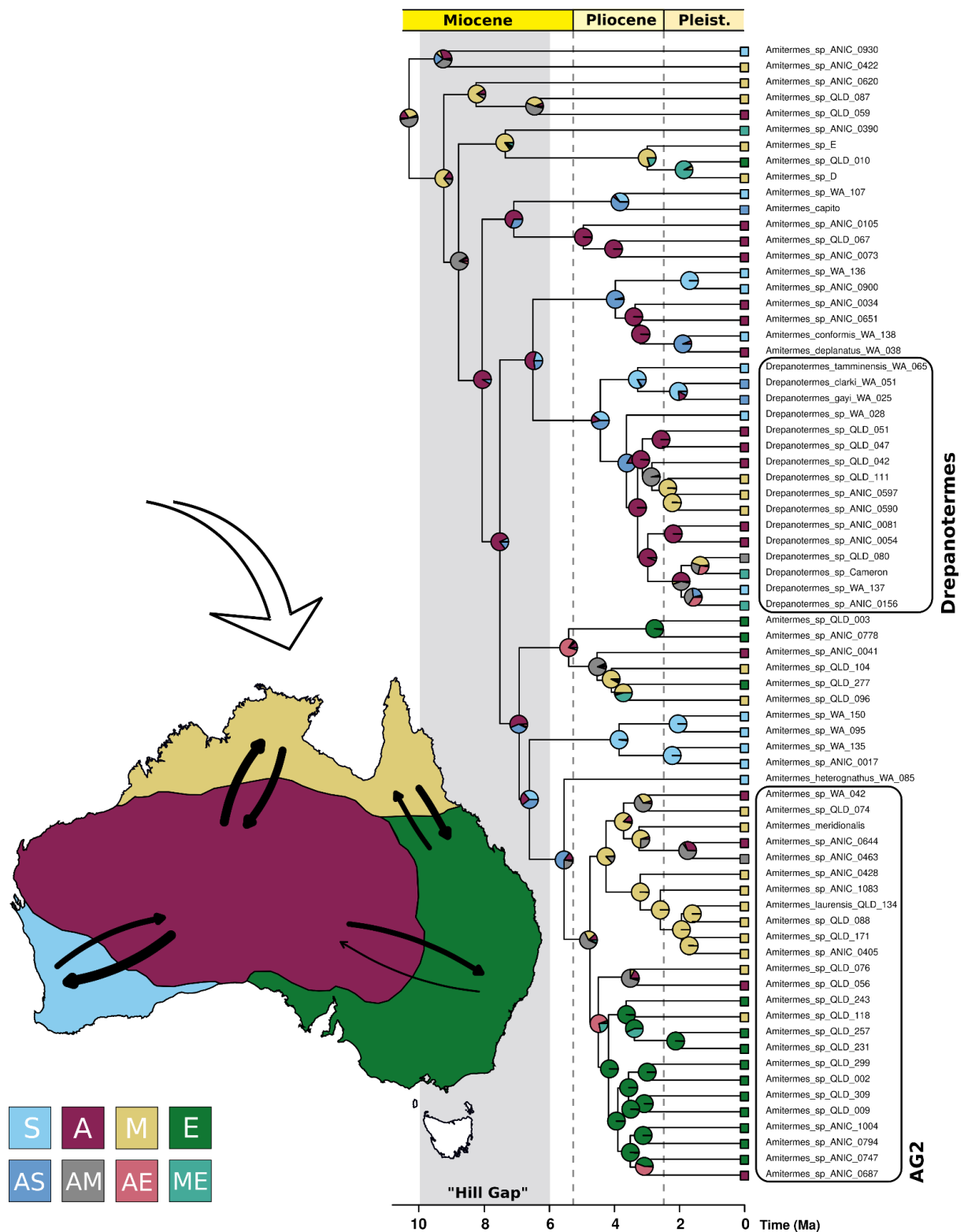
Figure 2. Ancestral range reconstruction of the AAG based on the DIVALIKE model. Relative probabilities of ancestral areas are shown in pie charts at nodes. Colored squares identify biomes: S, mesic south-western zone, A, arid zone, M, monsoonal tropics, E, mesic eastern zone. Combinations of biomes (*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) (see Tab. S4). The white arrow indicates the putative arrival direction of the ancestor of the AAG (see Discussion).

Table 2 Summary counts of 100 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.

	Range expansion	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

Model and Rates of Diversification

The multi-LTT plot suggests a rather continuous trend of increasing diversification from ~8-9 Ma with a sudden, abrupt incline from ~4 Ma, 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, $p < 0.0001 = 9.999e-05$) 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.
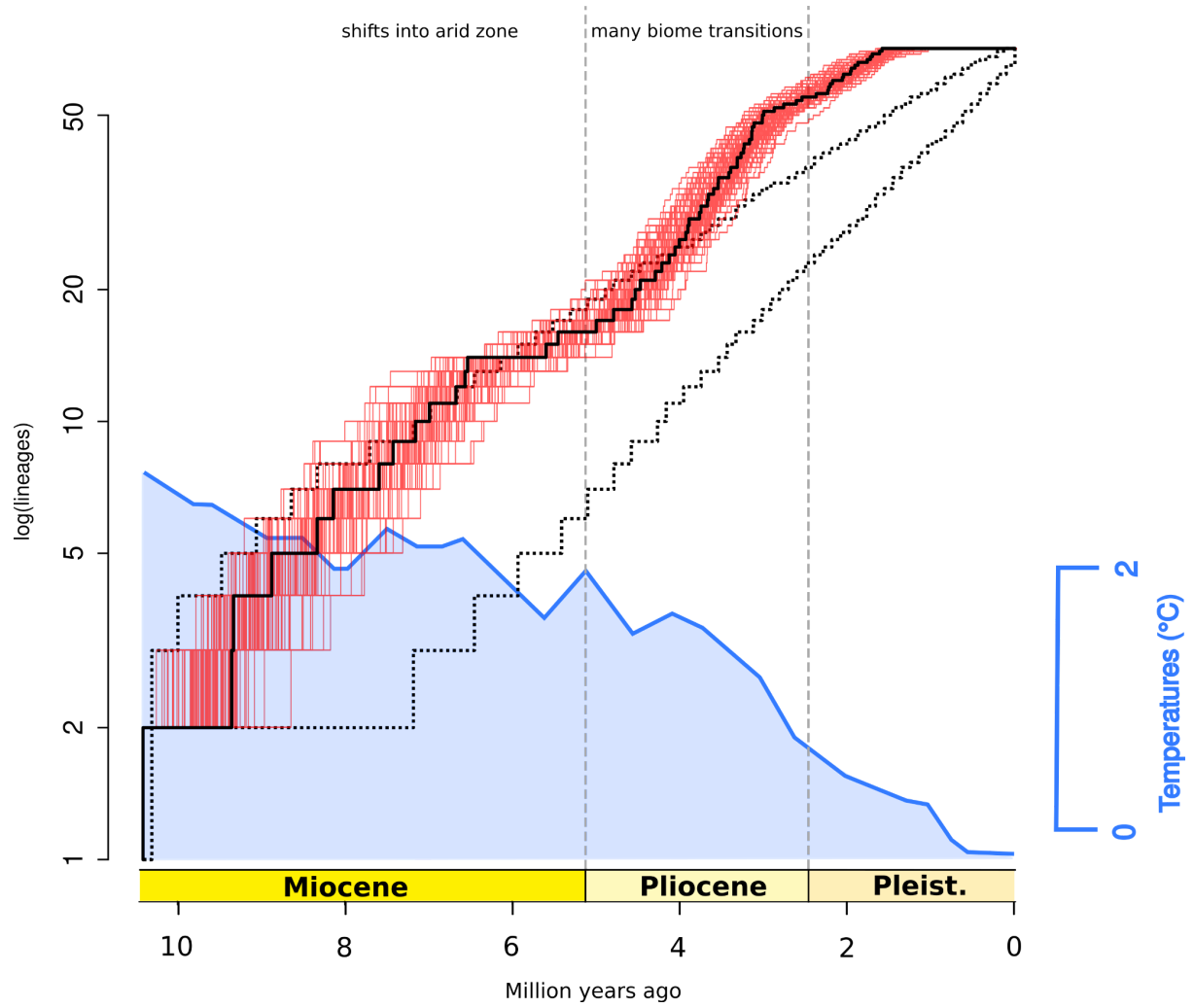
Figure 3. LTT curves of the MCC tree (black) and variation in relative branching times represented in the posterior sample, as generated from 100 posterior trees (red), show a sudden incline in diversification from ~4 Ma (exceeding the 95% confidence interval generated by simulated LTTs (dashed lines)), preceded by a period of continuously increasing diversification from 8 Ma. Periods of increased diversification correlate with major biome transitions.

Table 3 Comparison of alternative evolutionary models fitted to the diversification history of the 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.

Model	logL	λ	μ	AICc	ΔAICc
72/100					
Yule	-167	0.29	0	336 (337.2)	27.7 (25.6)
CR	-167	0.29	0	338.1 (339.3)	29.8 (27.7)
DDL+E	-151	0.74	5.9e-05	308.3 (311.6)	0
DDX+E	-179.5	0.57	0.35	365.3 (368.2)	57 (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	3.8e-06	310.1 (313.3)	0
DDX+E	-161.9	1.52	0.12	330.1 (330.5)	20 (17.2)
72/250					
Yule	-158.4	0.45	0	318.78 (320)	0.98 (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	323.52 (325.9)	5.72 (7.9)

BAMM analyses based on the MCC tree detected no major shifts in the rate of diversification within the AAG (Table S5 and Fig. S5), 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 (Table S5). 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 (Fig. S5). Consistent with a pattern of rapid diversification, the rate of diversification decreased markedly over time (Fig. S5), while the extinction rate remained near zero (mean extinction rate of ~0.05, Fig. S5).

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

In our PCoA, AG2 and *Drepanotermes* were clearly separated from AG1 and recovered in all phylogenetic analyses with high nodal support. 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. 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 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, Smissen and Rowe (2018) reported 12 transitions between biomes for 31 extant species of Australian rodents (Pseudomys division) in the last 5 Ma. 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 Ma, 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. 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 (Smissen

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. 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. 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 C_3 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. 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 C_4

grasslands in response to the establishment of the modern-like Australian monsoon regime ~3.5 Ma (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.* 2017) and cicadas (Owen *et al.* 2017).

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. meriodionalis*, *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.

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.* 2007). 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 increase 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, 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. 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 (Chouvenc *et al.* 2021). Despite these limitations, the large number of recent (< 2 Ma) 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 Gay 1991, Watson and Perry 1981, 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 (2006) 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) and cicadas (Owen *et al.* 2017) 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 Ma, which the authors' attributed to the expansion of C_4 grasslands in Africa (Pie *et al.* 2021). Similar expansions of C_4 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.

Chapter 2

Historical and future climate change fosters expansion of Australian harvester termites,

Drepanotermes

Bastian Heimburger, Santiago Soto Maurer, Leonie Schardt, Stefan Scheu, Tamara R. Hartke

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Past evolutionary adaptations to Australia's aridification can help us to understand potential responses of species in the face of global climate change. Here, we focus on the Australian-endemic genus *Drepanotermes*, also known as Australian harvester termites, which are mainly found in semi-arid and arid regions of Australia. We used species delineation, phylogenetic inference, and ancestral state reconstruction to investigate the evolution of mound-building in *Drepanotermes* and in relation to reconstructed past climatic conditions. Our findings suggest that mound-building evolved several times independently in *Drepanotermes*, apparently facilitating expansions into tropical and mesic regions of Australia. Phylogenetic signal of bioclimatic variables, especially of limiting environmental factors (*e.g.* precipitation of warmest quarter), suggests that climate exerts a strong selective pressure. Finally, we used environmental niche modeling to predict present and future habitat suitability for eight *Drepanotermes* species. Abiotic factors such as annual temperature contributed disproportionately to calibrations, while the inclusion of biotic factors like predators and vegetation cover improved ecological niche models in some species. A comparison between present and future habitat suitability under two different emission scenarios revealed continued suitability of current ranges as well as substantial habitat gains for most studied species. Human-mediated climate change is occuring more quickly than these termites can disperse into newly suitable habitat, however their role in stabilizing arid ecosystems may allow them to mitigate effects on some other organisms at a local level.

INTRODUCTION

Australia progressively aridified from the mid Miocene (~15 million years ago, hereafter Mya) onwards due to regional tectonic forcings (Pepper and Keogh 2021), leading to widespread contraction of rainforests and a massive loss of stabilizing vegetation cover (Martin 2006, Byrne *et al.* 2008, 2018). This resulted in unprecedented erosion, which paved the way for today's dominance of sclerophyllous and xeric vegetation (Byrne *et al.* 2008, 2011). The expansion of grasslands and the development of the arid zone in central Australia occurred in the context of global cooling caused by declining atmospheric CO_2 levels during the late Miocene (Herbert *et al.* 2016). Finally, sand and stone deserts, such as the Great Victoria Desert, formed during the Pleistocene (~2.58 Mya), when extreme climatic oscillations occurred during the interglacial periods (Fujioka *et al.* 2005). Current estimates suggest that climatic conditions in Australia may come to resemble those of hot and moist intervals in the Miocene within the next 100 years (Steinthorsdottir *et al.* 2021), as mean temperatures increase and rainfall patterns shift, *e.g.* increasing summer and decreasing winter rainfall (Dunlop *et al.* 2012). The arid zone, which now covers 75% of the continental landmass of Australia (Byrne *et al.* 2008), will expand in the future, because semi-arid and arid regions are expected to see a steeper temperature rise than other regions (Huang *et al.* 2016, Spinoni *et al.* 2021) resulting in higher levels of aridity.

Contrary to popular belief, the arid zone is anything but dead: it is home to an astonishing variety of arid-adapted organisms (reviewed in Crisp *et al.* 2004, Byrne *et al.* 2018, Pepper and Keogh 2021). Recent studies show that Australia's aridification triggered radiations in the past (Rabosky *et al.* 2007, Guzik *et al.* 2011), including the endemic termite genus *Drepanotermes* Silvestri, which is a prime example of an explosive radiation coinciding with intensifying arid conditions in the Plio-Pleistocene (Heimburger *et al.* 2021). The 23 described species primarily occur in arid and semi-arid regions of the continent (Watson and Perry 1981). Their success, especially in Australia's arid zone, has been attributed to an ability to exploit niches not occupied by *Amitermes* or other harvester termites (*e.g. Tumulitermes*, *Nasutitermes*; Watson 1974). *Drepanotermes* are unique among harvesting termites in that they also forage during the day, which is made possible by adaptations to

aridity such as heavily sclerotised and pigmented mature workers and soldiers (Watson and Perry 1981), which can tolerate high levels of desiccation stress and UV radiation (Nel and Hewitt 1969). Harvesting and storage of food material in nests (*e.g. Triodium, Acacia*, and other arid-zone plants; Hill 1942, Park *et al.* 1993, Tayasu *et al.* 2002) seems to be another key trait vital to the radiation of *Drepanotermes*, as this trait is also conserved throughout the genus (Watson and Perry 1981, Watson 1982) and clearly provides a selective advantage under adverse conditions (Korb 2011).

Most *Drepanotermes* are subterranean and build transverse or vertical gallery systems (Watson and Perry 1981). Some species are facultative or obligate mound-builders, and still others inhabit or take over nests built by other termites (Abensperg-Traun and Perry 1998). The great variability of nesting types has been related to differences in soil and food preferences (Watson and Perry 1981, Abensperg-Traun and Perry 1998), but has never been placed in the wider context of major ecological change coincident with Australia's intensifying aridification in the Plio-Pleistocene. Although termite mounds have been suggested to more effectively maintain environmental homeostasis and buffer environmental extremes of both heat and rainfall than other nest types (Korb 2003, 2007), little support for this has been found in other Australian mound-builders (Lee *et al.* 2015, Beasley-Hall *et al.* 2019).

The continental distribution of arid-adapted *Drepanotermes* presents a unique opportunity to investigate evolutionary and ecological patterns of nest-type variability in relation to past and future climatic conditions. To do this, we sampled colonies from across Australia and used DNA barcode sequencing to delineate species. A supermatrix alignment was used to infer the ancestral nesting habit, which was then related to reconstructed climatic niches. In general, mound-building termite species in Australia are more often found in regions with high temperatures and rainfall than subterranean species (Wijas *et al.* 2022), and we expect to see a similar pattern in *Drepanotermes*. Finally, current and future habitat suitability, based on abiotic and biotic factors such as bioclimatic variables and vegetation cover, were predicted for a selection of species with varying nesting habits. Under the prospect of global climate change, increasing aridity, hotter temperatures, and changing rainfall patterns are expected in Australia (Dunlop *et al.* 2012, Spinoni *et al.* 2021) and we hypothesise that

suitable habitat will increase in the future, independent of nesting preferences, as both mounds and subterranean nests buffer against long-term environmental change.

MATERIALS AND METHODS

Sample Collection

In total, specimens from 242 *Drepanotermes* colonies were included in this study. The collection comprised samples preserved in 70-100% EtOH or RNA*later* which we collected from Western Australia and Queensland in 2016 and 2019, respectively, as well as samples from the Australian National Insect Collection (ANIC) collected as part of a CSIRO/Atlas of Living Australia Project in 2008. See Supplementary Material, Tab. S1 for collection details.

DNA Extraction and Sequencing

Genomic DNA was extracted from the body, with head and gut removed, of one individual worker per colony using the Agencourt DNAdvance Magnetic Bead Kit (Beckman Coulter, USA). DNA quality and concentrations were checked with a Nanodrop 2000 Spectrophotometer (Thermo Fisher Scientific, USA) and a Qubit Fluorometer (Thermo Fisher Scientific, USA).

Three genetic markers were targeted for PCR amplification: the mitochondrial cytochrome c oxidase subunit 2 (COX2 mtDNA) and the nuclear internal transcribed spacer regions 1 and 2 (ITS1 and ITS2 nDNA, respectively). For primer sequences and PCR protocols see Supplementary Material (S1). All PCR products were visualized on a QIAxcel Advanced System (Qiagen, Germany), purified using the AMPure XP purification kit (Beckman Coulter, USA), and sent to Microsynth Seqlab (Germany) for bi-directional Sanger sequencing.

mOTU Delineation

We employed three different delineation methods, under default parameters of each, to assign specimens to molecular operational taxonomic units (mOTUs) using the COX2 mtDNA barcoding

sequences: bPTP (Zhang *et al.* 2013; https://species.h-its.org/ptp/, accessed on 23 June 2021), ABGD (Puillandre *et al.* 2011; https://bioinfo.mnhn.fr/abi/public/abgd/, accessed on 23 June 2021), and ASAP (Puillandre *et al.* 2021; https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html, accessed on 23 June 2021). bPTP uses a maximum likelihood (ML) tree as input, which was reconstructed on the PhyML 3.0 web-server (Guindon *et al.* 2010; http://www.atgc-montpellier.fr/phyml/).

Phylogenetic Inferences and Divergence Dating

We used the best partitioning scheme of ASAP (based on the lowest asap-score of 5.50) to divide the data set into 54 mOTUs, then selected representative sequences for each to use in downstream phylogenetic inference and divergence dating. To make our phylogenetic reconstructions as robust as possible, we selected representative mOTU sequences for which whole mitochondrial genome sequences were available from the same colony (Heimburger *et al.* 2021), or individuals for which at least two of the three targeted genes had been sequenced. Thus, our supermatrix alignment consisted of mitochondrial coding sequences (CDS), COX2 mtDNA, and ITS1 and ITS2 nDNA sequences.

We included eight outgroup sequences: six Australian *Amitermes* forming the sister clade to *Drepanotermes* (Heimburger *et al.* 2021), *Amitermes dentatus* from Southeast Asia, sister of Australian *Amitermes + Drepanotermes* (Bourguignon *et al.* 2015, 2017; Heimburger *et al.* 2021), and *Orthognathotermes aduncus* to root our phylogenies (Bourguignon *et al.* 2017). Accession numbers of mitogenomes and individual sequences can be found in Tab. S1.

Alignment was performed with the MUSCLE (Edgar 2004) plugin in Geneious Prime 2021.1.1 (Kearse *et al.* 2012) as follows: (i) CDS excluding COX2 mtDNA, were aligned separately as codons and partitioned into first, second, and third codon positions; (ii) COX2 mtDNA sequences were aligned as codons and partitioned into codon positions; and (iii) ITS1 and ITS2 nDNA sequences were aligned separately and gap characters retained. The final concatenated supermatrix alignment included 62 sequences with a total length of 11,823 bp (Tab. S1).

We used IQ-TREE version 2.0.6 (Minh *et al.* 2020) to reconstruct a maximum-likelihood (ML) phylogenetic tree and dated our phylogeny with BEAST v.2.6.6 (Bouckaert *et al.* 2019) using

two secondary calibrations, because no higher termite fossils are known from the Australian continent. For further details on phylogenetic inferences and divergence dating see Supplementary Material (S2).

Georeferenced Records and Predictor Variables

For mOTUs clearly attributable to described species (Fig. 1 and Tab. S2), we retrieved georeferenced records from the Global Biodiversity Information Facility (GBIF.org) using the R package rgbif (Chamberlain and Boettiger 2017). We did not retrieve georeferenced records for *D. perniger*-NE, *D. perniger*-SW, and *D. rubriceps*, because our molecular data support the suggestion that both *D. perniger* and *D. rubriceps* refer to species complexes (Watson and Perry 1981) widely distributed across the continent (see occurrence records from the Atlas of Living Australia). Therefore, we used only location data of samples collected in this study for *D. perniger* and *D. rubriceps*. We excluded unreliable records with the R package CoordinateCleaner (Zizka *et al.* 2019), namely: (a) coordinates assigned to the capital and province centroids, (b) sea coordinates, (c) zero coordinates, (d) coordinates assigned to biodiversity institutions, and (e) duplicated coordinates. Finally, filtered records were combined with our collected field records.

In total, we considered 30 predictor variables in this study: 26 abiotic and four biotic variables (Supplementary Material, Tab. S3). Abiotic variables included BIO01-BIO19 of the WorldClim 2 BioClim variable set (Fick and Hijmans 2017), soil parameters from the Australian Soil Resource Information System (ASRIS) (Grundy *et al.* 2015), elevation, and fire frequency. Biotic variables included species richness of three major termite predator groups including ants, lizards, and mammals (Supplementary Material S3 and Tab. S4) and Australia's Pre-1750 (pre-European, pre-clearing) native vegetation re-classified into 10 major vegetation groups from the Natural Vegetation Information System (NVIS) v6.0 (see Supplementary Material S3 and Tab. S5). Downloaded grid layers were transformed into Esri ASCII raster format and scaled to 30 arcsec in QGIS 3.20 (QGIS Development Team 2021).

All predictor variables were compared using pairwise Pearson's correlations in the R package raster (Hijmans 2021). One variable from each >75% correlated pair was randomly discarded, resulting in a final set of 16 uncorrelated predictor variables (Supplementary Material, Tab. S3 and S6).

Ancestral State Reconstruction of Nesting Habits

To reconstruct ancestral nesting habits, we excluded *Orthognathotermes aduncus* and *A. dentatus* from the divergence-dating tree. We assigned each tip to one of three nesting habits based on field records and literature data (Watson and Perry 1981, Abensperg-Traun and Perry 1998; Tab. S2): (1) 'subterranean', (2) 'subterranean + mound', and (3) 'mound'. 'Subterranean' is the broadest category and includes taxa that live in subterranean nests, decaying wood, under rocks and wood, as well as inquilines (*i.e.* termites living in nests of other termites). This category also includes mOTUs which could not be clearly assigned to one of the other two categories due to incomplete natural history information. The category 'mound' includes all obligate mound-builders, which construct either pavements or epigeal mounds (see Watson and Perry 1981), whereas mOTUs that included both subterranean and mound-building colonies were assigned as 'subterranean + mound', *i.e.* facultative mound-builders (Fig. 1 and Tab. S2).

We used the fitMk function of the R package phytools version 0.7-80 (Revell 2012) to test three different models: (1) an equal-rates model (ER), (2) an all-rate-different model (ARD), and (3) a symmetrical model (SYM). The best-fitting model was chosen on the basis of the highest Akaike weight.

Phylogenetic Signal

All biotic variables represent categorical traits and were excluded from phylogenetic signal analyses. Grand total means of each abiotic variable by mOTU/species were estimated to asses two different measures of phylogenetic signal, Blomberg's K (Blomberg *et al.* 2003) and Pagel's λ (Pagel 1999) using the R package phytools version 0.7-80. Values close to or above one indicate that closely related

species are more ecologically similar than expected based on their phylogenetic relationships, whereas lower values suggest the opposite (low phylogenetic dependence; Revell *et al.* 2008).

To investigate the acquisition of mound-building in relation to past climatic niches, we reconstructed ancestral states as a continuous trait using phytool's fastAnc function for two bioclimatic variables: BIO01 (mean annual temperature) and BIO18 (precipitation of warmest quarter). Both variables exhibited high phylogenetic signal (Fig. 3), suggesting that climatic niches are phylogenetically conserved over evolutionary time, so we also used them in ecological niche modelling (see below), to compare our reconstructions of past climatic niches with predictions of present and future habitat suitability.

Present and Future Habitat Suitability

Ecological niche models (ENMs) of eight representative taxa were predicted using MaxEnt 3.4.1 (Phillips *et al.* 2017). We included taxa with (i) nine or more georeferenced records, (ii) different geographic distributions (southwestern, central, northeastern) and (iii) different nesting habits ('subterranean', 'subterranean + mound', 'mound').

Standard model settings in MaxEnt tend to over- or underestimate niches depending on the study object and predictor variables (Radosavljevic and Anderson 2014), therefore several settings and subsets of predictor variables were tested. We used five different regularization multipliers (0.8, 1, 2, 3, and 5) to assess the importance of the 16 predictor variables. Additionally, we subsetted the predictor variables to assess the importance of abiotic vs. biotic factors, creating separate ENMs for abiotic (n = 12) and biotic variables (n = 4). All model runs allowed linear, quadratic, and product feature types, and automatic limiting of feature types was enabled. AICc values were estimated to assess model performance with the R package ENMTools (Warren *et al.* 2010) and model settings with the lowest AICc score (Tab. S7) were selected to calculate full ENMs with ten replicates to obtain the present habitat suitability. When AICc scores were equivalent (AICc difference less than 2), we used the more inclusive variable set (Tab. S7). We used complementary log-log (cloglog) as

model output (Phillips *et al.* 2017). For each model, we retained only variables with high permutation importance, *i.e.* permutation value higher than 15% (Tab. 1).

To project potential habitat suitability of each of the eight species under future climate scenarios, we first estimated full models with the current BioClim factors in our abiotic variable subset (BIO01, BIO02, BIO03, BIO09, and BIO18) using the best-fitting MaxEnt settings (see above). These estimated habitat suitability models were projected onto two future climate change predictions for the year 2061 implemented in the CSIRO-Mk3.6.0 climate system model (Rotstayn *et al.* 2012). Two different representative concentration pathway (RCP) scenarios were used: (1) RCP2.6, a moderate climate change scenario with an anticipated global mean temperature rise below 2°C by 2100; and (2) RCP8.5 representing the "business-as-usual" scenario with about 4°C of warming above pre-industrial levels by 2100 (O'Neill *et al.* 2016).

RESULTS

mOTU Delineation

The number of mOTUs varied between the three delineation approaches, reflecting their different power to detect cryptic lineages: ASAP sorted the 242 COX2 mtDNA sequences into 54 mOTUs, whereas ABGD and mPTP returned 65 and 62, respectively (Fig. 1). Unlike ASAP, which uses the sequence data directly to calculate pairwise genetic distances (Puillandre *et al.* 2021), mPTP and ABGD require either a phylogeny or *a priori* insight into intraspecific diversity, both of which can have a major influence on the number of resulting species partitions (Puillandre *et al.* 2021). Therefore, we chose to use the most conservative number of 54 mOTUs (delineated by ASAP) for downstream phylogenetic analyses (see also Tab. S2). The eight species used for ENM were almost always congruent between all three delimitation methods employed; only *D. perniger*-NE and *D. perniger*-SW showed very minor incongruencies (Fig. 1).

ASAP (n = 54)
ABGD (n = 65)
mPTP (n = 62)
nesting type

○ subterranean
◑ subterranean + mound
● mound

QLD_206
QLD_224
QLD_201
QLD_193
QLD_189
QLD_182
QLD_169
ANIC_0348   mOTU1 *D. rubriceps*
ANIC_0347
ANIC_0312
ANIC_0310
QLD_157
QLD_143
QLD_156
QLD_145
ANIC_0469   mOTU2
ANIC_0470
ANIC_0488   mOTU3
QLD_052
QLD_048
QLD_061
QLD_060
QLD_054   mOTU4
QLD_053
QLD_044
QLD_043
QLD_069
QLD_070   mOTU5
QLD_073   mOTU6
QLD_080
QLD_079
QLD_077   mOTU7
QLD_075
ANIC_0450
ANIC_0453   mOTU8
QLD_306
QLD_308
QLD_305
ANIC_0734
ANIC_0717   mOTU9
ANIC_0715
ANIC_0616
ANIC_0536
ANIC_0504
ANIC_0666   mOTU10
ANIC_0507   mOTU11
ANIC_0523
ANIC_0528
ANIC_0172   mOTU12
ANIC_0169
ANIC_0175
ANIC_0496   mOTU13
ANIC_0513
ANIC_0686
ANIC_0676
ANIC_0672   mOTU14
ANIC_0669
ANIC_0649
ANIC_0656
QLD_272   mOTU15
ANIC_0627   mOTU16
QLD_267
QLD_269
QLD_264
QLD_270
QLD_265
QLD_255
QLD_254
QLD_266
QLD_253
QLD_242
QLD_241
QLD_117
QLD_121
QLD_106
QLD_100
QLD_099
QLD_093
QLD_063
QLD_050
QLD_041
QLD_037
ANIC_0424   mOTU17 *D. perniger*-NE
ANIC_0423
ANIC_0415
ANIC_0411
QLD_015
QLD_026
QLD_281
QLD_283
QLD_028
QLD_280
QLD_279
QLD_273
QLD_271
QLD_033
QLD_031
QLD_021
QLD_013
QLD_008
QLD_007
QLD_035
ANIC_0472
ANIC_0156
ANIC_0642
ANIC_0520
ANIC_0121
ANIC_0623   mOTU18
ANIC_0474
ANIC_0111   mOTU19
ANIC_0131
ANIC_0128   mOTU20
ANIC_0112
ANIC_0633   mOTU21
WA_087
WA_059
WA_103
WA_080
WA_076   mOTU22
WA_073
WA_060
WA_023
ANIC_0913
WA_026
WA_028
WA_162
WA_015   mOTU23
WA_063
WA_055
WA_122
WA_151
WA_148
WA_128
WA_124   mOTU24
WA_121
WA_119
WA_116
WA_147

Figure 1. Concordance of molecular species delimitation using three different methods (ASAP, ABGD, and mPTP), illustrated on the unrooted PhyML tree. Representative sequences for each of the 54 mOTUs indicated in blue were used for downstream analyses. Red vertical squares and bars indicate mOTU limits proposed by each method. Nesting habits are denoted with colored circles and grey vertical bars mark mOTU limits as delineated by ASAP, except mOTU17 *D. perniger*-NE and mOTU48 (turquoise and green, respectively).

Molecular Phylogeny

Fifty of 54 mOTUs in the supermatrix alignment were represented by two or all three of the target genes (Tab. S1). Phylogenetic analyses based on Bayesian and ML inferences recovered mostly congruent topologies and comparable support values (Supplementary Figs. S1 and S2). The split between *A. dentatus* and (Australian *Amitermes* + *Drepanotermes*), and between Australian *Amitermes* and *Drepanotermes* was maximally supported (Figs. S1 and S2). Relationships within *Drepanotermes* showed lower nodal support values, consistent with the rapid diversification over the past five million years (see below and Heimburger *et al.* 2021).

Divergence Dating

BEAST analysis converged with ESS values >200 and divergence time estimates were largely congruent with previous studies (Bourguignon *et al.* 2017, Heimburger *et al.* 2021). The split between *A. dentatus* and (Australian *Amitermes* + *Drepanotermes*) was dated at 10.86 Mya (95% HDP: 8.27-14.27 Mya) (Fig. S1). *Drepanotermes* was found to have diverged from Australian *Amitermes* around 7.13 Mya (95% HDP: 6-8.39 Mya). The majority of lineages in this study originated within the Pleistocene (2.58 Mya to the present), many with divergence times around 1 Mya or less (Fig. S1).

Ancestral Nesting Habit and Phylogenetic Signal

The best-fitting ER model indicates subterranean nesting was the ancestral nesting habit (Akaike weight 0.46; fit of alternative rate models SYM = 0.37 and ARD = 0.17). Mound-building probably evolved independently three to six times within *Drepanotermes* (Fig. 2). Whereas mound-builders are more common in regions characterized by high temperatures and rainfall, subterranean species seem to prefer more arid conditions (Fig. 2).
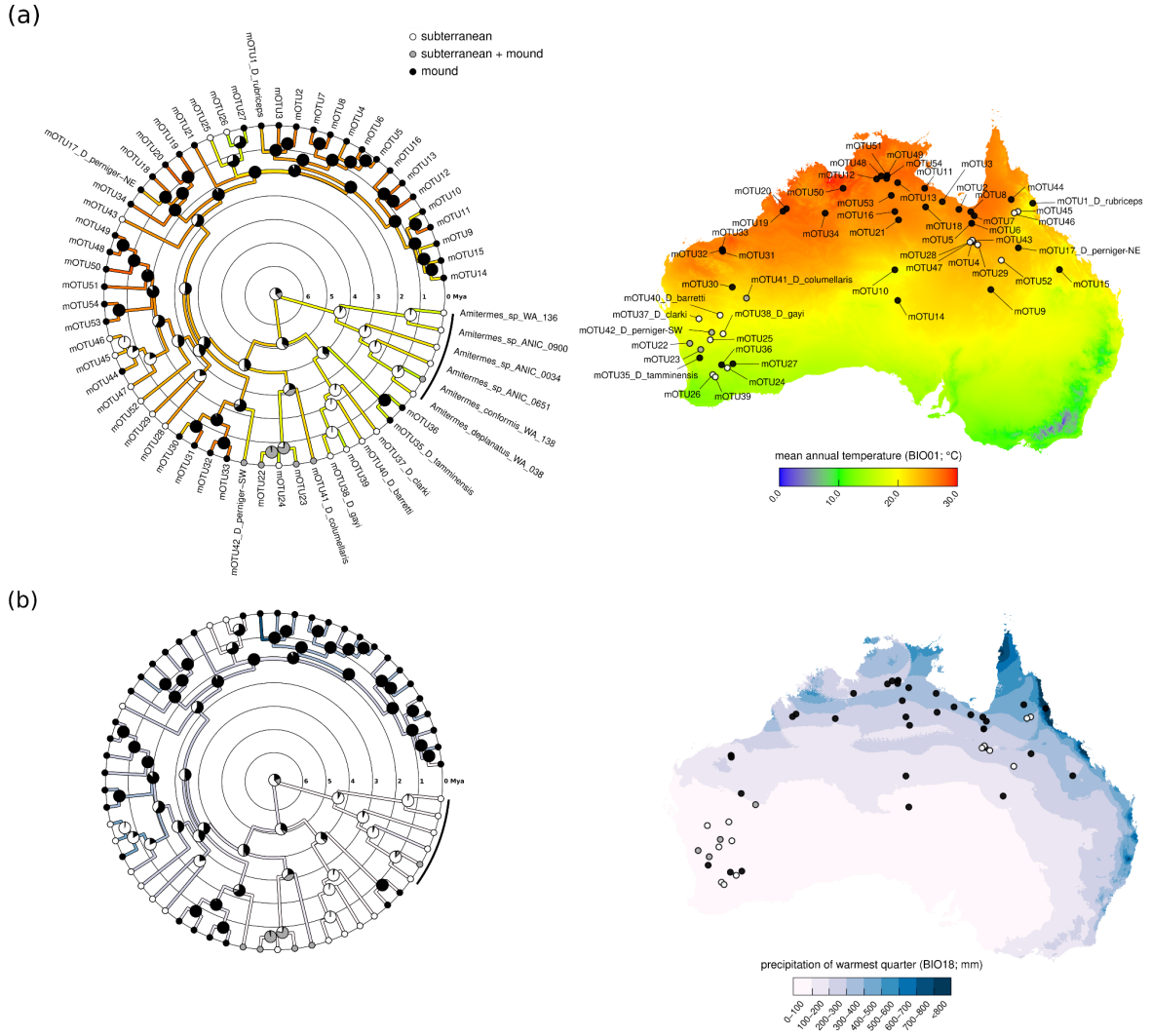
Figure 2 Ancestral state reconstruction of nesting habits related to two bioclimatic variables, (a) BIO01 (mean annual temperature) and (b) BIO18 (precipitation of warmest quarter). On each phylogeny, tip colour indicates nest type, and pies indicate inferred nest type for that node. White = 'subterranean', grey = 'subterranean + mound', black = 'mound'. Branch colours correspond to (a) mean annual temperature or (b) precipitation during the warmest quarter using the same scales as the maps, at the species range centroid (terminal branches) or as inferred by fastAnc (internal branches). Black bar indicates outgroup *Amitermes* sequences. Locations of mOTUs are given as centroids of georeferenced records.

Seventeen out of 19 bioclimatic variables showed evidence for phylogenetic signal (*p*-values <0.05) as measured by Blomberg's *K* and Pagel's λ (Fig. 3). We found high phylogenetic signal (λ ≤ 1

and *K* > 1) in bioclimatic variables that capture information about seasonal mean conditions and intra-year seasonality (BIO08, BIO11, BIO13, BIO15, BIO18, and BIO19), as well as annual temperature conditions (BIO01 and BIO03). Other abiotic variables that exhibited a significant phylogenetic signal included aridity index and, only for *K*, elevation (Fig. 3).
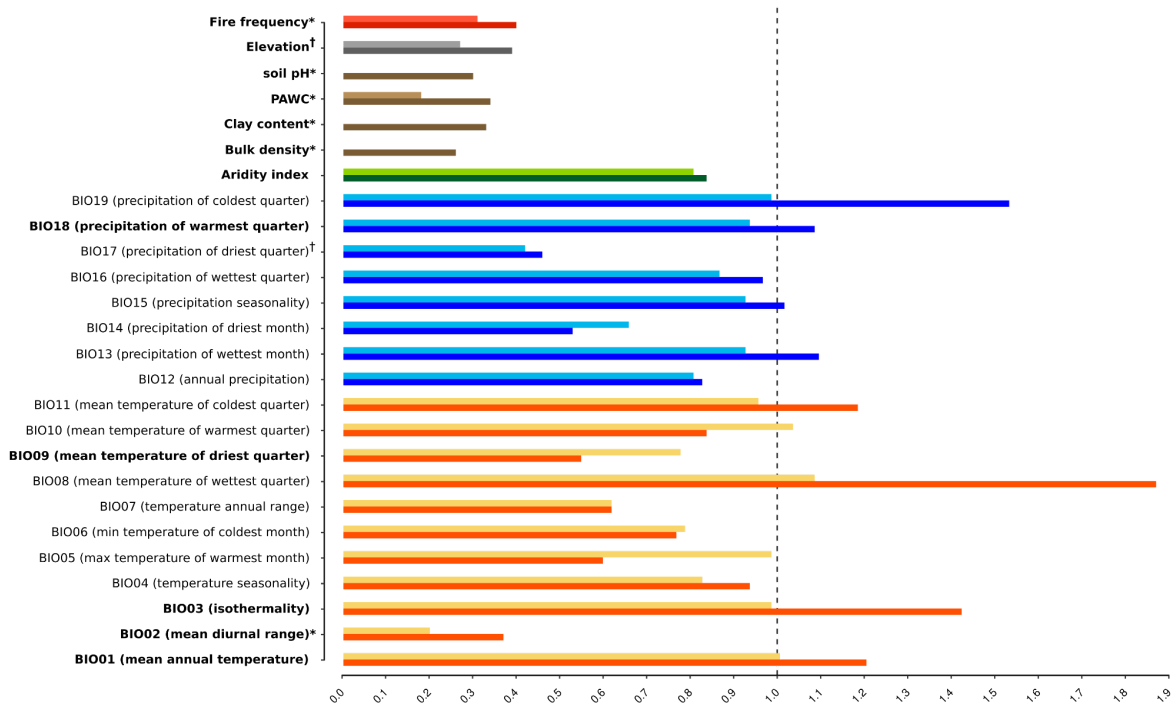
Figure 3   Phylogenetic signal as measured by Blomberg's *K* (darker shades) and Pagel's λ (brighter shades). *K* or λ values lower than 1.0 indicate low phylogenetic signal, interpreted as evolutionary lability. *K* or λ values above or close to 1.0 indicate that variables are phylogenetically conserved. Values below 0.1 were not visualized (λ: bulk density, clay content, and soil pH). * *K* and λ values not significant; † only *K* values significant.

Present Habitat Suitability

AICc values for the best-performing MaxEnt settings varied greatly between and among species, but were consistent for different model settings within the same species (Tab. S7). In five out of seven species, the abiotic variable set showed the lowest AICc score (often coupled with a low regularization multiplier), the biotic variable set never performed best (Tab. 1 and S7). Eight of the most important predictor variables were abiotic (aridity index, BIO01, BIO02, BIO03, BIO09, BIO18,

elevation and fire frequency) and two biotic (ant and lizard richness). For each species, only three or fewer predictor variables exceeded the permutation importance threshold of 15% (Fig. 4 and Tab. 1). Precipitation in the warmest quarter (BIO18) was the most frequent predictor variable with a permutation importance above 15%.

Table 1 Model settings used to calculate full ENMs with ten replicates to obtain the present habitat suitability. For each model, only predictor variables with a permutation importance above 15% are listed. BIO01: mean annual temperature; BIO02: mean diurnal range; BIO03: isothermality; BIO09: mean temperature of driest quarter; BIO18: precipitation of warmest quarter.

Species	Predictor variable (% of permutation importance)	Variable set	Reg. multiplier
D. barretti	BIO03 (75.2%), Aridity index (18.4%)	abiotic	2
D. clarki	BIO18 (39%), Clay content (16.5%), BIO01 (15.6%)	all	2
D. columellaris	Elevation (41.9%), BIO03 (34.5%), Aridity index (15.9%)	abiotic	5
D. gayi	BIO18 (44.7%), BIO03 (22.3%), BIO09 (15.1%)	all	5
D. perniger-NE	BIO18 (71%)	abiotic	1
D. perniger-SW	BIO18 (36.2%), Fire frequency (34.7%)	all	0.8
D. rubriceps	BIO02 (30.3%), BIO03 (25%), Fire frequency (15.1%)	abiotic	0.8
D. tamminensis	BIO18 (80.7%)	abiotic	0.8

In most cases, sampling sites were located within the largest contiguous portion of predicted suitable habitat (Fig. 4). Species in southwestern and central Australia (*D. barretti*, *D. clarki*, *D. columellaris*, *D. gayi*, *D. perniger*-SW) showed suitability ranges that overlap or lie exclusively within the arid zone, except *D. tamminensis*, which is endemic to the wheatbelt region (Fig. 4). Suitable ranges of the remaining species from northeastern Australia (*D. perniger*-NE and *D. rubriceps*) span mainly the north-northeastern margins of the arid zone, with the most suitable areas being the northeastern monsoonal tropics and eastern mesic regions (Fig. 4).
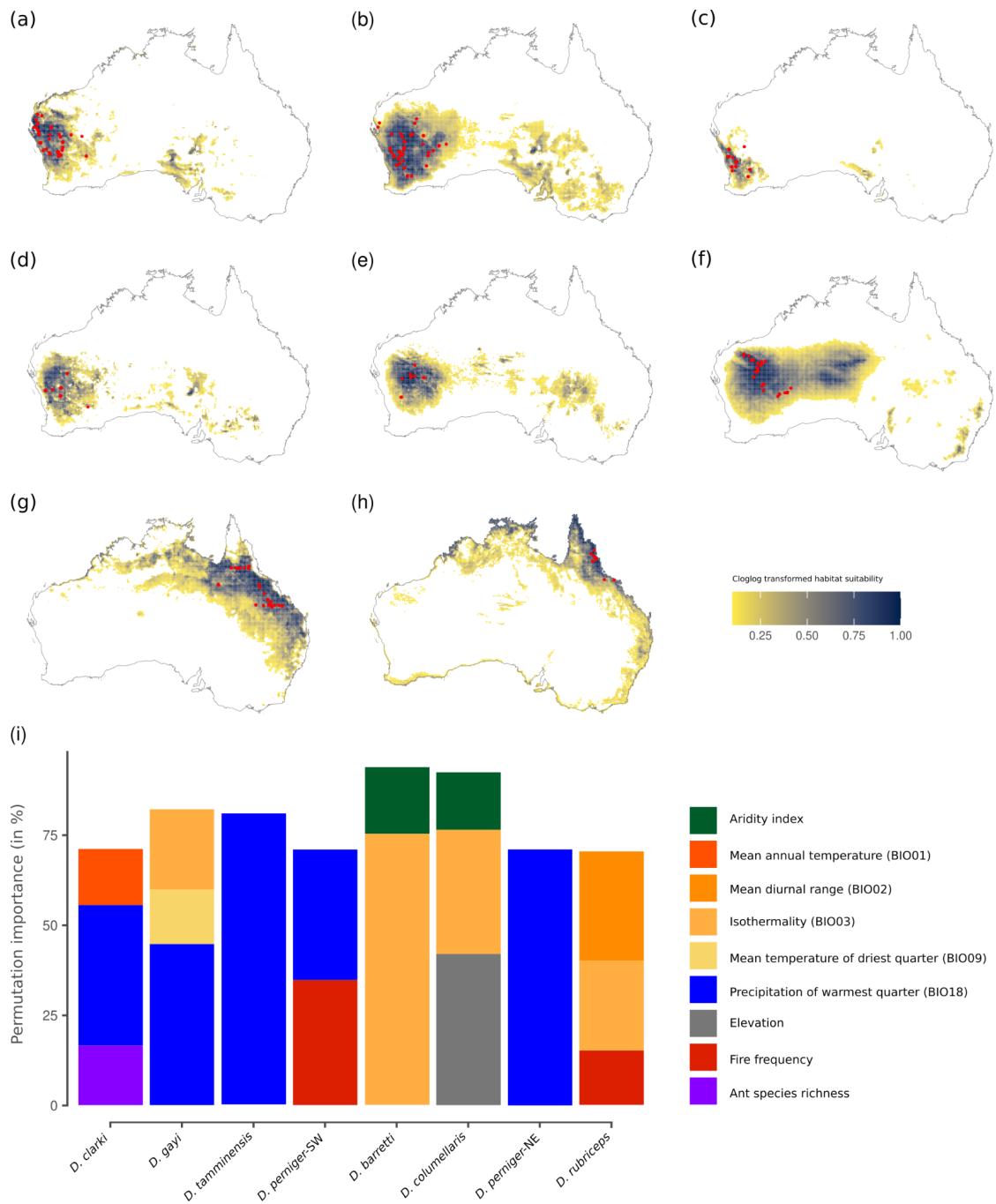
Figure 4 MaxEnt predictions of present-day habitat suitability for eight *Drepanotermes* species with nesting habitats given in parenthesis (subt. = subterranean). (a) *D. clarki* (subt.), (b) *D. gayi* (subt.), (c) *D. tamminensis* (mound), (d) *D. perniger*-SW (subt. + mound), (e) *D. barretti* (subt.), (f) *D. columellaris* (subt. + mound), (g) *D. perniger*-NE (mound), (h) *D. rubriceps* (mound). Red dots indicate georeferenced records for each species. Darker colors represent higher habitat suitability and brighter colors represent lower habitat suitability. (i) Bar chart shows permutation importance (>15%) of predictor variables for each species based on the best model (see also Tab. 1).

Future Habitat Suitability

Present-day ENMs analogous to future habitat models based on the uncorrelated bioclimatic variables (BIO01, BIO02, BIO03, BIO09, and BIO18) recovered larger and more disjunct areas of suitable habitat compared to full ENMs (Fig. 4 and 5). Even so, future habitat gain is predicted to be substantial for most species, particularly within the arid zone. This trend is stronger under the RCP 8.5 scenario than for RCP 2.6 (Fig. 5). *D. perniger*-NE is the only species which shows suitable habitat loss, suggesting range compression toward the coastline of Queensland and New South Wales.
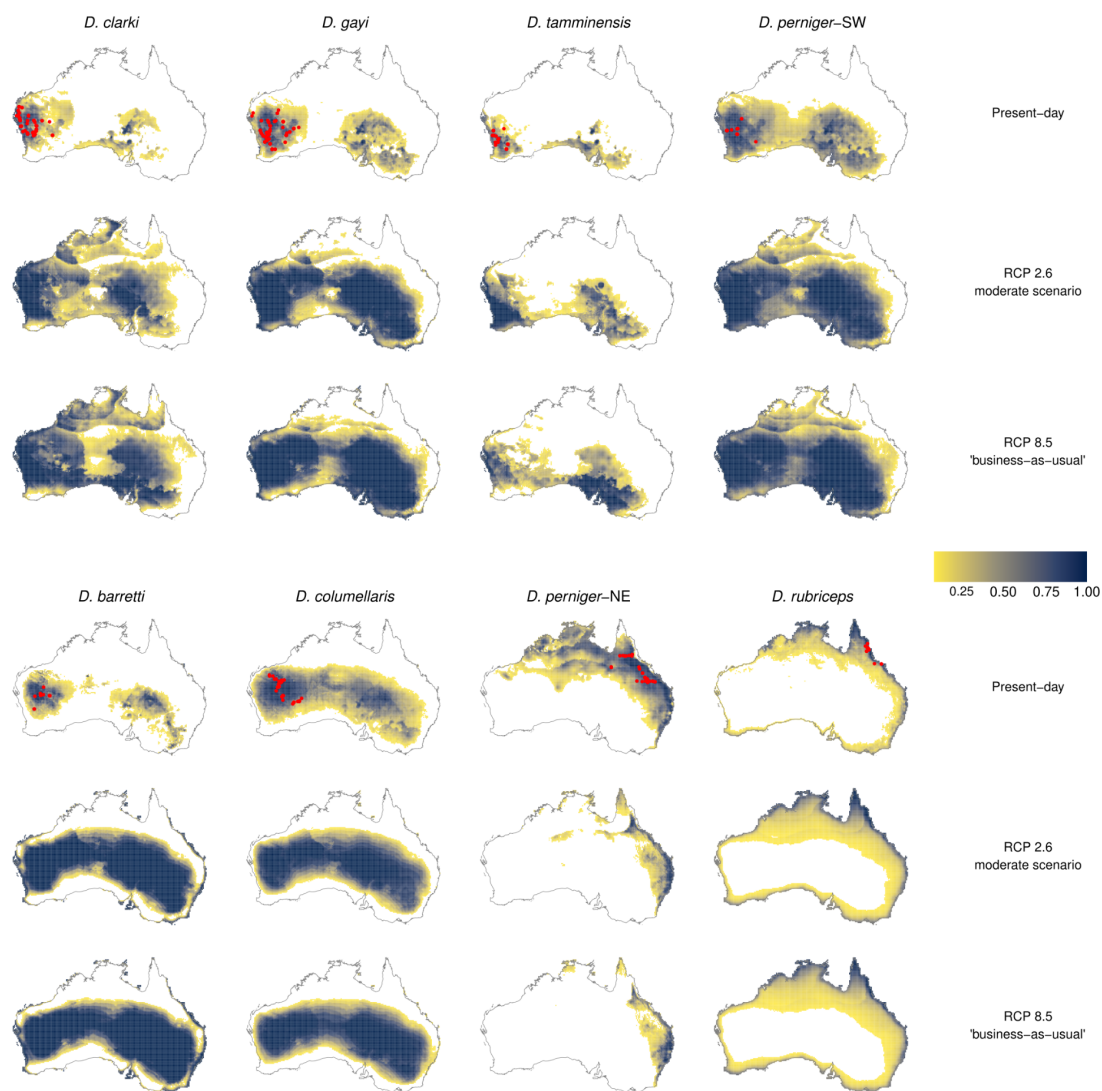
Figure 5　　　MaxEnt predictions of present and future habitat suitability by 2061, based on five bioclimatic variables and two climate-change scenarios. The majority of species show substantial

future habitat gains under both scenarios. Red dots indicate georeferenced records for each species. Darker colors represent higher habitat suitability and brighter colors represent lower habitat suitability.

DISCUSSION

Drepanotermes *Diversity*

Compared to other termite radiations within the last 5 Mya (Bourguignon *et al.* 2015, 2017), *Drepanotermes* are particularly species rich, only surpassed in Australia by *Amitermes* and possibly *Tumulitermes* (Watson and Abbey 1993, Abensperg-Traun and Steven 1997). Species delimitation, using both distance and phylogenetic methods under conservative parameters, indicates that the true diversity of *Drepanotermes* is much greater than the 23 species currently described (Krishna *et al.* 2013). The last major revision of the genus suggested that high morphological variability within described *Drepanotermes* species represents species clusters or intergradations (Watson and Perry 1981), and indeed our data demonstrated sufficient genetic divergence within several described species as to make taxonomic reconciliation with historical morphology-based records impracticable. Interpolating from our species delimitation results to the areas not sampled or dramatically undersampled in this study, including the center of *Drepanotermes* diversity in the Northwest Cape region (Watson and Abbey 1993), we estimate up to 75 to 100 independently evolving lineages (*i.e.* species) within *Drepanotermes*. Despite gaps in coverage of both described species and distributional areas (*e.g.* the Top End or Kimberley region), we are confident that our conservative species delimitation approach does not inflate these estimates.

Patterns of Plio-Pleistocene diversification coincide with Australia's intensifying aridification for many organisms, including plants, insects, and vertebrates (McLeish *et al.* 2007, Rabosky *et al.* 2007, reviewed in Byrne *et al.* 2018). Similarly, *Drepanotermes* radiated in concert with the formation and diversification of arid habitats from the Pliocene onwards (Heimburger *et al.* 2021). This study, covering the most *Drepanotermes* taxa to date, shows considerable species divergence in the past 1 Mya. During this time, dunefields formed across Australia (Fujioka *et al.* 2009, Hesse 2010, 2011,

Pepper and Keogh 2021) leading to habitat fragmentation. Indeed, Australia's ant megadiversity has been attributed to countless isolated refugia brought about by the large-scale movement of desert dunes (Andersen 2016), and a similar explanation has been invoked for lizards of the *Ctenophorus maculatus* species complex, which diverged in concert with dune habitats (Edwards *et al.* 2015). *Drepanotermes* also diversified within the proposed time frame of dune system formation and expansion (Fujioka *et al.* 2009, Fujioka and Chappell 2010), both within and beyond the arid zone. This implies that in addition to habitat fragmentation, which may have been important for speciation processes within the arid zone, other mechanisms must be invoked to explain recent radiation events in regions experiencing less dramatic changes (*e.g.* northern monsoonal tropics).

Watson (1982) proposed that speciation in *Drepanotermes* is mediated by species-specific differences in the timing of annual dispersal flights leading to reproductive isolation of populations, as demonstrated for sympatric *Reticulitermes* (Haverty *et al.* 2003). Resource partitioning may stabilize coexistence of *Drepanotermes* species (Watson 1982), which are often found in sympatric associations (Watson and Abbey 1993). It is currently not known whether interspecific hybridization occurs between Australian harvester termites, although it may occur among other termites (Hartke and Rosengaus 2011, Wu *et al.* 2020). More detailed natural history information, including reproductive strategies, diet, microbial symbionts, and relationships with other taxa will be needed to form a clearer picture of the forces driving *Drepanotermes* diversification within and beyond the arid zone.

Nesting habits and climate-related constraints

Our results indicate that the last common ancestor of *Drepanotermes* most likely lived in subterranean nests. This is consistent with the position of *Drepanotermes* as a crown group within Australian *Amitermes* (Heimburger *et al.* 2021), which are primarily soil-dwellers (Gay 1968, Gay and Calaby 1970). Many early-branching lineages are subterranean and occur near the North-West Cape in Western Australia, the likely origin of the genus (Watson and Perry 1981, Heimburger *et al.* 2021), while most extant mound-builders are found in the monsoonal tropics of northern Australia. Mound-building was acquired several times independently as this genus diversified across the

continent. Parallel evolution of mound-building has been shown before in Australian *Coptotermes* and Nasutitermitinae (Arab et. al. 2017, Lee *et al.* 2017).

We analyzed facultative mound-building as a distinct nesting habit following Watson and Perry (1981), however this may be an artifact of their limited set of morphological characters. Conspicuously, species described as facultative mound-builders (Watson and Perry 1981, Abensperg-Traun and Perry 1998) are characterized by (a) very large ranges (*D. daliensis, D. perniger*), (b) strong geographic variability in nesting habit (*D. columellaris, D. perniger*), or (c) contradictory records between observers (*D. septentrionalis*). Indeed, preliminary examination of "facultatively mound-building" populations of *D. perniger* from Western Australia recovered two very distinct genetic clades with different nesting habits (Sun, Heimburger, and Hartke, unpublished), confirming the long-held view that *D. perniger* is a species complex (Watson and Perry 1981). We believe a rigorous taxonomic revision will show that most species described as facultatively mound-building are actually divergent lineages with distinct nesting habits.

Strong phylogenetic signal, especially in bioclimatic factors, indicates that niches are phylogenetically constrained in *Drepanotermes*. This differs from previous studies on Australian Nasutitermitinae and *Coptotermes*, which found no phylogenetic signal for any abiotic variable and no relationship between abiotic variables and nesting habits (Lee *et al.* 2017, Beasley-Hall *et al.* 2019). However, our findings do support Wijas *et al.* (2022), which demonstrated that nesting habits of Australian termites in general are distributed along a temperature and rainfall gradient and thus subject to climatic controls. It appears therefore likely that the acquisition of mound-building in *Drepanotermes* played a crucial role for the expansion into tropical and mesic regions of Australia.

Drepanotermes mounds vary in size and shape from broad flat mounds with 20 cm peaks to half-meter spheroids or conical mounds with heights approaching 2 m (Watson and Perry 1981, personal observations). It has been suggested that subterranean nests are advantageous for maintaining homeostatic conditions in climates with large diurnal temperature swings, such as the Australian arid zone (Noirot and Darlington 2000, Korb 2003, Wijas *et al.* 2022), which may also explain some of the variation in mound form within *Drepanotermes*. However, beyond such predictable patterns, Australia's climate is exceptionally variable (Nicholls *et al.* 1997) and changes from year-to-year due

to the El Niño-Southern Oscillation (Delage and Power 2020). Tropical cyclones, heat waves, bushfires, droughts, and floods are often accompanied by El Niño-Southern Oscillation events (Forootan *et al.* 2016, Lin *et al.* 2020, Squire *et al.* 2021), and while most of these extremes do not occur every year, they could be critical to the establishment and maintenance of termite colonies (Noirot and Darlington 2000, Korb 2011). Thus mound-building might also be an evolutionary response to climate variability with many extremes (King *et al.* 2017), rather than to long-term climate means (*e.g.* annual precipitation).

Extreme (weather) events can exert a strong selection pressure on organisms and provoke significant evolutionary change, but it is challenging to quantify their impact (reviewed in Grant *et al.* 2017). Interestingly, fire frequency, the only direct measure of an extreme event in our analysis, apparently limits the extent of facultative and obligate mound-building species (*D. perniger*-SW and *D. rubriceps*, respectively). But it was not a significant explanatory factor for *D. tamminensis,* which also builds mounds and is known to live in fire-prone regions (Abensperg-Traun *et al.* 1996), or for other taxa. This may indicate ecological adaptation and thus tolerance to fire. It remains to be tested how the magnitude and frequency of other types of extremes (*e.g.* heat waves, droughts, floods) influence species distribution and nesting habits.

Estimates of phylogenetic signal can be distorted due to incomplete sampling of species and/or taxonomic over-splitting (Losos 2008; but see also Marcondes 2019). In both cases, levels of phylogenetic signal may be inflated because too many ecologically similar species cluster together in reconstructed phylogenies. Nonetheless, our conservative choices in species delimitation and nesting habit attribution give us confidence that the geographic variation of nesting habits reflects the strong selection pressure that climate places on them.

Habitat Suitability in Relation to Predation Pressure and Vegetation Cover

This is the first study addressing the influence of biotic variables on the ranges of Australian termites. Overall, abiotic variables were found to be more important predictors of habitat suitability than the biotic variables we included. Biotic-only models were never the best model, and ENMs calibrated

with both abiotic and biotic variables performed better than ENMs based only on abiotic variables in just 3 out of 8 species. Incorporation of biotic variables generally improves ENM predictions (*e.g.* Cunningham *et al.* 2016, Gherghel *et al.* 2018, Arumoogum *et al.* 2019, Flores-Tolentino *et al.* 2020, Kass *et al.* 2020; but see Silva *et al.* 2014) and biotic factors are associated with termite distribution and activity (Crist 1998, Gosling *et al.* 2016, da Cunha *et al.* 2018, Scholtz *et al.* 2021), so it is unclear whether this is not the case for *Drepanotermes* or whether we have not included the most relevant factors.

Species richness of predators was a dominant factor in only one out of eight species we tested, *D. clarki.* We had expected to see more species (ranges) affected by ants, which are frequent predators of termites in Australia (Holt 1990, Andersen 2007), and other predators such as lizards. Lizard diversity has been related to termite abundance within the arid zone (Pianka, 1989), where termites are their primary food source (Colli *et al.* 2006). However, our results may reflect the fact that colony survival is not at risk in most cases, *i.e.* predation is mainly opportunistic (Abensperg-Traun *et al.* 1991, Tuma *et al.* 2020), even though some specialized termite feeders are known (Abensperg-Traun 1994, Abensperg-Traun and Steven 1997). Of course, high predator richness does not necessarily correspond to high predation pressure, or *vice versa* (Basset 2020). Ants and lizards regularly prey upon dispersing *Drepanotermes* alates (Nutting 1979, Holt 1990, James 1991, Oonincx *et al.* 2015), but both mounds and subterranean nests are fortresses, readily protected by sealing off entrances (Noirot and Darlington 2000), resulting in different effects of predation on potential colony founders than on established colonies (Chouvenc *et al.* 2015). The relationship between termites and ants is complex, and in some cases even mutualistic (Holt and Greenslade 1980, Higashi and Ito 1989, Holt 1990), however predation pressure on foraging parties has clearly led to adaptation on the part of the termites. Forgoing the protection of foraging tunnels (as in *Amitermes*), *Drepanotermes* rely on large numbers of big, heavily scleoritized soldiers and fierce large workers, suggesting an evolutionary arms race between *Drepanotermes* and their predators, especially ants (Hölldobler and Wilson 1990, Chouvenc *et al.* 2021).

Unexpectedly, vegetation did not play a substantial role in predicting habitat suitability. This may be related to methodological limitations: we used broadly generalized vegetation groups, which

cannot completely reflect species-specific associations with plants. *Drepanotermes* clearly influence surrounding vegetation through nest construction and harvesting activity (Hill 1942, Watson and Perry 1981, Walsh *et al.* 2016), and we would expect to see a stronger signal toward particular food resources, such as *Triodia* and *Acacia*. We did consider including ranges for particular plant species, explicitly modeling suitable ranges of plant species (*e.g.* Silva *et al.* 2018) or incorporating existing ENMs or species distribution models of plants (see Hageer *et al.* 2017 for Australian shrubland species) in this study. However, concrete information on the diet of many Australian harvester termites is lacking (Tayasu *et al.* 2002), anecdotal (Watson 1982) or muddled by the multiple evolutionary lineages within currently described species, making the choice of candidate plants difficult and termite trait assignment impossible.

Drepanotermes in an Increasingly Extreme Environment

Future projections of habitat suitability show current ranges remaining habitable despite generally higher temperatures and shifting rainfall patterns, and an increase in suitable habitat for seven of the eight *Drepanotermes* we examined. Only *D. perniger*-NE shows a clear decrease in suitable habitat and its current range becoming unsuitable, more strongly under the "business-as-usual" scenario. Interestingly, its current range is decidedly smaller than the area of suitable habitat because the Top End and Cape York Peninsula constitute two biogeographic regions separated by the Carpentarian Gap (Bowman *et al.* 2010). *D. perniger*-NE occurs east of the Carpentarian Gap, and all other members of the clade (mOTU18-20 and 34) to the west; a pattern found in other plants and animals (Edwards *et al.* 2017, Jobson *et al.* 2017, Pepper *et al.* 2017, Peñalba *et al.* 2019), including clades of *Amitermes laurensis* (Ozeki *et al.* 2007). If mound-building is indeed an adaptation to climate variability, perhaps *D. perniger*-NE can persist in its current location, which is projected to receive more heavy/extreme rainfall alongside higher risk of drought (Kirono *et al.* 2020), and even expand its range down the east coast.

The clearest patterns of potential future habitat gain are found for *D. barretti* and *D. columellaris*. Under both emission scenarios, their projected ranges are largely congruent with

predicted increases of arid conditions on the continent by 2070 (Larkin *et al.* 2020, Fig. S3). Other south-western and central Australian species, *D. clarki*, *D. gayi*, *D. perniger*-SW, and *D. tamminensis*, are predicted to gain even more suitable areas of habitat, but we cannot predict whether they will be able to expand into these areas. For example, the low, almost treeless plateau of the Nullarbor Plain in southern Australia is currently devoid of *Drepanotermes* (Watson and Perry 1981, Watson and Abbey 1993); it is unclear why that is and whether *Drepanotermes* will be able to surmount whatever has been prohibiting their diversification into the Nullarbor.

Rates of expansion into newly suitable habitat will depend on not only dispersal of the termites themselves, but also availability of suitable food sources. Vegetation responses to climate change can lag behind by hundreds of years (Svenning and Sandel 2013), which suggests that *Drepanotermes* will not be limited or assisted by significant changes in vegetation composition in the near future. Termites themselves are generally poor dispersers (Eggleton 2000), and observations of annual dispersal flights in *Drepanotermes* indicate they may fly a couple of kilometers under favorable conditions (Watson and Perry 1981). While the Australian *Amitermes* group to which *Drepanotermes* belongs has undergone rapid diversification and range expansions since their arrival in Australia (Heimburger *et al.* 2021), those expansions must be measured in hundreds of thousands or millions of years, not the mere decades or centuries in which human-mediated climate change is occuring. Barring human-aided dispersal (Eyer *et al.* 2021), termite range expansion cannot keep pace with human-mediated climate change. One bright spot, however, is that termite mounds have been shown to stabilize arid ecosystems (Bonachela *et al.* 2015), so as climate change "winners", they might mitigate some local effects of global warming-induced environmental change for other organisms.

Conclusion

Drepanotermes are key components of many Australian ecosystems, but their natural history is still largely unexplored. Our results suggest that the number of species is much higher than currently known. Pleistocene divergence of many lineages correlates with the expansion of the arid zone,

including the formation of sand dunes and deserts (Pepper and Keogh 2021). Mound-building evolved several times independently, presumably presenting a selective advantage in the face of Australia's exceptionally variable climate. High phylogenetic signal in bioclimatic variables is reflected in distributional patterns of nesting habits along a temperature and precipitation gradient, *i.e.* subterranean nests are more common in arid environments, mounds in hot and moist environments. Present habitat suitability is mainly shaped by abiotic factors, especially bioclimatic variables, but inclusion of biotic factors may increase the predictive power of niche models. For the majority of *Drepanotermes* species in our study, current ranges remain habitable and potential future habitat gains are expected under both moderate and "business as usual" emission scenarios, regardless of nesting habit. *Drepanotermes* can thus be seen as potential climate change "winners", which can stabilize arid ecosystems and may mitigate local effects for some other organisms (Bonachela *et al.* 2015). However, expansion of potential habitat will be more rapid than any diversification this clade has ever experienced, so range expansion will likely lag due to limited dispersal capacities.

III General Discussion

Australia's climate has changed dramatically since the continent's complete separation from Gondwana ~35 Mya (McLoughlin 2001). Its subsequent northward drift changed both southern oceanic circulations and the position of Australia relative to subtropical high pressure cells (Pillans 2018), resulting in increasing aridity and large-scale environmental transformation. This eventually culminated in the development of the arid zone in central Australia (Pepper and Keogh 2021). Today, the arid zone is Australia's largest biome, covering roughly 70% of the continental landmass, and provides habitat for a unique flora and fauna (Byrne *et al.* 2018).

The arid-zone biota was assembled over millions of years and many organisms show genetic impacts of Australia's aridification (Pepper and Keogh 2021). In this thesis, continent-wide genetic sampling was used to disentangle the natural history of the most speciose and diverse group of higher termites in Australia, the Australian *Amitermes* Group (AAG) (**Chapter 1**). Results suggest that Australia's aridification has driven diversity and distributional patterns within the AAG. This is particularly clear in Australian harvester termites, a crown group which diverged from Australian *Amitermes* congruently with expansion of the arid zone. *Drepanotermes* are uniquely adapted to dry conditions and are widespread in semi-arid and arid environments. The evolution of mound-building appears to have facilitated the spread into more humid habitats in Australia (**Chapter 2**).

The arid zone: Origins of the fauna and flora

Arid zone biodiversity has been related to *in situ* diversification in central Australia pre-dating the Miocene and to independent species divergences from mesic ancestors coinciding with intensifying aridification of the Australian continent in the late Miocene and Plio-Pleistocene (Crisp and Cook 2013, Byrne *et al.* 2018). Numerous phylogenetic and phylogeographic studies have found evidence for arid lineages being derived from ancestral mesic groups, *e.g.* in arid-adapted shrubs (Crayn *et al.* 2006), eucalypts (Ladiges *et al.* 2011), *Hakea* (Cardillo *et al.* 2017), *Callistris* (Larter *et al.* 2017), birds (Toon *et al.* 2012, Schweizer *et al.* 2015), geckoes (Brennan *et al.* 2016), mammals (Mitchell *et al.* 2014, Kear *et al.* 2016), and invertebrates (Guzik *et al.* 2009, Owen *et al.* 2017).

Other arid lineages diversified from tropical ancestors, including old endemics with Gondwanan origin (Marin *et al.* 2012, Catullo and Keogh 2014), as well as younger lineages of

tropical Asian origin such as the plant family Atripliceae (Kadereit *et al.* 2010), Bynoe's gecko (Fujita *et al.* 2010), and rodents (Smissen and Rowe 2018). These immigrant taxa arrived in Australia via a northern route from Southeast Asia over the past ~20 million years (Yeates and Cassis 2017), similar to the AAG and several other termite families (Lee *et al.* 2015, Arab *et al.* 2017, Bourguignon *et al.* 2015, 2017, Heimburger *et al.* 2021). 'Stepping-stone' dispersal through the Indo-Australian Archipelago was made possible by shallow sea levels, numerous paleo-islands, and extensive carbonate reefs (Hall 1998, Metcalfe 2005) which formed after the collision of the Southeast Asian and Australian Plates 25 to 20 Mya (Hall 2002). Although far from constituting a permanent land connection between the two continents (Lohman *et al.* 2011), the emergent land masses undoubtedly facilitated the migration of plant and animal taxa to Australia (Morley 2002, Yeates and Cassis 2017). Using the largest phylogenomic data set of the AAG to date, this thesis provides conclusive evidence that the AAG is of Asian origin and that ancestral tropical lineages diversified into the developing arid zone during the late Miocene.

While the arid zone acts mainly as a sink of diversification, *i.e.* arid lineages deriving from mesic and tropical ancestors, diversification also occurs in the opposite direction (McLean *et al.* 2014, Brennan and Oliver 2017). For example, Toon *et al.* (2015) showed that hummock grasses of the genus *Triodia* evolved in the arid zone and diversified into northern savannah and southwestern mesic environments over time. A similar pattern can be observed in the radiations of the crown groups *Drepanotermes* and AG2 (**Chapter 1** and Heimburger *et al.* 2021), in which both mesic and tropical lineages diversified from arid ancestors in the Plio-Pleistocene. Phylogeographic analysis supports the idea that *Drepanotermes* radiated from north-western Australia across the continent (Watson and Perry 1981). The other crown group, AG2, apparently evolved at the interface of the arid zone and the monsoonal tropics, followed by divergence and diversification of lineages into tropical and mesic environments, as well as some movements back into the arid zone. Similar diversification patterns have been observed in the trapdoor spider genera *Aname* (Rix *et al.* 2021) and *Conothele* (Huey *et al.* 2019).

This thesis contributes substantially to our understanding of the biogeographic history of the AAG, which has not only been shaped by frequent biome shifts and *in situ* diversification, but also by vicariance. Many arid zone taxa show patterns of allopatric distributions along major geophysical barriers such as the Nullarbor Plain in southern Australia (Cracraft 1991, Crisp and Cook 2007, Nge *et al.* 2021), and the Carpentarian Gap in the northeast (Ozeki *et al.* 2007), both of which also appear to have structured the distribution of AAG taxa (Watson and Perry 1981, Watson and Abbey 1993, Ozeki *et al.* 2007). So far, the inhospitable, almost treeless Nullabor has only been inhabited by a handful of termite species (Abensperg-Traun and Steven 1997) including *Amitermes* (Watson and Abbey 1993), but ecological niche modeling in *Drepanotermes* suggests that this may change in the future under the impact of global climate change (**Chapter 2**).

Diversification in response to late Cenozoic climate change

Late Cenozoic climate change has shaped diversity patterns of Australian biota (Toon *et al.* 2015, Couzens and Prideaux 2018, Thornhill *et al.* 2019, Renner *et al.* 2020), including invertebrates (Braby and Pierce 2006, Chenoweth and Schwarz 2011, Kayaalp *et al.* 2013, Toussaint *et al.* 2015, Rix *et al.* 2021). However, diversification dynamics in Australian termites have remained virtually unexplored (but see Lee *et al.* 2017) despite their ubiquity and key ecological roles (Abensperg-Traun *et al.* 1995, Evans *et al.* 2011, Clement *et al.* 2021). This thesis provides the first empirical evidence for rapid diversification of a higher termite group on the Australian continent. Interestingly, the few studies on diversification patterns in termites (Davies *et al.* 2009, Legendre and Condamine 2018, Condamine *et al.* 2020, Pie *et al.* 2021) find that most taxa evolved rather constantly over time, with few instances of increasing speciation (*i.e.* radiation) in the recent past (<20 Mya), namely *Macrotermes* and some lineages of Nasutitermitinae (Pie *et al.* 2021).

While some astonishing adaptive radiations have been triggered by the initial formation of the arid zone (Rabosky *et al.* 2007, Brennan and Oliver 2017), this was not the case for the AAG. Their diversification rates appear to have remained stable during the late Miocene, followed by rapid diversification from the end of the early Pliocene and a subsequent decline to the present day. Such a pattern is often viewed as evidence of adaptive radiation (Harmon *et al.* 2003) or diversity-dependent

diversification (Phillimore and Price 2008), in which speciation accelerates in response to novel resources/environments and slows down as niches fill (Rundell and Price 2009). However, alternative biological causes may also explain slowdowns in diversification over time, including non-random extinctions (Condamine *et al.* 2013, Moen and Morlon 2014, Toussaint *et al.* 2015), geographic speciation (Losos and Glor 2003, Pigot *et al.* 2010, Givnish 2015), or protracted speciation (Etienne and Rosindell 2012).

It is evident from the fossil record that many, if not all, species will eventually become extinct, as they cannot keep pace with environmental change (Condamine *et al.* 2013, Quental and Marshall 2013). This results in non-random extinctions as, for example, Australian diving beetles experienced due to disappearing freshwater habitats during Pleistocene aridification (Toussaint *et al.* 2015). In comparison, the extinction rate of the AAG remained near zero over time, as is generally the case in termites (Legendre and Condamine 2018). A rigorous validation relating the slowdown to declining diversity (Quental and Marshall 2011) is currently not possible because there are no known fossils related to the AAG.

The importance of geographic speciation in slowing diversification has been emphasized by several authors (Moen and Morlon 2014, Givnish 2015, Czekanski-Moir and Rundell 2019). This may be more generally related to the ability of taxa to reach and colonize new territories; Pigot and Tobias (2013) have shown that poor dispersal abilities of furnariid birds constrained range expansions after allopatric speciation events, which resulted in lower speciation rates over time. Likewise, the AAG, and termites in general, are poor dispersers (Eggleton 2000). This, together with the concentration of allopatric speciation events, likely caused by range fragmentation during the Plio-Pleistocene, suggests that geographic speciation may have played a role in slowing diversification.

Speciation takes time (Avise 1999), but phylogenies can only roughly capture historical population splits, regardless of whether lineages have established complete reproductive isolation (Rosindell *et al.* 2010). As a consequence, recent speciation in populations often goes undetected, leading to the exclusion of branching events closest to the tips of a tree. This can result in reconstructed phylogenies which suggest decreasing present-day diversification rates attributed to diversity-dependent diversification (Etienne and Rosindell 2012).

These examples demonstrate how diversification patterns can be shaped by varying factors and caution against overly simplistic explanations. However, multiple lines of evidence, including a lineage-through-time plot, BAMM inferences, and model selection procedures (**Chapter 1**), suggest that the AAG followed a diversity-dependent pattern. This most likely resulted from new opportunities arising from expansion of the arid zone and C_4 grasslands during the Plio-Pleistocene (Byrne *et al.* 2008, Andrae *et al.* 2018, Pepper and Keogh 2021).

Mound-building: An adaptation to climate variability?

Termite mounds are some of the most intriguing structures built by invertebrates (Laidre *et al.* 2021). They can rise to a couple of meters in height (Korb 2011) and be inhabited by hundreds of thousands of individuals (Porter and Hawkins 2001). The function and structure of mounds has received much attention in recent years (Korb 2003, Ocko 2017, Claggett *et al.* 2018, Oberst *et al.* 2020), as has their role in stabilizing ecosystems in the face of global climate change (Bonachela *et al.* 2015), yet the evolution of this fascinating nesting habit remains enigmatic. It is likely that a complex interplay between multiple selective pressures (*e.g.* environmental factors, predator-prey relationships) has shaped the evolution of mound-building, as is often the case with such highly complex traits (Rossato *et al.* 2018).

Previous studies on Australian termites found no evidence that abiotic factors (*e.g.* temperature, rainfall, soil conditions.) played a crucial role in the acquisition of mound-building (Lee *et al.* 2017, Beasley-Hall *et al.* 2019). They concluded that biotic factors, *e.g.* interspecific competition, or the evolution of separate-piece nesting (see General Introduction: Nesting habits of termites) are more relevant factors, but results on *Drepanotermes* suggest otherwise. Most mound-building *Drepanotermes* are found in humid environments, while their subterranean congeners live under more arid conditions. This distributional pattern is supported by the more general findings of Wijas *et al.* (2022) using a continental-scale database including all Australian termite genera. They found that nesting habits are distributed along a temperature and rainfall gradient on the Australian continent, suggesting that climate exerts a strong selective pressure on nesting strategy (Wijas *et al.* 2022). Likewise, bioclimatic variables contributed disproportionately to ecological niche models of

Drepanotermes taxa, while the inclusion of biotic factors like predators and vegetation cover only marginally improved the calibrations (**Chapter 2**).

Termites are prone to desiccation (Collins 1969), so proper regulation of nest conditions, *i.e.* temperature and humidity, is of paramount importance to them. While living underground has been suggested to buffer against large diurnal temperature variation in arid landscapes (Noirot and Darlington 2000, Wijas *et al.* 2022), mounds are considered an adaptation to the rainy season and flooding in tropical regions, as the colony can shelter in the upper parts of the mound and store food reserves (Korb 2003, Ozeki *et al.* 2007). Moreover, certain mound shapes appear to be selectively favored under particular local environmental conditions (Lee and Wood 1971, Ozeki *et al.* 2007). For example, Ozeki *et al.* (2007) found that wedge- and dome-shaped mounds of *Amitermes laurensis* are associated with ill-drained and well-drained habitats, respectively. The wedge-shaped mounds have a higher surface to volume ratio which allows them to dry faster after heavy rainfall/flooding, which increases mound stability and protects stored food from spoiling (Ozeki *et al.* 2007).

This also suggests that mound-building may not simply be an adaptation to heavy rainfall but rather to frequent, more or less unpredictable, extreme events. Australia's climate is exceptionally variable from year-to-year, mostly driven by the El Niño-Southern Oscillation (ENSO). ENSO plays a strong role in shaping precipitation and temperature patterns over much of Australia and is known to modulate tropical cyclone activity (Santoso *et al.* 2017, Harris and Lucas 2019). Other extreme events such as heat waves, droughts, floods, and bushfires are also influenced by ENSO (Goddard and Gershunov 2020, Lin *et al.* 2020, Dey *et al.* 2021) and projected to become more intense and/or frequent under global climate change (Cai *et al.* 2020, Karamperidou *et al.* 2020).

Strong and significant phylogenetic signals of bioclimatic variables provide further evidence that species ranges and thus nesting habits are subject to climatic controls (**Chapter 2**). Mounds of *Drepanotermes* are often, but not exclusively, found in seasonally flooded areas (Watson and Perry 1981, personal observations), which makes it likely that they are also adapted to flooding. Pavement nests, on the other hand, rarely rise above ground-level (Watson and Perry 1981, Abensperg-Traun and Perry 1998) and are widespread in the arid zone (Walsh *et al.* 2016). They have a lower surface to volume ratio and thicker walls than aboveground mounds (Watson and Perry 1981), which likely

promotes humidity control under dry and cold conditions. Thus, it is not surprising that mean diurnal range did not show a significant phylogenetic signal (**Chapter 2**), as homeostatic nest conditions are presumably equally well maintained in subterranean and pavement nests of *Drepanotermes* spp. in the arid zone.

Additionally, pavement nests may be selectively favored in situations of fire (see Korb 2011). It is generally assumed that nests below the ground are better protected from direct effects of fire than mounds (Davis *et al.* 2018), as the soil temperature drops significantly with every centimeter of depth, increasing the chances of survival (Bradstock and Auld 1995). To my knowledge, no study has directly compared the impact of fire on nesting habits of *Drepanotermes*. However, Abensperg-Traun *et al.* (1996) showed that populations of mound-building *D. tamminensis* declined markedly following fire, as shown in other mound-building termites (Holt and Coventry 1990), yet they linked this to food shortages and ant predation in the burnt environments rather than to colony death in the fire (Abensperg-Traun *et al.* 1996). My results support Abensperg-Traun *et al.* (1996) in showing that fire (frequency) is not an important factor in predicting the distribution of *D. tamminensis*, suggesting that this species has adapted to fire. Colonies are protected by the hard structure of mounds (Abensperg-Traun and Milewski 1995) and may also take refuge in the underground chambers (extending up to 20 cm deep, Watson and Perry 1981) during fire. However, my results indicate that the distribution of one obligate and one facultative mound-building *Drepanotermes* has been limited by fire, but it is unclear why. Future comparative studies should focus on the relationship between nesting strategy (*i.e.*, subterranean nests, pavement nests, and mounds), nest phenology (height, depth, wall composition, and thickness), and kind of fire regime; grassland fires burn faster but less intensely than bushfires (Bradstock 2010), which presumably results in different selective pressures.

Surprisingly, Wijas *et al.* (2022) found that aboveground mounds were more often associated with lower clay content soils than subterranean nests, while my thesis and other studies showed no such association (Lee *et al.* 2017, Beasley-Hall *et al.* 2018). The dataset of Wijas *et al.* (2022) included 182 of the 258 species in the GBIF database, covering all Australian genera. This and other studies used only specific termite genera, encompassing 8 to 54 taxa. This may be a sample size effect or a bias in the data available to the different studies; Lee *et al.* (2017), Beasley-Hall *et al.* (2018), and

my study include undescribed taxa and collecting notes on nesting habits, which are not in the GBIF database. In addition, definitions of "mound" vary between the studies, in particular the classification of pavement nests.

All in all, Australia's exceptionally variable climate with many extremes clearly exerts a strong selection pressure on nesting habits. The parallel evolution of mound-building in several lineages played a crucial role in the expansion of *Drepanotermes* into warmer and wetter regions of northern Australia; early-branching lineages are mostly subterranean and often occur in northwestern Australia, the putative origin of the genus (Watson and Perry 1981). A comparison between present and future habitat suitability under two different emission scenarios (*i.e.*, moderate and "business-as-usual") revealed continued suitability of current species ranges as well as substantial habitat gains for most studied *Drepanotermes* species, regardless of nesting strategy. Although global climate change is occuring more quickly than *Drepanotermes* can disperse into newly suitable habitat, these ecosystem engineers may buffer their present arid ecosystems against increasing aridification in the future (Bonachela *et al.* 2015).

Synthesis and outlook

This thesis joins the rank of other continent-wide phylogenetic studies which show that Australia's aridification resulted in complex distributional and diversification patterns, *e.g.* in plants (Cardillo *et al.* 2017, Dale *et al.* 2020, Renner *et al.* 2020), animals (Owen *et al.* 2017, Ashman *et al.* 2018, Smissen and Rowe 2018, Roycroft *et al.* 2020, Rix *et al.* 2021), and fungi (Sheedy *et al.* 2016). The AAG diversified through periods of severe climate and environmental change, which helps to predict the potential distribution and diversification of termites in the face of current global climate change. To date, the AAG is the only example of a termite group that has diversified rapidly in Australia. In accordance with recent findings, I demonstrated that nesting habits of *Drepanotermes* are distributed along a climatic gradient, which opens avenues to explore their functional roles in ecosystems.

This study has made a big leap forward in our understanding of the AAG, yet there is still much unexplored. Molecular sequence and genomic data generated in this study has not been fully evaluated, but suggests that there is much undescribed biodiversity within the AAG; preliminary

results suggest the clade may number over 250 species, 2.5 times more than known today. Recently initiated stable isotope analysis of the same colonies in combination with sequencing of the trnL region of the chloroplast genome (Platell 2019) may show promise to detect inter- and intra-specific dietary differences that may help elucidate the ecological role of AAG species. Nonetheless, a greater representation of taxa, particularly from the arid-zone, the Kimberly, and the Northwest Cape regions and more detailed natural history information (*e.g.* reproductive strategies, diet, microbial symbionts) are ultimately required to fully understand the evolutionary history of the AAG.

IV References

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V Supplementaries

Research Chapter 1

__Rapid Diversification of the Australian__ Amitermes __group during late Cenozoic Climate Change__

Mitochondrial Genome Sequencing

Sequences were obtained from a total of 87 AAG samples preserved in 70 - 100 % ethanol or RNA*later*, including samples from our own collections (sampled in 2016 and 2019) and the Australian National Insect Collection (ANIC) (see Table S1).

We used two different sequencing and assembly strategies: (1) long-range PCR followed by deep-amplicon sequencing and (2) ultra-low coverage (1X) whole-genome sequencing (WGS). For the first strategy, whole genomic DNA (gDNA) was extracted from soldier heads using the DNeasy Blood and Tissue extraction kit (Qiagen, Hilden, Germany) following manufacturer's instructions. Long-range PCRs were performed with PrimeSTAR GXL DNA Polymerases (Takara Bio Europe). Initial sequences generated following Bourguignon *et al.* (2015) were used to develop more effective primers for this group using Primer3 version 2.3.7 (Untergasser *et al.* 2012) implemented in Geneious Prime 2020.2.3 (Kearse *et al.* 2012). We used the available mitochondrial genome sequences of Australian *Amitermes* to design two pairs of primers spanning (a) ~8 kb and (b) ~10 kb fragments of the mitochondrial genome to ensure sufficient overlap between fragments. We used following forward and reverse primers: (a) nad1_ter_1 (ATCAAARGGWGTHCGATTMGTYTC) and cox2_ter_2 (TTTGCYCCRCARATYTCWGARCATTG), and (b) cox2_ter_3 (TGGCAGATAAGTGCRBTGGATTTAAG) and 16s_ter_4 (GAAGGGCCGCGGTATTTGACC).

The PrimeStar GXL polymerase (Takara Bio Europe) was used to amplify both fragments in a touchdown PCR procedure. The first 20 iterations were run as follows: the denaturing temperature was set to 98 °C (30 s), the initial annealing temperature of 60 °C (15 s) was gradually decreased to 50 °C with a step of 0.5 °C per cycle, and the elongation temperature was set to 62 °C (10 min). This was followed by 10 iterations of 98 °C (10 s), denaturing temperature, 50 °C (15 s), annealing temperature, and 62 °C (10 min), elongation temperature. The resulting ~8 kb and ~10 kb fragments were mixed in equimolar concentrations and sequenced as paired-end 300 bp reads on an Illumina

MiSeq at the Göttingen Genomics Laboratory (G2L, Germany). Amplicon sequencing reads were quality-trimmed using Trimmomatic (Bolger *et al.* 2014) and assembled with the SPAdes 3.13.0 (Nurk *et al.* 2013) plugin in Geneious Prime using default settings.

For the second strategy, gDNA was extracted from a pool of 4-6 individuals per colony (digestive tracts removed), using the Agencourt DNAdvance Magnetic Bead Kit (Beckman Coulter) or the MagAttract HMW DNA Kit (Qiagen). DNA quality was assessed visually using a 1% agarose gel, quality and concentration were also checked with a Nanodrop 2000 Spectrophotometer (Thermo Fisher Scientific), and a Qubit 2.0 Fluorometer (Thermo Fisher Scientific). Whole genome sequencing (WGS) was performed on a MGISEQ-2000 (Beijing Genomics Institute, BGI, China) resulting in paired-end 150 bp reads. Reads were pre-trimmed by BGI using SOAPnuke1.5.5 (Chen *et al.* 2018).

To retrieve mitochondrial reads from WGS data, we filtered all reads against a customised database of termite whole mitochondrial genome sequences (mitogenomes, Table S1) using Kraken 2 (Wood *et al.* 2019). Filtered mitochondrial reads were assembled with MitoZ version 2.4 (Meng *et al.* 2019) using the 'all' module for paired-end data with default settings (read length: 150 bp, insert size: 300 bp). The resulting mitogenomes were visually checked in Geneious Prime. Unresolved residues and gap characters were manually corrected and the MITOS web server was used for annotation (Bernt *et al.* 2013).

Control regions of mitogenomes were omitted, as they are generally poorly assembled with short reads due to their highly repetitive character. Each gene was aligned individually using the Muscle algorithm (Edgar 2004) implemented in Geneious Prime with default settings. Protein-coding genes were aligned as codons. Although, there was no evidence for saturation at third codon positions of protein-coding genes (NumOTU = 32, Iss = 0.265, Iss.cAsym = 0.554) using Xia's method in DAMBE v.7.2.4 (Xia 2018), a test for compositional homogeneity using p4 (Foster 2004, https://github.com/pgfoster/p4-phylogenetics) detected heterogeneity among sequences at the third codon position (chi-square = 1332.07, df = 372, p < 0.0001). Therefore, we excluded those third codon positions from all further analyses.

Genetic Distances and Phylogenetic Relationships

Principal Coordinates Analysis (PCoA) was used to visualize genetic (dis)similarity among AAG sequences. Thus, we excluded non-*Amitermes* sequences and *Amitermes* sequences from outside Australia from the final concatenated sequence alignment. SNPs were called with the R package 'adegenet' ver. 2.1.1 (Jombart 2008, Jombart and Ahmed 2011) using R version 3.6.3 (R Core Team 2020). The PCoA was performed in R with vegan ver. 2.5-6 (Oksanen *et al.* 2019).

The final concatenated sequence alignment was analyzed in a maximum likelihood framework using IQ-TREE ver. 2.0.6 (Minh *et al.* 2020). We used the implemented algorithm of PartitionFinder (Lanfear *et al.* 2012) to search for the best-fitting partitioning scheme, which increases model fit by reducing overparameterization. The model selection procedure was immediately followed by tree reconstruction ('-MFP+MERGE' command). We performed 1000 replicates each for both ultrafast bootstraps (ufBS) ('-bb' command) and SH-aLRT tests ('-alrt' command). Nodes were classified as "robust", if recovered support values for SH-aLRT/ufBS were ≥ 75 %.

To date our phylogeny, we used four termite fossils as internal calibrations (see Table S2): (1) †*Nanotermes isaacae*, (2) †*Reticulitermes antiquus,* (3) †*Microcerotermes insularis* and (4) †*Amitermes lucidus.* †*Nanotermes isaacae* is the oldest known Termitidae fossil and at least 47.8 million years old (Engel *et al.* 2011), we used it to calibrate the Termitidae + sister group. †*Reticulitermes antiquus* is known from Baltic amber (Engel *et al.* 2007) (minimum age of 33.9 million years) and likely represents a stem group *Reticulitermes* according to Bucek *et al.* (2019), so we used it to calibrate *Reticulitermes* + sister group. (3) †*Microcerotermes insularis* and (4) †*Amitermes lucidus* are both known from Dominican amber (minimum age of 13.8 million years) and their generic assignment is clearly established (Krishna and Grimaldi 2009). The fossil calibrations were implemented as exponential priors using the aforementioned minimum fossil ages as reported on the Paleobiology Database (www.paleobiodb.org, accessed 30 July 2020) as minimum age constraints. Soft maximum bonds (97.5 % probability) were deliberately chosen to be very old (Table S2), because the fossil record of termites is highly fragmentary, which can lead to underestimated node ages (Ho and Philips 2009).

For each partition of the final concatenated sequence alignment, we used the bModelTest package (Bouckaert and Drummond 2017) to average over all transition/transversion split models (31

different models in total, see Bouckaert and Drummond 2017) implemented in BEAST 2.6.1 (Bouckaert *et al.* 2019) using reversible jump Markov Chain Monte Carlo (rjMCMC). This approach takes into account uncertainty in the model selection process and subsequent bias in estimates based on single models (Bouckaert *et al.* 2017). In all analyses, we used an uncorrelated lognormal relaxed clock model of rate variation across branches (Drummond *et al.* 2006) and a birth-death speciation process as tree prior.

We performed three independent MCMC runs, sampling tree and parameter values every 25,000 steps over a total of 500 million generations. Convergence and effective sample sizes were checked with Tracer v1.7.1. (Rambaut *et al.* 2018), with a quarter of samples removed as burn-in. MCMC runs were combined with LogCombiner v2.6.2 (Drummond and Rambaut 2007) and a maximum-clade-credibility tree was obtained using TreeAnnotator v2.6.0.

Supplementary Figure S1.   Maximum likelihood tree inferred with IQ-TREE ver. 2.0.6. The AAG is indicated by the grey box, with *Drepanotermes* and AG2 in black boxes. Nodes are labelled with SH-aLRT/ufBS values.
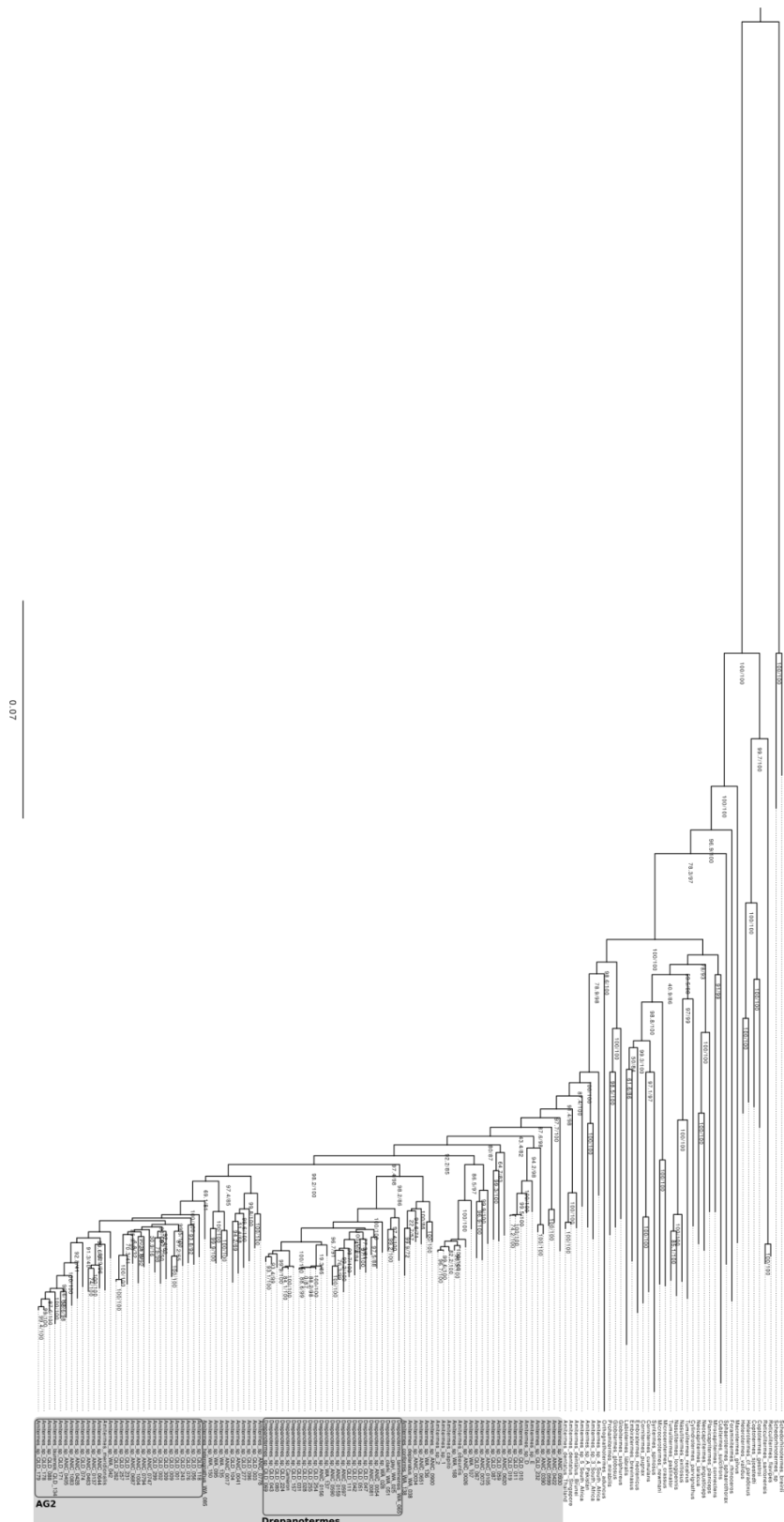
Supplementary Figure S2. Bayesian phylogenetic chronogram inferred with BEAST 2.6.1. The AAG is indicated by the grey box, with *Drepanotermes* and AG2 in black boxes. The scale bar is given in millions of years. Node bars represent the 95% credibility intervals of node-time estimates. Nodes are labelled with posterior probabilities.
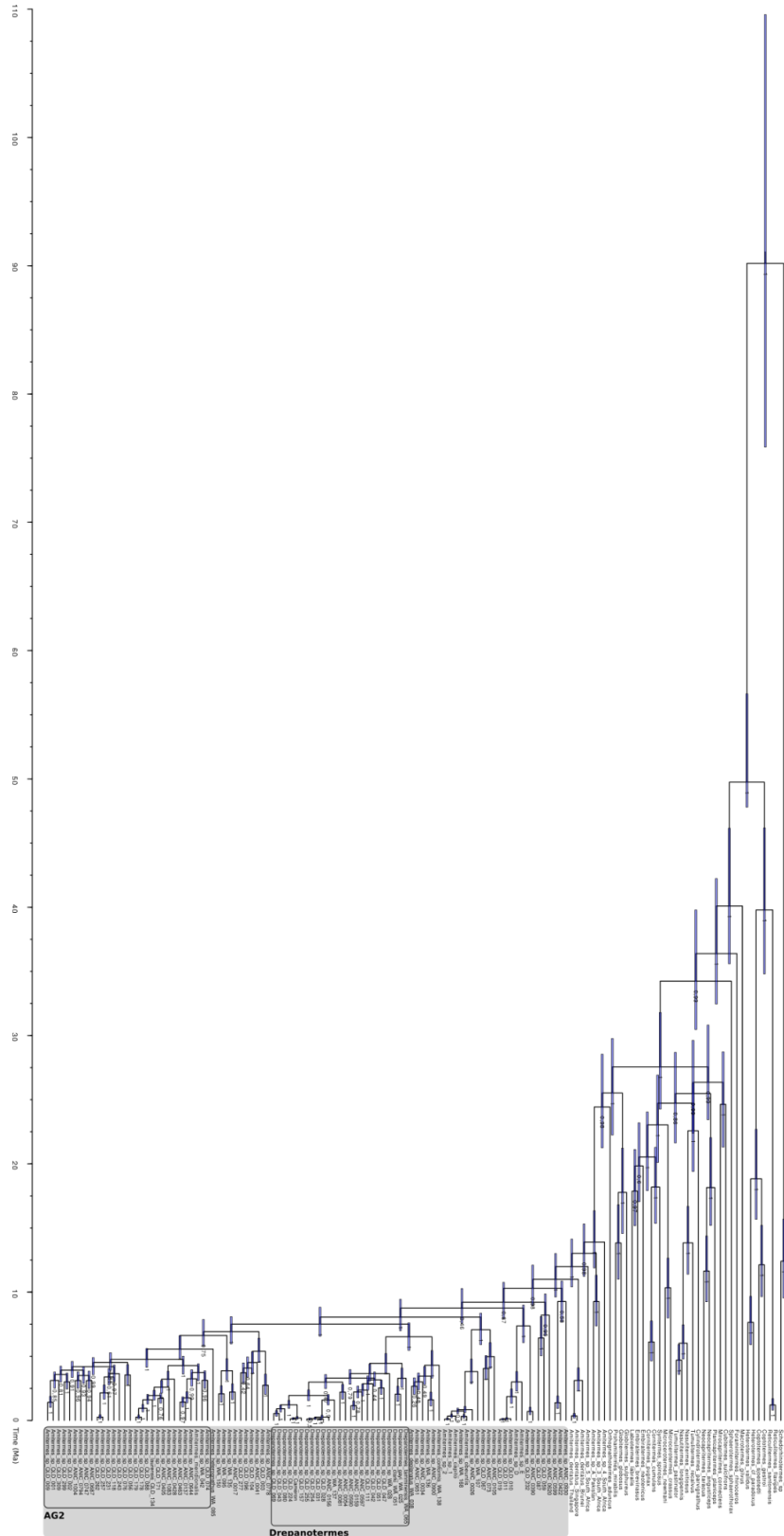
Supplementary Figure S3. Ancestral range reconstruction based on (a) DEC and (b) BAYAREALIKE models using BioGeoBEARS. Relative probabilities of ancestral areas are shown in pie charts at nodes. Colored squares identify biomes: S, mesic south-western zone, A, arid zone, M, monsoonal tropics, E, mesic 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.
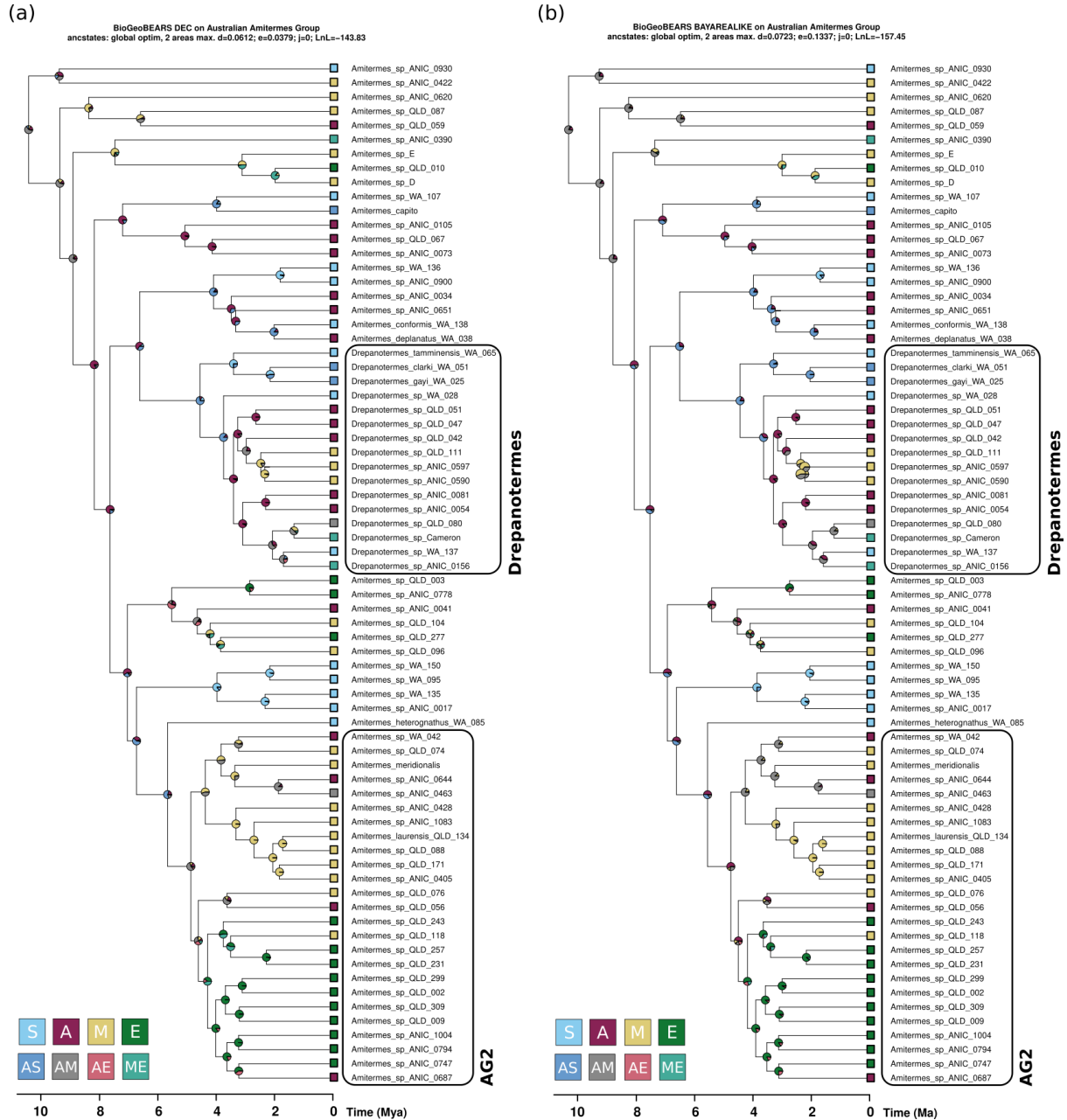
Supplementary Figure S4. Frequency histogram of AICc values of DEC, DIVALIKE, and BAYAREALIKE summarized from 100 posterior trees. The position of the MCC tree is indicated by a colored point.
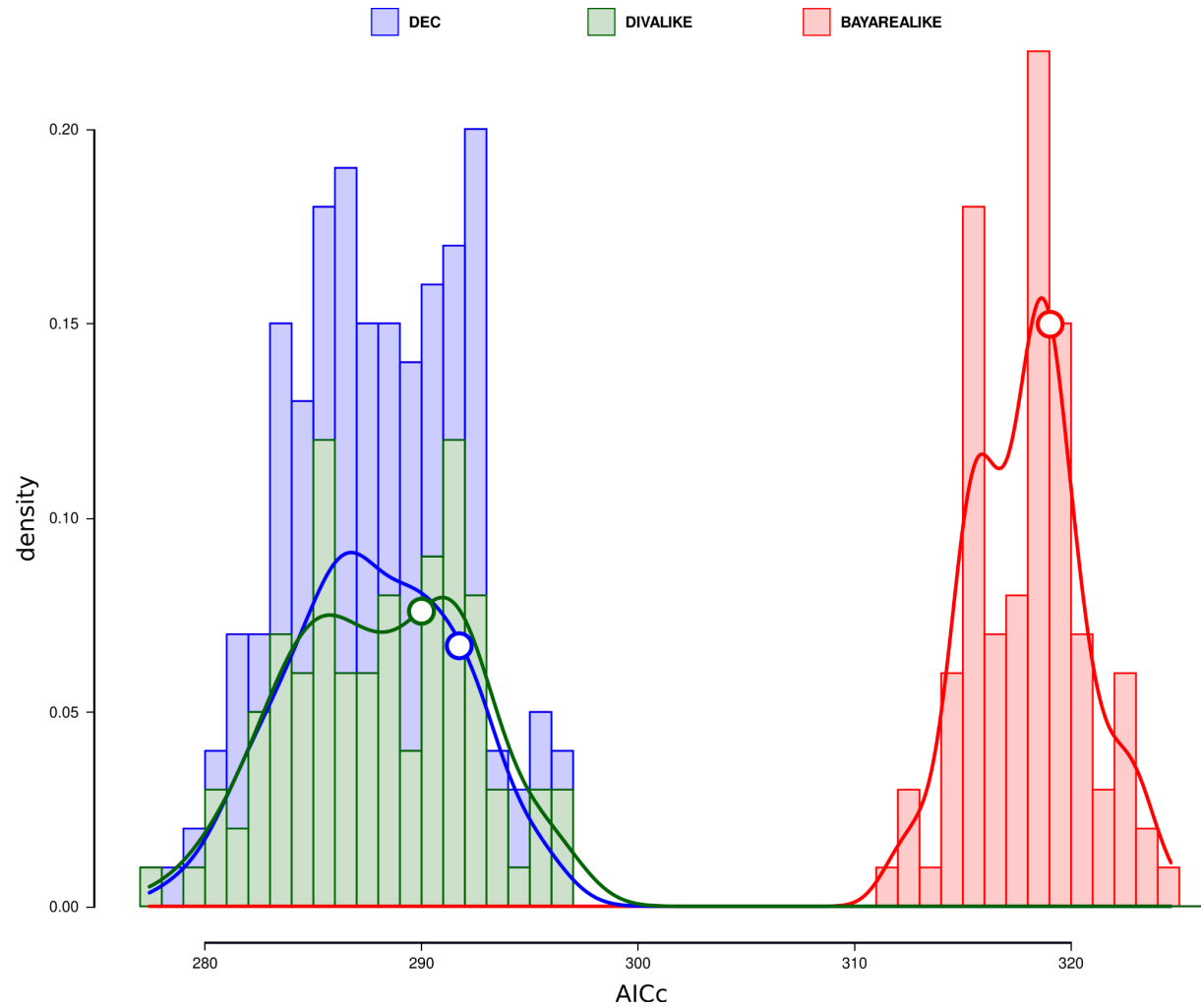
Supplementary Figure S5. Diversification pattern of the AAG inferred with BAMM 2.5.0. (a) The best-fitting run showed no rate shift(s) in diversification. Warmer colors denote faster rates of diversification. Numbers at nodes indicate the number of rate shifts tested for the 100 posterior trees. Ninety-eight trees showed no rate shift, while two trees showed one rate shift (red arrow indicates location of rate shift) after computing the best shift configuration. Inset plot shows the mean diversification rate and mean extinction rate in blue and red lines, respectively. (b) Plots depict the most likely distinct shift configurations for the best-fitting run (see Table S5), gray circles denote locations of rate shifts for each distinct shift configuration.
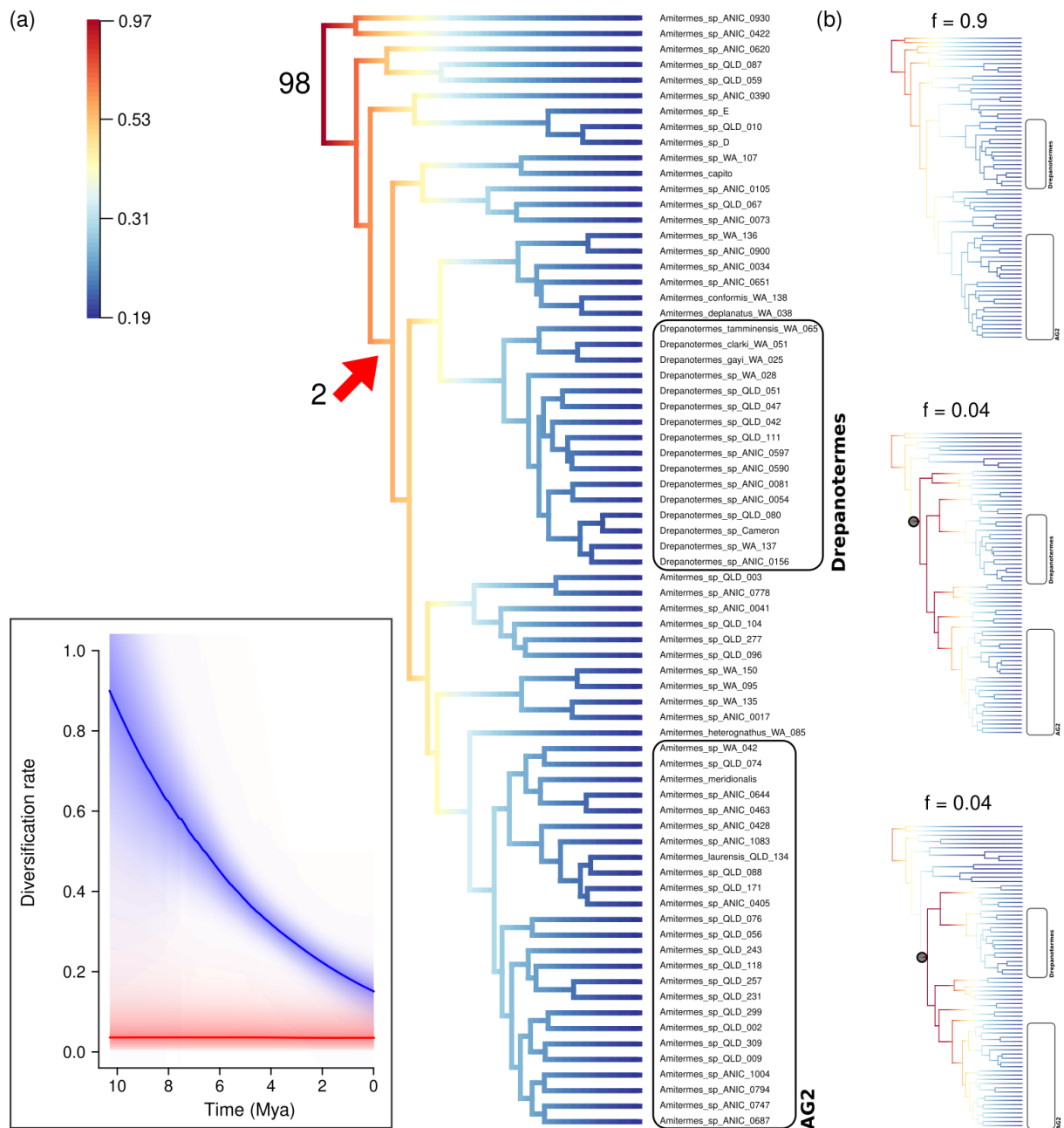
Supplementary Tables

Supplementary Table S1.   Summary of sample information, including sample ID, collection locality, GenBank accession numbers, sequencing platform, and PCoA group. Sequences used for the customized mitochondrial database in Kraken2 are indicated by an asterisk.

Species	Sample ID	Collecting locality	Latitude	Longitude	Reference	Accession Number	Sequencing platform (read length)	PCoA group
Amitermes capito*		Western Australia, Australia			Bourguignon *et al.* 2017	KY224432		AG1
Amitermes dentatus*		Brunei, Asia			Bourguignon *et al.* 2017	KY224593		
Amitermes dentatus*		Singapore, Asia			Bourguignon *et al.* 2017	KY224549		
Amitermes dentatus*		Thailand, Asia			Bourguignon *et al.* 2017	KY224513		
Amitermes meridionalis*		Darwin, Northern Territory, Australia			Bourguignon *et al.* 2017	KY224487		AG2
Amitermes obeuntis*		Western Australia, Australia			Bourguignon *et al.* 2017	KY224650		AG1
Amitermes sp 1*		Western Australia, Australia			Bourguignon *et al.* 2017	KY224629		AG1
Amitermes sp 2*		Western Australia, Australia			Bourguignon *et al.* 2017	KY224602		AG1
Amitermes sp 3*		South Africa, Africa			Bourguignon *et al.* 2017	KY224581		
Amitermes sp 4*		South Africa, Africa			Bourguignon *et al.* 2017	KY224426		
Amitermes sp 5*		South Africa, Africa			Bourguignon *et al.* 2017	KY224528		
Amitermes sp A*		Pakistan, Asia			Bourguignon *et al.* 2017	KY224621		
Amitermes sp D*		Cairns, Queensland, Australia			Bourguignon *et al.* 2017	KY224695		AG1
Amitermes sp E*		Cairns, Queensland, Australia			Bourguignon *et al.* 2017	KY224564		AG1
Drepanotermes sp*	Cameron	Queensland, Australia			Cameron *et al.* 2012	JX144938		DRE
Amitermes sp	ANIC_0017	Western Australia, Australia	-30.2	116		MZ008479	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0026	Western Australia, Australia	-29.7	116.2		MZ008480	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0034	Western Australia, Australia	-28.1	117.8		MZ008481	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0041	Western Australia, Australia	-27.4	117.9		MZ008482	MGISEQ-2000 (150 bp)	AG1
Drepanotermes sp	ANIC_0054	Western Australia, Australia	-26	118.7		MZ008483	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	ANIC_0073	Western Australia, Australia	-23.2	119.5		MZ008484	MGISEQ-2000 (150 bp)	AG1
Drepanotermes sp	ANIC_0081	Western Australia, Australia	-21.7	118.8		MZ008485	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	ANIC_0105	Western Australia,	-19.8	121.1		MZ008486	MGISEQ-2000 (150 bp)	AG1

		Australia					
Amitermes sp	ANIC_0137	Western Australia, Australia	-18.7	126.2	MZ008487	MGISEQ-2000 (150 bp)	AG2
Drepanotermes sp	ANIC_0156	Western Australia, Australia	-15.8	128.8	MZ008488	MGISEQ-2000 (150 bp)	DRE
Drepanotermes sp	ANIC_0159	Northern Territory, Australia	-16.1	129.2	MZ008489	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	ANIC_0390	Queensland, Australia	-17.6	145.4	MZ008490	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0405	Queensland, Australia	-17.9	144.9	MZ008491	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	ANIC_0422	Queensland, Australia	-18.3	143.4	MZ008492	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0428	Queensland, Australia	-18.2	142.9	MZ008493	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	ANIC_0463	Queensland, Australia	-17.9	139.3	MZ008494	MGISEQ-2000 (150 bp)	AG2
Drepanotermes sp	ANIC_0590	Northern Territory, Australia	-14.7	132.7	MZ008495	MGISEQ-2000 (150 bp)	DRE
Drepanotermes sp	ANIC_0597	Northern Territory, Australia	-14.7	132.7	MZ008496	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	ANIC_0599	Northern Territory, Australia	-15.3	133.1	MZ008497	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0620	Northern Territory, Australia	-16.9	133.4	MZ008498	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0644	Northern Territory, Australia	-21	134.2	MZ008499	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	ANIC_0651	Northern Territory, Australia	-23.1	133.7	MZ008500	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0687	Southern Australia, Australia	-28.1	135.8	MZ008501	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	ANIC_0747	New South Wales, Australia	-33.5	145.5	MZ008502	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	ANIC_0778	Queensland, Australia	-27.6	152.9	MZ008503	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0794	Queensland, Australia	-24.3	146.7	MZ008504	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	ANIC_0900	Western Australia, Australia	-28.7	115.2	MZ008505	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_0930	Western Australia, Australia	-33.3	115.8	MZ008506	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	ANIC_1004	New South Wales, Australia	-34.4	147.6	MZ008507	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	ANIC_1083	Queensland, Australia	-12.6	143.4	MZ008508	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_001	Queensland, Australia	-26.5	151.8	MZ008509	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_002	Queensland, Australia	-26.5	151.8	MZ008510	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_003	Queensland, Australia	-25.6	151.6	MZ008511	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_009	Queensland, Australia	-23.7	149.6	MZ008512	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_010	Queensland, Australia	-23.7	149.6	MZ008513	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_011	Queensland, Australia	-23.7	149.6	MZ008514	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_019	Queensland, Australia	-23.6	149.2	MZ008515	MGISEQ-2000 (150 bp)	AG1
Drepanotermes sp	QLD_028	Queensland, Australia	-23.5	148	MZ008516	MGISEQ-2000 (150 bp)	DRE

Drepanotermes sp	QLD_031	Queensland, Australia	-23.5	147.8	MZ008517	MGISEQ-2000 (150 bp)	DRE
Drepanotermes sp	QLD_042	Queensland, Australia	-22.3	143	MZ008518	MGISEQ-2000 (150 bp)	DRE
Drepanotermes sp	QLD_043	Queensland, Australia	-21.1	141.1	MZ008519	MGISEQ-2000 (150 bp)	DRE
Drepanotermes sp	QLD_047	Queensland, Australia	-21	140.9	MZ008520	MGISEQ-2000 (150 bp)	DRE
Drepanotermes sp	QLD_051	Queensland, Australia	-20.7	140.5	MZ008521	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	QLD_056	Queensland, Australia	-20.8	140.2	MZ008522	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_059	Queensland, Australia	-20.8	140.2	MZ008523	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_067	Queensland, Australia	-19.9	140.2	MZ008524	MGISEQ-2000 (150 bp)	AG1
Drepanotermes sp	QLD_069	Queensland, Australia	-19.9	140.2	MZ008525	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	QLD_074	Queensland, Australia	-19.1	140.4	MZ008526	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_076	Queensland, Australia	-18.7	140.5	MZ008527	MGISEQ-2000 (150 bp)	AG2
Drepanotermes sp	QLD_080	Queensland, Australia	-18.5	140.7	MZ008528	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	QLD_087	Queensland, Australia	-17.7	141	MZ008529	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_088	Queensland, Australia	-18	141.4	MZ008530	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_096	Queensland, Australia	-18.2	142.3	MZ008531	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_104	Queensland, Australia	-18.2	142.9	MZ008532	MGISEQ-2000 (150 bp)	AG1
Drepanotermes sp	QLD_111	Queensland, Australia	-18.1	144.4	MZ008533	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	QLD_118	Queensland, Australia	-18	144.9	MZ008534	MGISEQ-2000 (150 bp)	AG2
Amitermes laurensis	QLD_134	Queensland, Australia	-17.1	145.1	MZ008535	MGISEQ-2000 (150 bp)	AG2
Drepanotermes sp	QLD_157	Queensland, Australia	-16.5	145.1	MZ008536	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	QLD_171	Queensland, Australia	-15.8	144.7	MZ008537	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_178	Queensland, Australia	-15.7	144.6	MZ008538	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_179	Queensland, Australia	-15.6	144.5	MZ008539	MGISEQ-2000 (150 bp)	AG2
Drepanotermes sp	QLD_224	Queensland, Australia	-19.9	146.6	MZ008540	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	QLD_231	Queensland, Australia	-20.3	146.2	MZ008541	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_232	Queensland, Australia	-20.3	146.2	MZ008542	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_243	Queensland, Australia	-21	146.4	MZ008543	MGISEQ-2000 (150 bp)	AG2
Drepanotermes sp	QLD_254	Queensland, Australia	-21.9	147	MZ008544	MGISEQ-2000 (150 bp)	DRE
Drepanotermes sp	QLD_255	Queensland, Australia	-22.8	147.6	MZ008545	MGISEQ-2000 (150 bp)	DRE
Amitermes sp	QLD_257	Queensland, Australia	-22.8	147.6	MZ008546	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_262	Queensland, Australia	-22.8	147.6	MZ008547	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_277	Queensland, Australia	-23.1	148	MZ008548	MGISEQ-2000 (150 bp)	AG1
Amitermes sp	QLD_299	Queensland, Australia	-25.7	148.7	MZ008549	MGISEQ-2000 (150 bp)	AG2
Amitermes sp	QLD_309	Queensland, Australia	-26.7	150.3	MZ008550	MGISEQ-2000 (150 bp)	AG2
Drepanotermes gayi	WA_025	Western Australia, Australia	-30.3	116.7	MZ008551	Illumina MiSeq (300 bp)	DRE
Drepanotermes sp	WA_028	Western Australia, Australia	-30.3	116.7	MZ008552	Illumina MiSeq (300 bp)	DRE
Amitermes	WA_038	Western	-29.3	117.7	MZ008553	Illumina MiSeq	AG1

deplanatus		Australia, Australia					(300 bp)	
Amitermes sp	WA_042	Western Australia, Australia	-29.3	117.7		MZ008554	Illumina MiSeq (300 bp)	AG2
Drepanotermes clarki	WA_051	Western Australia, Australia	-27.9	117.9		MZ008555	Illumina MiSeq (300 bp)	DRE
Drepanotermes tamminensis	WA_065	Western Australia, Australia	-28.5	115.6		MZ008556	Illumina MiSeq (300 bp)	DRE
Amitermes heterognathus	WA_085	Western Australia, Australia	-29.5	115.4		MZ008557	Illumina MiSeq (300 bp)	AG1
Amitermes sp	WA_095	Western Australia, Australia	-30	116.1		MZ008558	Illumina MiSeq (300 bp)	AG1
Amitermes sp	WA_107	Western Australia, Australia	-31.7	116.5		MZ008559	Illumina MiSeq (300 bp)	AG1
Amitermes sp	WA_135	Western Australia, Australia	-30.8	121.6		MZ008560	Illumina MiSeq (300 bp)	AG1
Amitermes sp	WA_136	Western Australia, Australia	-31.3	119.7		MZ008561	Illumina MiSeq (300 bp)	AG1
Drepanotermes sp	WA_137	Western Australia, Australia	-31.3	119.7		MZ008562	Illumina MiSeq (300 bp)	DRE
Amitermes conformis	WA_138	Western Australia, Australia	-32.4	118.4		MZ008563	Illumina MiSeq (300 bp)	AG1
Amitermes sp	WA_150	Western Australia, Australia	-32.5	118.1		MZ008564	Illumina MiSeq (300 bp)	AG1
Amitermes obeuntis	WA_168	Western Australia, Australia	-32.1	117.8		MZ008565	Illumina MiSeq (300 bp)	AG1
Coptotermes gestroi						Bourguignon *et al.* 2016	NC_030014	
Coptotermes sjoestedti						Bourguignon *et al.* 2016	NC_030020	
Cornitermes cumulans						Bourguignon *et al.* 2017	NC_034086	
Cornitermes pugnax						Bourguignon *et al.* 2017	NC_034055	
Cubitermes sulcifrons						Bourguignon *et al.* 2017	NC_034109	
Cylindrotermes parvignathus						Bourguignon *et al.* 2017	KY224565	
Embiratermes brevinasus						Bourguignon *et al.* 2017	NC_034101	
Embiratermes neotenicus						Bourguignon *et al.* 2017	NC_034930	
Foraminitermes rhinoceros						Bourguignon *et al.* 2017	NC_034116	
Globitermes globosus						Bourguignon *et al.* 2017	NC_034095	
Globitermes sulphureus						Bourguignon *et al.* 2017	NC_034139	
Heterotermes cf *paradoxus*						Bourguignon *et al.* 2016	NC_030023	
Heterotermes validus						Bourguignon *et al.* 2016	NC_030034	
Labiotermes labralis						Herve and Brune, 2017	NC_034929	
Macrotermes gilvus						Bourguignon *et al.* 2017	NC_034110	
Microcerotermes crassus						Bourguignon *et al.* 2017	NC_034036	
Microcerotermes newmani						Bourguignon *et al.* 2017	NC_034021	
Mirocapritermes connectens						Bourguignon *et al.* 2017	NC_034085	

Species	Reference	Accession
Nasutitermes exitiosus	Bourguignon *et al.* 2017	NC_034115
Nasutitermes longipennis	Bourguignon *et al.* 2017	NC_034060
Neocapriterme s angusticeps	Bourguignon *et al.* 2017	NC_034053
Neocapriterme s taracua	Dietrich and Brune, 2016	NC_026116
Orthognathoter mes aduncus	Bourguignon *et al.* 2015	KP026289
Planicapriterm es planiceps	Bourguignon *et al.* 2017	NC_034090
Prohamitermes mirabilis	Bourguignon *et al.* 2017	NC_034039
Reticulitermes flavipes	Cameron and Whiting, 2007	EF206314
Reticulitermes santonensis	Cameron and Whiting, 2007	EF206315
Schedorhinoter mes breinli	Cameron *et al.* 2012	NC_018126
Schedorhinoter mes sp	Wang *et al.* 2019	MK246859
Sphaerotermes sphaerothorax	Bourguignon *et al.* 2017	NC_034103
Syntermes spinosus	Bourguignon *et al.* 2015	KP026293
Tumulitermes pastinator	Bourguignon *et al.* 2017	NC_034098
Tumulitermes recalvus	Bourguignon *et al.* 2017	NC_034051

Supplementary Table S2. Fossils used as internal calibrations for divergence dating with BEAST 2.6.1. Fossil age estimates were taken from the Paleobiology Database (www.paleobiodb.org, accessed 30 July 2020).

Species	Minimum age constraint (Ma)	Calibration group	Soft maximum bound (97.5% probability)	Note on maximum bond
Nanotermes isaacae	47.8	Termitidae + *Reticulitermes* + *Coptotermes* + *Heterotermes*	93.5	*Archeorhinotermes rossi*, first fossil of Rhinotermitidae
Reticulitermes antiquus	33.9	*Reticulitermes* + *Coptotermes* + *Heterotermes*	93.5	
Microcerotermes insularis	13.8	*Microcerotermes* + Syntermitinae	47.8	
Amitermes lucidus	13.8	Amitermes + Globitermes + Orthognathotermes+ Prohamitermes	47.8	*Nanotermes isaacae*, first fossil of Termitidae

Supplementary Table S3.   AAG taxa included in ancestral range reconstruction. Biogeographical distribution in the four major biomes given by presence (1) or absence (0). Biomes are abbreviated as follows: S, mesic south-western zone, A, arid zone, M, monsoonal tropics, E, mesic eastern zone. Sequences pruned from the best-time calibrated tree are given with sample ID (see Table S1) after their corresponding species.

Species	Sample ID	Pruned sequences	S	A	M	E
Amitermes capito		*Amitermes* sp 1, *Amitermes* sp 2, *Amitermes obeuntis*, WA_168, ANIC_0026	1	1	0	0
Amitermes meridionalis			0	0	1	0
Amitermes sp D			0	0	1	0
Amitermes sp E			0	0	1	0
Drepanotermes sp		QLD_157, QLD_224	0	0	1	1
Amitermes sp	ANIC_0017		1	0	0	0
Amitermes sp	ANIC_0034		0	1	0	0
Amitermes sp	ANIC_0041		0	1	0	0
Drepanotermes sp	ANIC_0054		0	1	0	0
Amitermes sp	ANIC_0073		0	1	0	0
Drepanotermes sp	ANIC_0081		0	1	0	0
Amitermes sp	ANIC_0105		0	1	0	0
Drepanotermes sp	ANIC_0156	QLD 028, QLD 031, QLD 254, QLD 255	0	0	1	1
Amitermes sp	ANIC_0390	QLD_232	0	0	1	1
Amitermes sp	ANIC_0405		0	0	1	0
Amitermes sp	ANIC_0422	ANIC_0599	0	0	1	0
Amitermes sp	ANIC_0428		0	0	1	0
Amitermes sp	ANIC_0463	ANIC_0137	0	1	1	0
Drepanotermes sp	ANIC_0590	ANIC_0159	0	0	1	0
Drepanotermes sp	ANIC_0597		0	0	1	0
Amitermes sp	ANIC_0620		0	0	1	0
Amitermes sp	ANIC_0644		0	1	0	0
Amitermes sp	ANIC_0651		0	1	0	0
Amitermes sp	ANIC_0687		0	1	0	0
Amitermes sp	ANIC_0747		0	0	0	1
Amitermes sp	ANIC_0778		0	0	0	1
Amitermes sp	ANIC_0794		0	0	0	1
Amitermes sp	ANIC_0900		1	0	0	0
Amitermes sp	ANIC_0930		1	0	0	0
Amitermes sp	ANIC_1004		0	0	0	1
Amitermes sp	ANIC_1083		0	0	1	0
Amitermes sp	QLD_002		0	0	0	1
Amitermes sp	QLD_003		0	0	0	1
Amitermes sp	QLD_009	QLD_001	0	0	0	1
Amitermes sp	QLD_010	QLD_011, QLD_019	0	0	0	1
Drepanotermes sp	QLD_042		0	1	0	0

Drepanotermes sp	QLD_047		0	1	0	0
Drepanotermes sp	QLD_051		0	1	0	0
Amitermes sp	QLD_056		0	1	0	0
Amitermes sp	QLD_059		0	1	0	0
Amitermes sp	QLD_067		0	1	0	0
Amitermes sp	QLD_074		0	0	1	0
Amitermes sp	QLD_076		0	0	1	0
Drepanotermes sp	QLD_080	QLD_043, QLD_069	0	1	1	0
Amitermes sp	QLD_087		0	0	1	0
Amitermes sp	QLD_088	QLD_178, QLD_179	0	0	1	0
Amitermes sp	QLD_096		0	0	1	0
Amitermes sp	QLD_104		0	0	1	0
Drepanotermes sp	QLD_111		0	0	1	0
Amitermes sp	QLD_118		0	0	1	0
Amitermes laurensis	QLD_134		0	0	1	0
Amitermes sp	QLD_171		0	0	1	0
Amitermes sp	QLD_231		0	0	0	1
Amitermes sp	QLD_243		0	0	0	1
Amitermes sp	QLD_257	QLD_262	0	0	0	1
Amitermes sp	QLD_277		0	0	0	1
Amitermes sp	QLD_299		0	0	0	1
Amitermes sp	QLD_309		0	0	0	1
Drepanotermes gayi	WA_025		1	1	0	0
Drepanotermes sp	WA_028		1	0	0	0
Amitermes sp	WA_038		0	1	0	0
Amitermes sp	WA_042		0	1	0	0
Drepanotermes clarki	WA_051		1	1	0	0
Drepanotermes tamminensis	WA_065		1	0	0	0
Amitermes sp	WA_085		1	0	0	0
Amitermes sp	WA_095		1	0	0	0
Amitermes sp	WA_107		1	0	0	0
Amitermes sp	WA_135		1	0	0	0
Amitermes sp	WA_136		1	0	0	0
Drepanotermes sp	WA_137		1	0	0	0
Amitermes sp	WA_138		1	0	0	0
Amitermes sp	WA_150		1	0	0	0

Supplementary Table S4. Dispersal event counts estimated with biogeographical stochastic mapping (BSM), averaged across 100 BSMs. Rows indicate where the lineage dispersed from and columns where the lineage dispersed to. Standard deviations are given in parentheses. On the margins (in grey), the sum and percentages of events (in parentheses) involving each area are given, in which rows denote the starting point of dispersal, and columns the dispersal destination. Biomes are abbreviated as follows: S, mesic south-western zone; A, arid zone; M, monsoonal tropics; E, mesic eastern zone.

		to				
		S	**A**	**M**	**E**	
	S		3.37 (±1.87)	0	0	3.37 (9%)
from	**A**	9.22 (±1.82)		7.45 (±2.08)	2.88 (±0.9)	19.55 (52.1%)
	M	0	5.81 (±1.75)		4.88 (±1.07)	10.69 (28.5%)
	E	0	1.39 (±0.67)	2.51 (±1.24)		3.9 (10.4%)
		9.22 (24.6%)	10.57 (28.1%)	9.96 (26.6%)	7.76 (20.7%)	37.51 (100%)

Supplementary Table S5. Summary of models compared across a range of Poisson rate priors using BAMM version 2.5.0 and BAMMtools v.2.1. The selected model according to the highest posterior distribution per number of shifts is indicated in bold (see also Figure S5). Note that core shift(s) may occur at different branches in the phylogenetic tree (indicated by asterisk).

		Poisson rate prior									
		0.1	**0.2**	**0.3**	**0.4**	**0.5**	**0.6**	**0.7**	**0.8**	**0.9**	**1**
ESS N shifts		681.3	678.14	681.53	827.79	945.97	1093.51	890.57	945.57	1064.32	1628.1
ESS lnL		721.81	657.35	569.34	702.81	795.11	868.05	649.8	691.94	735.25	1056.45
Posterior distribution per number of shifts	**0**	**0.9**	0.84	0.79	0.71	0.66	0.59	0.62	0.62	0.61	0.62
	1*	0.04	0.06	0.08	0.1	0.12	0.15	0.14	0.14	0.14	0.14
	1*	0.04	0.06	0.07	0.1	0.12	0.15	0.14	0.14	0.14	0.14
	1*	NA	NA	0.03	0.04	0.05	0.06	0.06	0.06	0.06	0.06
	1*	NA	NA	NA	NA	NA	0.05	NA	NA	NA	NA

Research Chapter 2

Historical and future climate change fosters expansion of Australian harvester termites, **Drepanotermes**

S1   Primer Sequences and PCR Protocols

COX2 mtDNA fragments were amplified using the primer pair COX2_Termites_F (modified from Miura *et al.* 2000: 5′-CAG AYA AGT GCD KTG GAT TT-3′) and COX2_Termites_R (modified from Simon *et al.* 1994: 5′-TTT AAG AGA CCA TTA CTT G-3′). PCR was carried out in 25 µl reactions, including 30 ng of gDNA. The PCR mix comprised 12.5 µl 2x SuperHot Mastermix (Genaxxon, Germany), 1.5 µl $MgCl_2$ (25mM), 1 µl of forward/reverse primer (10 ppmol), 1 µl Bovine Serum albumin (BSA) and 6 µL H_20. After activating the polymerase at 95°C for 15 min, the reaction was exposed to 28 cycles of denaturation at 95°C for 30 sec, annealing at 54°C for 60 sec, elongation at 72°C for 60 sec. Final elongation was at 72°C for 10 min.

ITS1 and ITS2 nDNA were amplified in two fragments using primers designed with Primer3 (Rozen and Skaletsky 2000) implemented in Geneious Prime 2021.1.1 (Kearse *et al.* 2012). ITS1 was amplified with ITS_F (5′-ATG CCC GAA CTT GAT CAT TT-3′) and ITS_5.8S_R (5′-GAA ACG TCG ATG TTC ATG T-3′) and ITS2 with ITS_R (5′-TGC TTA AAT TCA GCG GGT A-3′) and ITS_5.8_F (5′-AGG ACA CAT GAA CAT CGA-3′). PCR was carried out in 25 μl reactions, including 30 ng of gDNA. The PCR mix comprised 12.5 µl 2x SuperHot Mastermix (Genaxxon, Germany), 1.5 µl $MgCl_2$ (25mM), 1 µl of forward/reverse primer (10 ppmol), 3 µl PCR enhancer (Top-Bio, Czech Republic) and 5.5 µL H_20. After activating the polymerase at 95°C for 15 min, the reaction was exposed to 25 cycles of denaturation at 95°C for 30 sec, annealing at 51°C for 60 sec, elongation at 72°C for 60 sec. Final elongation was at 72°C for 10 min.

S2   Phylogenetic Analyses and Divergence Dating

We used IQ-TREE version 2.0.6 (Minh *et al.* 2020) to reconstruct a maximum-likelihood (ML) phylogenetic tree using the implemented ModelFinder algorithm (Kalyaanamoorthy *et al.* 2017) to

select a substitution model for each of the eight partitions based on the corrected Akaike information criterion (-MFP+MERGE -merit AICc). The resulting scheme (six partitions: ITS1 + ITS2 nDNA, second codon position COX2 + CDS, and separate partitions for first and third codons of COX2 and CDS) was used to perform a thorough and slow tree search under Maximum Likelihood (ML) criteria using a random starting tree, a candidate set of up to 50 trees (during ML tree search), smaller perturbation strength, and up to 500 unsuccessful iterations before stopping the search algorithm (-p -t RAND -nbest 50 -pers 0.2 -nstop 500). To estimate node support, tree reconstruction was immediately followed by 1,000 ultrafast bootstraps (ufBS) and 1,000 replicates of single-branch tests (SH-aLRT) (-bb 1000 -alrt 1000). Clades are considered robust if SH-aLRT $\geq$ 80% and ufBS $\geq$ 95%.

We dated our phylogeny with BEAST v.2.6.6 (Bouckaert *et al.* 2019) using unlinked site models, linked partition trees, linked clocks for mtDNA sequences and two unlinked clocks for nDNA sequences. For each partition of the supermatrix alignment, the bModelTest package (Bouckaert and Drummond 2017) was used to average over 31 transition/transversion split models. We performed three independent MCMC runs, sampling tree and parameter values every 25,000 steps over a total of 250 million generations. Convergence and effective sample sizes were checked with Tracer v1.7.1. (Rambaut *et al.* 2018), with a quarter of samples removed as burn-in. MCMC runs were combined with LogCombiner v2.6.2 (Drummond and Rambaut 2007) and a maximum-clade-credibility tree with mean node heights was obtained using TreeAnnotator v2.6.0 (Drummond and Rambaut, 2007). For three basal nodes, the topology was constrained by enforcing monophyly for Australian *Amitermes + Drepanotermes*, Australian *Amitermes*, and *Drepanotermes*. We calibrated the root node of our phylogeny using a uniform prior with a lower bound of 26.50 and an upper bound of 28.60 Mya, representing the estimated range of the pairwise divergence time for *Amitermes + Orthognathotermes* taken from the TimeTree database (timetree.org, accessed on 22 September 2021; Kumar *et al.* 2017).

The fossil record of termites is sparse and no higher termite (Termitidae) fossil is known from Australia (Engel *et al.* 2009), so we dated the split between Australian *Amitermes* and *Drepanotermes* using a secondary calibration derived from Heimburger *et al.* 2021. We used a lognormal prior with a mean of 1.875 and a standard deviation of 0.095, which resulted in a distribution centred around 6.5

Mya with a 95% probability range from 5.5 to 7.5 Mya. This corresponds to the divergence estimate of the most recent common ancestor of Australian *Amitermes* and *Drepanotermes* (Heimburger *et al.* 2022).

S3   Predictor Variables: Biotic Factors

To investigate the influence of predator-prey interactions on habitat suitability in *Drepanotermes*, we created predictor variables from major termite predator groups in Australia: (1) ants, (2) lizards, and (3) mammals. We used a literature search with the terms "prey", "predator", "termites" and "Australia". Species/genera noted in the literature as predating on *Drepanotermes* spp. or *Amitermes* spp. were selected; for details on species/genera in each predator group and references see Tab. S4. Occurrence records of each predator species/genus were downloaded from the Atlas of Living Australia and used to create ENMs using MaxEnt 3.4.1 (Phillips *et al.* 2017) with default settings. To convert habitat suitability scores to binary suitability (suitable/unsuitable), we used the 10% training threshold rule, which rejects the lowest 10% of predicted values (Liu *et al.* 2013). The resulting binary models of species/genera for each predator group were summed to calculate the potential species 'richness' for ants, lizards, and mammals, respectively. Estimates do not represent species richness *per se*; they reflect the suitability of each grid cell in respect to the total number of species in each predator group (Hageer *et al.* 2017). For example, we have included six ant species in total, a value of 2 would mean that a given grid cell is suitable for two out of six ant species.

We used the latest summary information on Australia's Pre-1750 native vegetation (http://www.awe.gov.au) to investigate the influence of land-cover types on ENMs. The major vegetation groups (MVGs) reflect the dominant vegetation before the arrival of Europeans and the widespread clearing of vegetation. We have re-classified the original 33 MVGs into 10 MVGs (see Tab. S5) to better assess the importance of particular food resources of *Drepanotermes* (hummock grasses, eucalypts, mallee; Watson and Perry 1981, Watson 1982, Tayasu *et al.* 2002) on habitat suitability.

Supplementary Tables

Supplementary Table 1   Samples used in this study, including collection location and GenBank accession numbers. ID names in bold indicate representative mOTU sequences used in downstream phylogenetic analyses. Note: sequences generated during this study are being prepared for GenBank submission and do not yet have accession numbers.

| | | | | | mitochondrial DNA | | nuclear DNA | | |
ID	Genus	Species	Latitude	Longitude	COX2	CDS	ITS1	ITS2	Reference
ANIC_0001	*Drepanotermes*	*tamminensis*	-31.04	116.05					
ANIC_0021	*Drepanotermes*	*tamminensis*	-29.67	116.19					
ANIC_0031	*Drepanotermes*	*perniger*-SW	-28.09	117.84					
ANIC_0052	*Drepanotermes*	*perniger*-SW	-26.02	118.68					
ANIC_0054	*Drepanotermes*	*perniger*-SW	-26.02	118.68	MZ008483	MZ008483			Heimburger *et al.* 2021
ANIC_0056	*Drepanotermes*	sp	-24.65	119.61					
ANIC_0060	*Drepanotermes*	*columellaris*	-24.44	119.68					
ANIC_0081	*Drepanotermes*	sp	-21.54	118.77	MZ008485	MZ008485			Heimburger *et al.* 2021
ANIC_0098	*Drepanotermes*	sp	-21.40	118.75					
ANIC_0102	*Drepanotermes*	sp	-21.39	118.74					
ANIC_0111	*Drepanotermes*	sp	-18.02	122.60					
ANIC_0112	*Drepanotermes*	*perniger*-NE	-18.02	122.60					
ANIC_0121	*Drepanotermes*	*perniger*-NE	-17.65	123.22					
ANIC_0128	*Drepanotermes*	sp	-17.84	124.31					
ANIC_0131	*Drepanotermes*	sp	-18.09	125.41					
ANIC_0143	*Drepanotermes*	sp	-18.23	127.67					
ANIC_0156	*Drepanotermes*	*perniger*-NE	-15.82	128.81					

ANIC_0159	*Drepanotermes*	sp	-16.07	129.23	MZ008489	MZ008489	Heimburger *et al.* 2021
ANIC_0169	*Drepanotermes*	sp	-15.64	130.45			
ANIC_0172	*Drepanotermes*	sp	-15.64	130.45			
ANIC_0175	*Drepanotermes*	sp	-15.54	131.29			
ANIC_0310	*Drepanotermes*	sp	-19.96	148.10			
ANIC_0312	*Drepanotermes*	sp	-19.96	148.10			
ANIC_0347	*Drepanotermes*	sp	-16.88	145.42			
ANIC_0348	*Drepanotermes*	sp	-16.88	145.42			
ANIC_0411	*Drepanotermes*	*perniger*-NE	-18.19	144.20			
ANIC_0415	*Drepanotermes*	*perniger*-NE	-18.31	144.78			
ANIC_0423	*Drepanotermes*	*perniger*-NE	-18.30	143.35			
ANIC_0424	*Drepanotermes*	*perniger*-NE	-18.27	143.22			
ANIC_0450	*Drepanotermes*	sp	-18.01	140.57			
ANIC_0453	*Drepanotermes*	sp	-18.10	140.31			
ANIC_0469	*Drepanotermes*	sp	-17.90	139.28			
ANIC_0470	*Drepanotermes*	sp	-17.90	139.28			
ANIC_0472	*Drepanotermes*	*perniger*-NE	-17.90	139.28			
ANIC_0474	*Drepanotermes*	*perniger*-NE	-17.90	139.28			
ANIC_0488	*Drepanotermes*	sp	-17.23	137.84			
ANIC_0496	*Drepanotermes*	sp	-15.92	132.36			
ANIC_0504	*Drepanotermes*	sp	-16.07	136.31			
ANIC_0507	*Drepanotermes*	sp	-16.07	136.31			
ANIC_0513	*Drepanotermes*	sp	-15.24	135.55			
ANIC_0520	*Drepanotermes*	*perniger*-NE	-15.24	135.55			
ANIC_0523	*Drepanotermes*	sp	-14.69	134.34			
ANIC_0528	*Drepanotermes*	sp	-14.77	134.16			
ANIC_0536	*Drepanotermes*	sp	-14.77	134.16			

ANIC_0544	*Drepanotermes*	sp	-14.67	132.10			
ANIC_0554	*Drepanotermes*	sp	-14.16	132.01			
ANIC_0558	*Drepanotermes*	sp	-14.96	133.05			
ANIC_0559	*Drepanotermes*	sp	-14.96	133.05			
ANIC_0562	*Drepanotermes*	sp	-14.96	133.05			
ANIC_0590	*Drepanotermes*	sp	-14.67	132.67	MZ008495	MZ008495	Heimburger *et al.* 2021
ANIC_0597	*Drepanotermes*	sp	-14.67	132.67	MZ008496	MZ008496	Heimburger *et al.* 2021
ANIC_0600	*Drepanotermes*	sp	-15.50	133.18			
ANIC_0604	*Drepanotermes*	sp	-15.50	133.18			
ANIC_0610	*Drepanotermes*	sp	-16.51	133.38			
ANIC_0612	*Drepanotermes*	sp	-16.51	133.38			
ANIC_0615	*Drepanotermes*	sp	-16.86	133.43			
ANIC_0616	*Drepanotermes*	sp	-16.86	133.43			
ANIC_0623	*Drepanotermes*	sp	-17.48	133.50			
ANIC_0627	*Drepanotermes*	sp	-18.09	133.72			
ANIC_0633	*Drepanotermes*	sp	-18.81	134.04			
ANIC_0642	*Drepanotermes*	sp	-21.02	134.21			
ANIC_0649	*Drepanotermes*	sp	-23.15	133.72			
ANIC_0656	*Drepanotermes*	sp	-23.15	133.72			
ANIC_0666	*Drepanotermes*	sp	-23.15	133.72			
ANIC_0669	*Drepanotermes*	sp	-25.84	133.30			
ANIC_0672	*Drepanotermes*	sp	-27.30	133.62			
ANIC_0676	*Drepanotermes*	sp	-27.30	133.62			
ANIC_0686	*Drepanotermes*	sp	-28.13	135.81			
ANIC_0715	*Drepanotermes*	sp	-31.97	141.40			
ANIC_0717	*Drepanotermes*	sp	-31.97	141.40			

ANIC_0734	*Drepanotermes*	sp	-32.40	142.43				
ANIC_0908	*Drepanotermes*	*perniger*-SW	-28.50	115.50				
ANIC_0913	*Drepanotermes*	sp	-29.79	115.94				
ANIC_0920	*Drepanotermes*	*tamminensis*	-31.04	116.04				
ANIC_1019	*Drepanotermes*	*tamminensis*	-29.48	115.67				
QLD_007	*Drepanotermes*	*perniger*-NE	-23.72	149.67				
QLD_008	*Drepanotermes*	*perniger*-NE	-23.72	149.64				
QLD_013	*Drepanotermes*	*perniger*-NE	-23.72	149.60				
QLD_015	*Drepanotermes*	*perniger*-NE	-23.59	149.13				
QLD_021	*Drepanotermes*	*perniger*-NE	-23.62	149.21				
QLD_026	*Drepanotermes*	*perniger*-NE	-23.60	148.55				
QLD_028	*Drepanotermes*	*perniger*-NE	-23.54	148.03	MZ008516	MZ008516		Heimburger *et al.* 2021
QLD_031	*Drepanotermes*	*perniger*-NE	-23.54	147.75				
QLD_033	*Drepanotermes*	*perniger*-NE	-23.55	147.74				
QLD_035	*Drepanotermes*	*perniger*-NE	-23.60	147.65				
QLD_037	*Drepanotermes*	*perniger*-NE	-23.66	146.96				
QLD_041	*Drepanotermes*	*perniger*-NE	-23.57	145.84				
QLD_042	*Drepanotermes*	sp	-22.32	142.96	MZ008518	MZ008518	NA	Heimburger *et al.* 2021
QLD_043	*Drepanotermes*	sp	-21.12	141.09	MZ008519	MZ008519	NA	Heimburger *et al.* 2021
QLD_044	*Drepanotermes*	sp	-20.97	140.91				
QLD_047	*Drepanotermes*	sp	-20.97	140.91	MZ008520	MZ008520		Heimburger *et al.* 2021
QLD_048	*Drepanotermes*	sp	-20.72	140.46				
QLD_050	*Drepanotermes*	*perniger*-NE	-20.72	140.46				
QLD_051	*Drepanotermes*	sp	-20.72	140.46	MZ008521	MZ008521		Heimburger *et al.* 2021

QLD_052	*Drepanotermes*	sp	-20.72	140.46				
QLD_053	*Drepanotermes*	sp	-20.72	140.46				
QLD_054	*Drepanotermes*	sp	-20.72	140.46				
QLD_057	*Drepanotermes*	sp	-20.75	140.24				
QLD_058	*Drepanotermes*	sp	-20.75	140.24				
QLD_060	*Drepanotermes*	sp	-20.76	140.21				
QLD_061	*Drepanotermes*	sp	-20.76	140.21				
QLD_062	*Drepanotermes*	sp	-20.57	140.44				
QLD_063	*Drepanotermes*	*perniger*-NE	-20.57	140.44				
QLD_066	*Drepanotermes*	sp	-20.57	140.44				
QLD_069	*Drepanotermes*	sp	-19.86	140.22				
QLD_070	*Drepanotermes*	sp	-19.11	140.39				
QLD_073	*Drepanotermes*	sp	-19.11	140.39				
QLD_075	*Drepanotermes*	sp	-18.70	140.51				
QLD_077	*Drepanotermes*	sp	-18.53	140.66				
QLD_079	*Drepanotermes*	sp	-18.53	140.66				
QLD_080	*Drepanotermes*	sp	-18.53	140.65	MZ008528	MZ008528		Heimburger *et al.* 2021
QLD_084	*Drepanotermes*	sp	-17.96	140.90				
QLD_086	*Drepanotermes*	sp	-17.73	141.05				
QLD_093	*Drepanotermes*	*perniger*-NE	-18.23	142.28				
QLD_099	*Drepanotermes*	*perniger*-NE	-18.23	142.28				
QLD_100	*Drepanotermes*	*perniger*-NE	-18.19	142.90				
QLD_106	*Drepanotermes*	*perniger*-NE	-18.28	143.59				
QLD_110	*Drepanotermes*	sp	-18.21	144.09				
QLD_111	*Drepanotermes*	sp	-18.09	144.41	MZ008533	MZ008533		Heimburger *et al.* 2021
QLD_117	*Drepanotermes*	*perniger*-NE	-17.98	144.86				

QLD_119	*Drepanotermes*	sp	-17.98	144.86			
QLD_121	*Drepanotermes*	*perniger*-NE	-17.98	144.86			
QLD_124	*Drepanotermes*	sp	-17.98	144.86			
QLD_143	*Drepanotermes*	sp	-17.29	144.98			
QLD_145	*Drepanotermes*	sp	-17.29	144.98			
QLD_156	*Drepanotermes*	sp	-16.53	145.14			
QLD_157	*Drepanotermes*	sp	-16.53	145.14	MZ008536	MZ008536	Heimburger *et al.* 2021
QLD_160	*Drepanotermes*	sp	-16.34	144.73			
QLD_163	*Drepanotermes*	sp	-16.34	144.73			
QLD_169	*Drepanotermes*	sp	-15.68	145.19			
QLD_174	*Drepanotermes*	sp	-15.75	144.69			
QLD_182	*Drepanotermes*	sp	-16.21	144.73			
QLD_183	*Drepanotermes*	sp	-16.21	144.73			
QLD_189	*Drepanotermes*	sp	-16.68	145.33			
QLD_193	*Drepanotermes*	sp	-16.68	145.33			
QLD_201	*Drepanotermes*	sp	-16.99	145.46			
QLD_206	*Drepanotermes*	sp	-16.99	145.46			
QLD_224	*Drepanotermes*	sp	-19.90	146.64			
QLD_241	*Drepanotermes*	*perniger*-NE	-20.61	146.28			
QLD_242	*Drepanotermes*	*perniger*-NE	-21.04	146.42			
QLD_253	*Drepanotermes*	*perniger*-NE	-21.89	147.04			
QLD_254	*Drepanotermes*	*perniger*-NE	-21.89	147.04			
QLD_255	*Drepanotermes*	*perniger*-NE	-22.82	147.58			
QLD_264	*Drepanotermes*	*perniger*-NE	-22.81	147.55			
QLD_265	*Drepanotermes*	*perniger*-NE	-22.81	147.55			
QLD_266	*Drepanotermes*	*perniger*-NE	-22.81	147.55			
QLD_267	*Drepanotermes*	*perniger*-NE	-22.81	147.55			

QLD_269	*Drepanotermes*	*perniger*-NE	-22.81	147.55			
QLD_270	*Drepanotermes*	*perniger*-NE	-22.81	147.54			
QLD_271	*Drepanotermes*	*perniger*-NE	-23.11	148.01			
QLD_272	*Drepanotermes*	sp	-23.13	148.01			
QLD_273	*Drepanotermes*	*perniger*-NE	-23.13	148.01			
QLD_279	*Drepanotermes*	*perniger*-NE	-23.10	148.01			
QLD_280	*Drepanotermes*	*perniger*-NE	-23.83	148.13			
QLD_281	*Drepanotermes*	*perniger*-NE	-23.83	148.13			
QLD_283	*Drepanotermes*	*perniger*-NE	-23.83	148.13			
QLD_305	*Drepanotermes*	sp	-26.42	148.80			
QLD_306	*Drepanotermes*	sp	-26.67	150.27			
QLD_308	*Drepanotermes*	sp	-26.67	150.27			
WA_006	*Drepanotermes*	*tamminensis*	-31.55	116.09			
WA_009	*Drepanotermes*	*tamminensis*	-30.96	116.61			
WA_011	*Drepanotermes*	*tamminensis*	-30.96	116.61			
WA_012	*Drepanotermes*	*tamminensis*	-30.96	116.61			
WA_014	*Drepanotermes*	*tamminensis*	-30.96	116.61			
WA_015	*Drepanotermes*	sp	-30.96	116.61			
WA_016	*Drepanotermes*	*tamminensis*	-30.39	116.64			
WA_017	*Drepanotermes*	*tamminensis*	-30.22	116.75			
WA_019	*Drepanotermes*	*tamminensis*	-30.39	116.64			
WA_020	*Drepanotermes*	*tamminensis*	-30.39	116.64			
WA_021	*Drepanotermes*	*tamminensis*	-30.39	116.64			
WA_022	*Drepanotermes*	*tamminensis*	-30.39	116.64			
WA_023	*Drepanotermes*	sp	-30.25	116.68			
WA_025	*Drepanotermes*	*gayi*	-30.25	116.68	MZ008551	MZ008551	Heimburger *et al.* 2021
WA_026	*Drepanotermes*	sp	-30.25	116.69			

WA_028	*Drepanotermes*	sp	-30.25	116.69	MZ008552	MZ008552	Heimburger *et al.* 2021
WA_031	*Drepanotermes*	*tamminensis*	-30.25	116.69			
WA_032	*Drepanotermes*	*tamminensis*	-30.22	116.75			
WA_033	*Drepanotermes*	*tamminensis*	-30.22	116.75			
WA_034	*Drepanotermes*	*tamminensis*	-30.22	116.75			
WA_039	*Drepanotermes*	*perniger*-SW	-29.27	117.77			
WA_040	*Drepanotermes*	*perniger*-SW	-29.28	117.70			
WA_041	*Drepanotermes*	*perniger*-SW	-29.26	117.70			
WA_044	*Drepanotermes*	sp	-29.23	117.70			
WA_046	*Drepanotermes*	*perniger*-SW	-29.23	117.70			
WA_047	*Drepanotermes*	*perniger*-SW	-28.10	117.84			
WA_048	*Drepanotermes*	*perniger*-SW	-28.10	117.84			
WA_049	*Drepanotermes*	*perniger*-SW	-28.11	117.84			
WA_050	*Drepanotermes*	*tamminensis*	-28.11	117.84			
WA_051	*Drepanotermes*	*clarki*	-27.89	117.87	MZ008555	MZ008555	Heimburger *et al.* 2021
WA_055	*Drepanotermes*	sp	-28.15	117.70			
WA_057	*Drepanotermes*	*perniger*-SW	-28.15	117.70			
WA_058	*Drepanotermes*	*perniger*-SW	-28.36	116.55			
WA_059	*Drepanotermes*	sp	-28.45	115.56			
WA_060	*Drepanotermes*	sp	-28.45	115.56			
WA_061	*Drepanotermes*	*perniger*-SW	-28.45	115.56			
WA_062	*Drepanotermes*	*perniger*-SW	-28.52	115.59			
WA_063	*Drepanotermes*	sp	-28.52	115.59			
WA_064	*Drepanotermes*	*perniger*-SW	-28.52	115.59			
WA_065	*Drepanotermes*	*tamminensis*	-28.50	115.63	MZ008556	MZ008556	Heimburger *et al.* 2021
WA_066	*Drepanotermes*	*tamminensis*	-28.50	115.63			

WA_067	*Drepanotermes*	*tamminensis*	-28.50	115.63			
WA_068	*Drepanotermes*	*tamminensis*	-28.50	115.63			
WA_069	*Drepanotermes*	*tamminensis*	-28.50	115.64			
WA_073	*Drepanotermes*	sp	-29.09	115.98			
WA_076	*Drepanotermes*	sp	-29.24	116.12			
WA_077	*Drepanotermes*	*tamminensis*	-29.53	115.68			
WA_078	*Drepanotermes*	*tamminensis*	-29.53	115.68			
WA_079	*Drepanotermes*	*tamminensis*	-29.53	115.68			
WA_080	*Drepanotermes*	sp	-29.54	115.64			
WA_083	*Drepanotermes*	*tamminensis*	-29.52	115.45			
WA_084	*Drepanotermes*	*tamminensis*	-29.53	115.45			
WA_087	*Drepanotermes*	sp	-30.04	115.76			
WA_102	*Drepanotermes*	*tamminensis*	-30.97	116.04			
WA_103	*Drepanotermes*	sp	-30.97	116.04			
WA_111	*Drepanotermes*	*tamminensis*	-31.37	118.62			
WA_112	*Drepanotermes*	*tamminensis*	-31.38	118.68			
WA_113	*Drepanotermes*	*tamminensis*	-31.38	118.68			
WA_114	*Drepanotermes*	*tamminensis*	-31.39	118.68			
WA_115	*Drepanotermes*	sp	-31.40	118.68			
WA_116	*Drepanotermes*	sp	-31.23	119.37			
WA_119	*Drepanotermes*	sp	-31.28	119.65			
WA_121	*Drepanotermes*	sp	-31.28	119.65			
WA_122	*Drepanotermes*	sp	-31.27	119.65			
WA_124	*Drepanotermes*	sp	-31.27	119.65			
WA_128	*Drepanotermes*	sp	-31.27	119.98			
WA_134	*Drepanotermes*	*perniger*-SW	-30.85	121.66			
WA_137	*Drepanotermes*	sp	-31.31	119.66	MZ008562	MZ008562	Heimburger *et al.* 2021

WA_139	*Drepanotermes*	*tamminensis*	-32.41	118.38					
WA_140	*Drepanotermes*	*tamminensis*	-32.41	118.38					
WA_141	*Drepanotermes*	*tamminensis*	-32.41	118.39					
WA_143	*Drepanotermes*	*tamminensis*	-32.41	118.39					
WA_145	*Drepanotermes*	*tamminensis*	-32.39	118.39					
WA_147	*Drepanotermes*	sp	-32.50	118.26					
WA_148	*Drepanotermes*	sp	-32.50	118.26					
WA_149	*Drepanotermes*	sp	-32.46	118.14					
WA_151	*Drepanotermes*	sp	-32.44	118.14					
WA_155	*Drepanotermes*	*gayi*	-32.39	117.96					
WA_158	*Drepanotermes*	*gayi*	-32.40	118.00					
WA_161	*Drepanotermes*	sp	-32.26	117.92					
WA_162	*Drepanotermes*	sp	-32.26	117.92					
WA_164	*Drepanotermes*	*gayi*	-32.22	117.86					
WA_173	*Drepanotermes*	*barretti*	-28.45	115.56					
ANIC_0034	*Amitermes*	sp	-28.08	117.83	MZ008481	MZ008481			Heimburger *et al.* 2021
ANIC_0651	*Amitermes*	sp	-23.14	133.71	MZ008500	MZ008500			Heimburger *et al.* 2021
ANIC_0900	*Amitermes*	sp	-28.68	115.22	MZ008505	MZ008505			Heimburger *et al.* 2021
WA_038	*Amitermes*	*deplanatus*	-29.27	117.70	MZ008553	MZ008553			Heimburger *et al.* 2021
WA_136	*Amitermes*	sp	-31.29	119.65	MZ008561	MZ008561	NA	NA	Heimburger *et al.* 2021
WA_138	*Amitermes*	*conformis*	-32.39	118.36	MZ008563	MZ008563	NA	NA	Heimburger *et al.* 2021

KY224513	*Amitermes*	*dentatus*		KY224513	KY224513	NA	NA	Bourguignon *et al.* 2017
KP026289	*Orthognathotermes*	*aduncus*		KP026289	KP026289	NA	NA	Bourguignon *et al.* 2014

Supplementary Table S2   Summary of mOTUs based on the best partitioning scheme of ASAP, including nesting habits used for ancestral state reconstruction and representative sequences used for downstream phylogenetic analyses. Lineages for which ENMs have been modelled are indicated in bold.

ID	Species name	Included sequences	n	Nesting habit	References	Representative sequence
mOTU1	***Drepanotermes rubriceps***	ANIC_0310, ANIC_0312, ANIC_0347, ANIC_0348, QLD_169, QLD_182, QLD_189, QLD_193, QLD_201, QLD_206, QLD_143, QLD_156, QLD_157, QLD_224, QLD_145	15	mound		QLD_157
mOTU2	*Drepanotermes* sp	ANIC_0469, ANIC_0470	2	mound		ANIC_0469
mOTU3	*Drepanotermes* sp	ANIC_0488	1	mound		ANIC_0488
mOTU4	*Drepanotermes* sp	QLD_043, QLD_044, QLD_053, QLD_054, QLD_060, QLD_061, QLD_048, QLD_052, QLD_069	9	mound		QLD_043
mOTU5	*Drepanotermes* sp	QLD_070	1	mound		QLD_070
mOTU6	*Drepanotermes* sp	QLD_073	1	mound		QLD_073
mOTU7	*Drepanotermes* sp	ANIC_0450, QLD_075, QLD_077, QLD_079, QLD_080	5	mound		QLD_080
mOTU8	*Drepanotermes* sp	ANIC_0453	1	mound		ANIC_0453
mOTU9	*Drepanotermes* sp	ANIC_0504, ANIC_0536, ANIC_0616, ANIC_0715, ANIC_0717, ANIC_0734, QLD_305, QLD_306, QLD_308	9	mound		ANIC_0717
mOTU10	*Drepanotermes* sp	ANIC_0666	1	mound		ANIC_0666
mOTU11	*Drepanotermes* sp	ANIC_0507	1	mound		ANIC_0507

mOTU12	*Drepanotermes* sp	ANIC_0169, ANIC_0172, ANIC_0523, ANIC_0528, ANIC_0175	5	mound	ANIC_0169
mOTU13	*Drepanotermes* sp	ANIC_0496, ANIC_0513	2	mound	ANIC_0496
mOTU14	*Drepanotermes* sp	ANIC_0649, ANIC_0656, ANIC_0669, ANIC_0672, ANIC_0676, ANIC_0686	6	mound	ANIC_0649
mOTU15	*Drepanotermes* sp	QLD_272	1	mound	QLD_272
mOTU16	*Drepanotermes* sp	ANIC_0627	1	mound	ANIC_0627
mOTU17	***Drepanotermes perniger*-NE**	ANIC_0112, ANIC_0156, ANIC_0411, ANIC_0415, ANIC_0424, QLD_037, QLD_041, QLD_050, QLD_063, QLD_093, QLD_099, QLD_100, QLD_106, QLD_241, QLD_242, QLD_253, QLD_255, QLD_265, QLD_266, QLD_270, ANIC_0423, QLD_007, QLD_008, QLD_013, QLD_021, QLD_033, QLD_271, QLD_273, QLD_279, QLD_280, QLD_281, QLD_283, QLD_117, QLD_121, QLD_254, QLD_264, QLD_267, QLD_269, QLD_015, QLD_026, QLD_028, QLD_031, QLD_035,	47	mound	QLD_028

		ANIC_0520, ANIC_0642, ANIC_0121, ANIC_0472				
mOTU18	*Drepanotermes* sp	ANIC_0474, ANIC_0623	2	mound		ANIC_0474
mOTU19	*Drepanotermes* sp	ANIC_0111, ANIC_0131	2	mound		ANIC_0111
mOTU20	*Drepanotermes* sp	ANIC_0128	1	mound		ANIC_0128
mOTU21	*Drepanotermes* sp	ANIC_0633	1	mound		ANIC_0633
mOTU22	*Drepanotermes* sp	ANIC_0913, WA_023, WA_059, WA_060, WA_073, WA_076, WA_080, WA_103, WA_087	9	mound + subterranean		WA_073
mOTU23	*Drepanotermes* sp	WA_015, WA_162, WA_026, WA_028, WA_055, WA_063	6	mound + subterranean		WA_028
mOTU24	*Drepanotermes* sp	WA_116, WA_119, WA_121, WA_122, WA_124, WA_128, WA_148, WA_147, WA_151	9	subterranean		WA_116
mOTU25	*Drepanotermes* sp	WA_044	1	subterranean		WA_044
mOTU26	*Drepanotermes* sp	WA_161	1	subterranean		WA_161
mOTU27	*Drepanotermes* sp	WA_137	1	mound		WA_137
mOTU28	*Drepanotermes* sp	QLD_051, QLD_057, QLD_062	3	subterranean		QLD_051
mOTU29	*Drepanotermes* sp	QLD_047	1	subterranean		QLD_047
mOTU30	*Drepanotermes* sp	ANIC_0056	1	mound		ANIC_0056
mOTU31	*Drepanotermes* sp	ANIC_0081	1	mound		ANIC_0081
mOTU32	*Drepanotermes* sp	ANIC_0098	1	mound		ANIC_0098
mOTU33	*Drepanotermes* sp	ANIC_0102	1	mound		ANIC_0102
mOTU34	*Drepanotermes* sp	ANIC_0143	1	mound		ANIC_0143
mOTU35	***Drepanotermes tamminensis***	ANIC_0001, ANIC_0021, ANIC_0920, WA_009, WA_011, WA_012, WA_016,	40	mound	Watson and Perry 1981	WA_065

		WA_017, WA_019, WA_020, WA_021, WA_022, WA_031, WA_102, WA_111, WA_113, WA_114, WA_139, WA_140, WA_141, WA_143, WA_145, WA_006, WA_050, WA_032, WA_033, WA_034, WA_112, ANIC_1019, WA_014, WA_065, WA_066, WA_068, WA_069, WA_077, WA_078, WA_079, WA_083, WA_084, WA_067				
mOTU36	*Drepanotermes* sp	WA_115	1	mound		WA_115
mOTU37	**Drepanotermes clarki**	WA_051	1	subterranean	Watson and Perry 1981	WA_051
mOTU38	**Drepanotermes gayi**	WA_025, WA_155, WA_158, WA_164	4	subterranean	Watson and Perry 1981	WA_025
mOTU39	*Drepanotermes* sp	WA_149	1	subterranean		WA_149
mOTU40	**Drepanotermes barretti**	WA_173	1	subterranean	Watson and Perry 1981	WA_173
mOTU41	**Drepanotermes columellaris**	ANIC_0060	1	mound + subterranean	Watson and Perry 1981	ANIC_0060
mOTU42	**Drepanotermes perniger-SW**	ANIC_0031, ANIC_0908, WA_040, WA_041, WA_047, WA_049, WA_057, WA_058, WA_061, WA_064, ANIC_0052, WA_039,	17	mound + subterranean		ANIC_0054

		WA_046, WA_048, WA_062, WA_134, ANIC_0054				
mOTU43	*Drepanotermes* sp	QLD_066	1	subterranean		QLD_066
mOTU44	*Drepanotermes* sp	QLD_084, QLD_160, QLD_163, QLD_174, QLD_183, QLD_086, QLD_124, QLD_119	8	mound		QLD_084
mOTU45	*Drepanotermes* sp	QLD_111	1	subterranean		QLD_111
mOTU46	*Drepanotermes* sp	QLD_110	1	subterranean		QLD_110
mOTU47	*Drepanotermes* sp	QLD_058	1	subterranean		QLD_058
mOTU48	*Drepanotermes* sp	ANIC_0544, ANIC_0554, ANIC_0612, ANIC_0590	4	mound		ANIC_0590
mOTU49	*Drepanotermes* sp	ANIC_0562	1	mound		ANIC_0562
mOTU50	*Drepanotermes* sp	ANIC_0159	1	mound		ANIC_0159
mOTU51	*Drepanotermes* sp	ANIC_0558, ANIC_0559	2	mound		ANIC_0558
mOTU52	*Drepanotermes* sp	QLD_042	1	subterranean		QLD_042
mOTU53	*Drepanotermes* sp	ANIC_0610, ANIC_0615	2	mound		ANIC_0610
mOTU54	*Drepanotermes* sp	ANIC_0597, ANIC_0600, ANIC_0604	3	mound		ANIC_0597
	Amitermes sp	ANIC_0034		subterranean		
	Amitermes sp	ANIC_0651		subterranean		
	Amitermes sp	ANIC_0900		subterranean		
	Amitermes deplanatus	WA_038		subterranean	Gay 1968	
	Amitermes sp	WA_136		subterranean		
	Amitermes conformis	WA_138		mound + subterranean	Abensperg-Traun and Perry 1998	

Supplementary Table S3   Predictor variables and sources. Gray-shaded variables were used for ecological niche modeling. Remaining variables were involved in pairwise Pearson's correlations above 75% (Table S6) and thus discarded prior to ecological niche modeling.

	Description	Source
BIO01	Annual Mean Temperature (ºC)	https://worldclim.org/
BIO02	Mean Diurnal Range (Mean of monthly (max temp - min temp)) (ºC)	https://worldclim.org/
BIO03	Isothermality (BIO02/BIO07) (×100)	https://worldclim.org/
BIO04	Temperature Seasonality (standard deviation ×100)	https://worldclim.org/
BIO05	Max Temperature of Warmest Month (ºC)	https://worldclim.org/
BIO06	Min Temperature of Coldest Month (ºC)	https://worldclim.org/
BIO07	Temperature Annual Range (BIO5-BIO6) (ºC)	https://worldclim.org/
BIO08	Mean Temperature of Wettest Quarter (ºC)	https://worldclim.org/
BIO09	Mean Temperature of Driest Quarter (ºC)	https://worldclim.org/
BIO10	Mean Temperature of Warmest Quarter (ºC)	https://worldclim.org/
BIO11	Mean Temperature of Coldest Quarter (ºC)	https://worldclim.org/
BIO12	Annual Precipitation (mm)	https://worldclim.org/
BIO13	Precipitation of Wettest Month (mm)	https://worldclim.org/
BIO14	Precipitation of Driest Month (mm)	https://worldclim.org/
BIO15	Precipitation Seasonality (Coefficient of Variation)	https://worldclim.org/
BIO16	Precipitation of Wettest Quarter (mm)	https://worldclim.org/
BIO17	Precipitation of Driest Quarter (mm)	https://worldclim.org/
BIO18	Precipitation of Warmest Quarter (mm)	https://worldclim.org/
BIO19	Precipitation of Coldest Quarter (mm)	https://worldclim.org/
Aridity index	Mean annual aridity index (BIO12/annual potential evaporation)	https://www.asris.csiro.au/
Bulk density	Bulk density in the first 30cm of soil	https://www.asris.csiro.au/
Clay content	Percentage of clay content in the first 30 cm of soil	https://www.asris.csiro.au/
Elevation	Meters above sea level (m)	https://www.ga.gov.au/data-pubs/maps
Fire frequency	National fire return frequency for Australia (1988 - 2015)	https://data.gov.au/dataset/ds-dga-491fa8ce-5add-4d07-ba35-b7a8bd1d2c4d/details
PAWC	Plant available water capacity (PAWC), maximum amount of water stored in a soil profile that can be used by plants	https://www.asris.csiro.au/
soil pH	pH as measured with $CaCl_2$ for the first 30 cm of soil	https://www.asris.csiro.au/
Ant species richness	Number of ant species modeled to occur according to ENMs 10% top suitable area	https://ala.org.au/ and this study
Lizard species richness	Number of lizard species modeled to occur according to ENMs 10% top suitable area	https://ala.org.au/ and this study
Mammal species richness	Number of mammal species modeled to occur according to ENMs 10% top suitable area	https://ala.org.au/ and this study
MVG	Pre-1750 (pre-European, pre-clearing) native vegetation reclassified into 10 MVGs	https://www.environment.gov.au/ and this study

Supplementary Table S4   Taxa included in predator groups.

Genus	Species	Predator Group	References
Iridomyrmex	*sanguineus*	ants	Higashi and Ito 1989
Iridomyrmex	*rufoniger*	ants	Abensperg-Traun and Perry 1998
Iridomyrmex	*greensladei*	ants	Abensperg-Traun and Perry 1998
Iridomyrmex	*rubriceps*	ants	Heterick and Shattuck 2011
Iridomyrmex	*pallidus*	ants	Heterick and Shattuck 2011
Iridomyrmex	*purpureus*	ants	Holt and Greenslade 1980
Chlamydosaurus	*kingii*	lizards	Griffiths and Christian 1996
Diplodactylus	*conspicillatus*	lizards	Abensperg‑Traun 1994
Pogona	*vitticeps*	lizards	Oonincx *et al.* 2015
Pogona	*barbata*	lizards	Oonincx *et al.* 2015
Pogona	*minor*	lizards	Oonincx *et al.* 2015
Diplodactylus	*conspicillatus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*klugei*	lizards	Abensperg‑Traun 1994
Diplodactylus	*ameyi*	lizards	Abensperg‑Traun 1994
Diplodactylus	*laevis*	lizards	Abensperg‑Traun 1994
Diplodactylus	*kenneallyi*	lizards	Abensperg‑Traun 1994
Diplodactylus	*barraganae*	lizards	Abensperg‑Traun 1994
Diplodactylus	*mitchelli*	lizards	Abensperg‑Traun 1994
Diplodactylus	*galaxias*	lizards	Abensperg‑Traun 1994
Diplodactylus	*wiru*	lizards	Abensperg‑Traun 1994
Diplodactylus	*nebulosus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*ornatus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*platyurus*	lizards	Abensperg‑Traun, 1994
Diplodactylus	*capensis*	lizards	Abensperg‑Traun 1994
Diplodactylus	*custos*	lizards	Abensperg‑Traun 1994
Diplodactylus	*lateroides*	lizards	Abensperg‑Traun 1994
Diplodactylus	*calcicolus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*furcosus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*vittatus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*polyophthalmus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*tessellatus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*hillii*	lizards	Abensperg‑Traun 1994
Diplodactylus	*galeatus*	lizards	Abensperg‑Traun 1994
Diplodactylus	*granariensis*	lizards	Abensperg‑Traun 1994
Diplodactylus	*pulcher*	lizards	Abensperg‑Traun 1994
Diplodactylus	*bilybara*	lizards	Abensperg‑Traun 1994
Diplodactylus	*fulleri*	lizards	Abensperg‑Traun 1994
Diplodactylus	*savagei*	lizards	Abensperg‑Traun 1994
Isoodon	*auratus*	mammals	Keiper and Johnson 2004
Isoodon	*obesulus*	mammals	Keiper and Johnson 2004

Isoodon	*macrourus*	mammals	Keiper and Johnson 2004
Macrotis	*lagotis*	mammals	Southgate and Carthew 2006
Perameles	*nasuta*	mammals	Thums *et al.* 2005
Tachyglossus	*aculeatus*	mammals	Abensperg-Traun 1991, 1994
Ningaui	spp	mammals	Bos and Carthew 2007, Abensperg‑Traun 1994

Supplementary Table S5 Summarisation scheme of Australia's 33 Pre-1750 (pre-European, pre-clearing) native Major Vegetation Groups (MVGs) to 10 reclassified MVGs highlighting acacia, eucalypts, and tussock and hummock grasses as important food resources for *Drepanotermes*.

| Original #	MVGs	New #	Reclassified MVGs
1	Rainforests and Vine Thickets	1	Rainforest
2	Eucalypt Tall Open Forests	2	Eucalypt dominated
3	Eucalypt Open Forests	2	Eucalypt dominated
4	Eucalypt Low Open Forests	2	Eucalypt dominated
5	Eucalypt Woodlands	2	Eucalypt dominated
6	Acacia Forests and Woodlands	3	Acacia dominated
7	Callitris Forests and Woodlands	4	Other forests and woodlands
8	Casuarina Forests and Woodlands	4	Other forests and woodlands
9	Melaleuca Forests and Woodlands	4	Other forests and woodlands
10	Other Forests and Woodlands	4	Other forests and woodlands
11	Eucalypt Open Woodlands	2	Eucalypt dominated
12	Tropical Eucalypt Woodlands/Grasslands	2	Eucalypt dominated
13	Acacia Open Woodlands	3	Acacia dominated
14	Mallee Woodlands and Shrublands	2	Mallee dominated
15	Low Closed Forests and Tall Closed Shrublands	4	Other forests and woodlands
16	Acacia Shrublands	3	Acacia dominated
17	Other Shrublands	5	Other shrublands
18	Heathlands	6	Heathlands
19	Tussock Grasslands	7	Tussock Grasslands
20	Hummock Grasslands	8	Hummock Grasslands
21	Other Grasslands, Herblands, Sedgelands and Rushlands	9	Other grasslands
22	Chenopod Shrublands, Samphire Shrublands and Forblands	9	Other grasslands
23	Mangroves	10	Other
24	Inland Aquatic - freshwater, salt lakes, lagoons	10	Other
25	Cleared, non-native vegetation, buildings	10	Other
26	Unclassified native vegetation	10	Other
27	Naturally bare - sand, rock, claypan, mudflat	10	Other
28	Sea and estuaries	10	Other
29	Regrowth, modified native vegetation	10	Other
30	Unclassified forest	4	Other forests and woodlands
31	Other Open Woodlands	4	Other forests and woodlands
32	Mallee Open Woodlands and Sparse Mallee Shrublands	2	Mallee dominated
99	Unknown/no data	10	Other

Supplementary Table S6   Pariwise Pearson's correlations for all 30 predictor variables. Correlations above 75% are highlighted in red. Ant = ant species richness, Aridity = aridity index, Bulk = bulk density, Clay = clay content, Elev = elevation, Fire = fire frequency, Lizard = lizard species richness, Mam = mammal species richness, soil = soil pH.

|	Ant	Aridity	Bulk	BIO01	BIO02	BIO03	BIO04	BIO05	BIO06	BIO07	BIO08	BIO09	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19	Clay	Elev	Fire	Lizard	Mam	MVG	PAWC	soil
Ant																														
Aridity	0.45																													
Bulk	0.12	-0.10																												
BIO01	-0.26	-0.26	0.21																											
BIO02	-0.50	-0.66	0.05	0.59																										
BIO03	0.20	0.34	0.18	0.54	0.12																									
BIO04	-0.46	-0.67	-0.11	-0.14	0.42	-0.83																								
BIO05	-0.45	-0.56	0.16	0.90	0.81	0.20	0.29																							
BIO06	0.05	0.16	0.23	0.86	0.17	0.81	-0.61	0.55																						
BIO07	-0.55	-0.78	-0.06	0.13	0.72	-0.60	0.93	0.54	-0.40																					
BIO08	-0.32	-0.31	0.13	0.82	0.60	0.24	0.14	0.85	0.58	0.34																				
BIO09	-0.08	-0.05	0.17	0.49	0.13	0.45	-0.34	0.33	0.55	-0.20	0.03																			
BIO10	-0.42	-0.52	0.18	0.92	0.73	0.21	0.25	0.99	0.61	0.47	0.85	0.36																		
BIO11	-0.07	-0.01	0.23	0.94	0.37	0.77	-0.47	0.70	0.97	-0.21	0.67	0.57	0.74																	
BIO12	0.52	0.90	0.02	0.02	-0.52	0.58	-0.80	-0.34	0.45	-0.82	-0.11	0.09	-0.28	0.29																
BIO13	0.39	0.66	0.14	0.40	-0.24	0.79	-0.82	0.03	0.75	-0.73	0.18	0.32	0.08	0.64	0.89															
BIO14	0.38	0.62	-0.23	-0.79	-0.63	-0.34	-0.07	-0.80	-0.57	-0.31	-0.59	-0.51	-0.81	-0.69	0.38	-0.05														
BIO15	-0.01	0.11	0.17	0.83	0.32	0.74	-0.50	0.59	0.90	-0.26	0.56	0.54	0.61	0.91	0.37	0.69	-0.59													
BIO16	0.41	0.69	0.13	0.36	-0.28	0.79	-0.84	-0.02	0.73	-0.76	0.14	0.31	0.04	0.61	0.92	0.99	-0.02	0.66												
BIO17	0.38	0.65	-0.24	-0.77	-0.64	-0.33	-0.09	-0.80	-0.55	-0.32	-0.58	-0.50	-0.80	-0.67	0.41	-0.02	0.99	-0.56	0.01											
BIO18	0.40	0.60	0.11	0.38	-0.20	0.65	-0.68	0.06	0.66	-0.61	0.29	0.13	0.10	0.56	0.83	0.89	0.05	0.60	0.88	0.08										
BIO19	0.30	0.63	-0.23	-0.73	-0.67	-0.28	-0.15	-0.78	-0.47	-0.38	-0.72	-0.17	-0.77	-0.59	0.37	0.00	0.77	-0.41	0.03	0.79	-0.08									
Clay	0.18	0.02	-0.20	-0.11	-0.04	-0.08	0.04	-0.09	-0.11	0.02	-0.01	-0.20	-0.09	-0.12	0.02	-0.05	0.19	-0.16	-0.04	0.18	0.05	0.01								
Elev	-0.10	0.06	-0.09	-0.21	0.00	-0.29	0.25	-0.10	-0.30	0.19	-0.03	-0.29	-0.14	-0.29	-0.01	-0.10	0.21	-0.07	-0.11	0.20	0.00	0.13	-0.21							
Fire	0.09	0.24	0.17	0.52	0.14	0.71	-0.55	0.28	0.66	-0.36	0.29	0.37	0.30	0.65	0.45	0.65	-0.34	0.63	0.65	-0.33	0.46	-0.30	-0.23	-0.09						
Lizard	0.21	-0.11	0.06	-0.36	-0.24	-0.20	0.05	-0.32	-0.30	-0.05	-0.36	-0.13	-0.31	-0.33	-0.14	-0.22	0.12	-0.39	-0.20	0.11	-0.24	0.14	0.08	-0.19	-0.21					
Mam	-0.29	-0.22	-0.13	0.11	0.24	-0.20	0.30	0.23	-0.07	0.32	0.21	-0.08	0.21	-0.02	-0.24	-0.19	-0.14	0.06	-0.21	-0.13	-0.14	-0.10	-0.18	0.25	-0.09	-0.06				
MVG	-0.43	-0.36	-0.09	0.21	0.38	-0.12	0.30	0.34	-0.01	0.39	0.23	0.08	0.31	0.08	-0.40	-0.28	-0.29	0.04	-0.30	-0.29	-0.27	-0.25	0.01	-0.11	-0.11	-0.19	0.21			
PAWC	0.00	0.11	-0.35	-0.12	0.00	-0.04	0.02	-0.10	-0.11	0.01	-0.05	-0.17	-0.11	-0.12	0.07	-0.01	0.20	-0.08	-0.01	0.20	0.03	0.10	0.19	0.05	-0.07	-0.04	0.06	0.01		
soil	-0.25	-0.49	-0.10	-0.03	0.31	-0.22	0.35	0.14	-0.24	0.40	0.04	-0.08	0.11	-0.15	-0.52	-0.46	-0.19	-0.26	-0.47	-0.21	-0.41	-0.25	0.35	-0.19	-0.31	0.21	0.01	0.32	0.05	

Supplementary Table S7   The five best performing model setting combinations for each predictor variable set (all, abiotic or biotic) and regularization multiplier (0.8, 1, 2, 3 or 5) are shown. The model settings with the lowest AICc score (in bold) were used to calculate full ENMs.

Species	AICc	Variable set	Regularization multiplier
D. barretti	**357.03**	**abiotic**	**2**
	361.16	abiotic	3
	369.84	all	5
	371.02	abiotic	5
	373.76	biotic	2
D. clarki	**1543.77**	**all**	**2**
	1556.31	all	3
	1556.42	abiotic	8
	1558.04	all	5
	1561.02	all	0.8
D. columellaris	**923.52**	**abiotic**	**5**
	928.54	abiotic	3
	928.89	abiotic	2
	928.96	abiotic	1
	932.01	all	3
D. gayi	**1778.31**	**all**	**5**
	1787.22	all	2
	1791.15	all	3
	1793.01	abiotic	3
	1794.56	abiotic	5
D. perniger-NE	**982.07**	**abiotic**	**1**
	983.08	abiotic	0.8
	988.12	abiotic	2
	991.24	all	3
	992.8	abiotic	3
D. perniger-SW	**-4.06**	**all**	**0.8**
	2.25	all	1
	404.47	abiotic	3
	414	abiotic	5
	417.19	biotic	3
D. rubriceps	**80.33**	**abiotic**	**0.8**
	277.63	biotic	2
	278.53	biotic	1
	281.36	biotic	3
	284.96	biotic	0.8
D. tamminensis	**515.67**	**abiotic**	**0.8**
	516.61	abiotic	2
	520.31	all	2
	522.04	abiotic	3
	522.31	abiotic	1

Supplementary Figures

Supplementary Figure S1   Bayesian phylogenetic chronogram inferred with BEAST 2.6.6. The scale bar represents millions of years. Node bars represent the 95% credibility intervals of node-time estimates. Nodes are labeled with posterior probabilities. See Tab. S2 for sample(s) and representative sequence belonging to each mOTU.
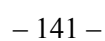
Supplementary Figure S2 Maximum likelihood tree inferred with IQ-TREE ver. 2.0.6. Nodes are labeled with SH-aLRT/ufBS values. See Tab. S2 for sample(s) and representative sequence belonging to each mOTU.
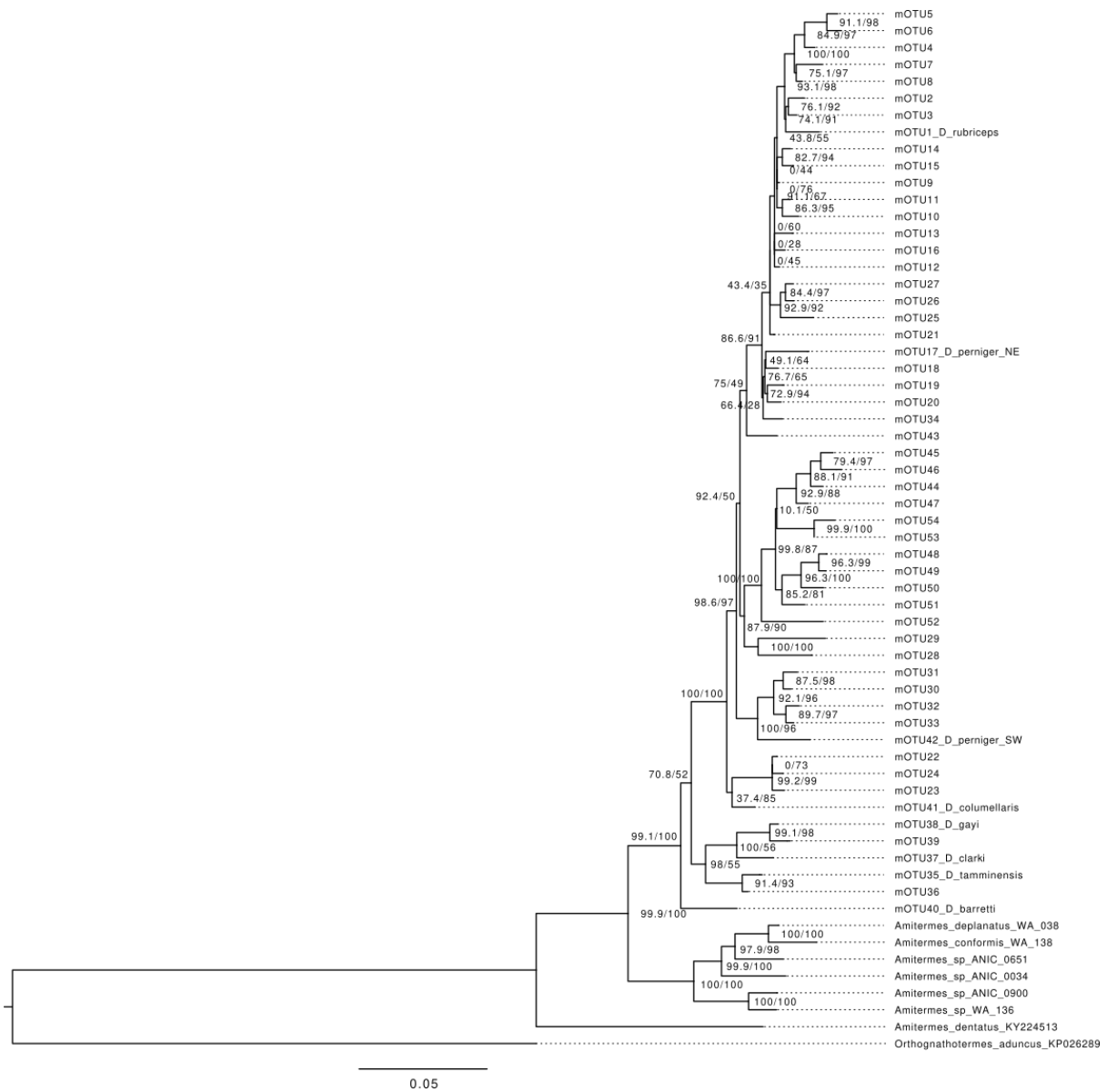
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Publication list

Peer reviewed articles

Brandt A., Anselmetti Y., Bluhm C., Dumas Z., François C. M., Galtier N., **Heimburger B.**, Jaron K. S., Labédan M., Maraun M., Robinson-Rechavi M., Schaefer I., Scheu S., Simion P., Tran-Van P., Schwander T. & Bast J. (2021) Haplotype divergence supports obligate asexuality in the oribatid mite *Oppiella nova*. *PNAS* **38**:e2101485118**.**

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Articles emerging from this thesis

Heimburger B., Schardt S., Brandt A., Scheu S. & Hartke T. R. (2021) Rapid diversification of the Australian *Amitermes* group during late Cenozoic climate change. – *bioRxiv* 2021.04.12.439430. *Submitted for publication in the journal* Ecography.

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Statutory Declaration

I, hereby, declare that this dissertation has not been presented to any other examining body either in its present or a similar form. Furthermore, I also affirm that I have not applied for a dissertation at any other higher school of education.

Bastian Heimburger

Göttingen, 11 February 2022

I, hereby, solemnly declare that this dissertation was undertaken independently and without any unauthorized aid.

Bastian Heimburger

Göttingen, 11 February 2022