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

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Past evolutionary adaptations to Australia’s aridification can help us to understand the 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 semiarid 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. The phylogenetic signal of bioclimatic variables, especially limiting environmental factors (e.g., precipitation of the warmest quarter), suggests that the climate exerts a strong selective pressure. Finally, we used environmental niche modeling to predict the 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 such as 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 occurs 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.

**KEY WORDS:** ancestral state reconstruction, climate change, *Drepanotermes*, ecological niche modeling, mound-building, species delineation.

Australia progressively aridified from the mid-Miocene (∼15 million years ago) onward 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 CO₂ 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 million years ago), when extreme climatic oscillations occurred during the interglacial periods (Fujioka et al. 2005). Current estimates suggest that climatic conditions in Australia may resemble those of hot and moist intervals in the Miocene within the next 100 years (Steinthorsdottir et al. 2021), as the 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 (Pepper and Keogh 2021), will expand in the future because semiarid 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 radiation in the past (Rabosky et al. 2007, Guzik et al. 2011), including the endemic termite genus Drepanotermes Silvestri, which is a prime example of explosive radiation coinciding with intensifying arid conditions in the Plio-Pleistocene (Heimburger et al. 2022). The 23 described species primarily occur in arid and semiarid 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 1982). 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 sclerotized 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., Triodia, 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 through the soil (Watson and Perry 1981). Drepanotermes are responsible for crucial amounts of carbon mineralization in the habitats in which they occur (Holt 1987) and can be considered keystone species (Whitford et al. 1992). 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, Evans et al. 2011) but also provide vital living space and food resources for ants (Holt and Greenslade 1980, Holt 1990), reptiles (Morton and James 1988, Abensperg-Traun 1994), and small mammals (Moro et al. 2014). Some Drepanotermes 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 hypothesize 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 Supporting Information, Table S1 for collection details.

DNA EXTRACTION AND SEQUENCING

Genomic DNA was extracted from the body, with the head and gut removed, of one individual worker per colony using the Agencourt DNA Advance 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: mitochondrial cytochrome c oxidase subunit 2 (COX2 mtDNA) and nuclear internal transcribed spacer regions 1 and 2 (ITS1 and ITS2 nDNA, respectively). ITS1 and ITS2 nDNA have been
frequently used in termites (Kutnik et al. 2004, Jenkins et al. 2007, Lee et al. 2017) because they are relatively easy to amplify and align compared to other candidate nuclear markers.

For primer sequences and PCR protocols, see Supporting Information (S1). All PCR products were visualized on a QiAxAcel Advanced System (Qiagen, Germany), purified using the AMPure XP purification kit (Beckman Coulter, USA), and sent to Microsynth Seqlab (Germany) for bidirectional 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. 2012; 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/) using default settings and Smart Model Selection (Lefort et al. 2017) in PhyML. bPTP models branching events (i.e., speciation) with regard to the number of substitutions (Zhang et al. 2013), whereas ABGD and ASAP use pairwise genetic distances (Puillandre et al. 2012, 2021). For ABGD, the user has to define a priori the maximal genetic intraspecific divergence ($P$; Puillandre et al. 2012), which is often unknown; therefore, we used the default settings ($P_{\text{max}} = 0.1$). ASAP overcomes this by providing several partitions ranked by a scoring system without having to define $P$ (Puillandre et al. 2021).

**PHYLOGENETIC INFERENCE 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 and 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. 2022) 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 (Heimburger et al. 2022).

We included eight outgroup sequences: six Australian *Amiitermes* forming the sister clade to *Drepanotermes* (Heimburger et al. 2022), *Amiitermes dentatus* from Southeast Asia, sister of Australian *Amiitermes + Drepanotermes* (Bourguignon et al. 2015, 2017; Heimburger et al. 2022), and *Orthognathotermes aduncus* to root our phylogenies (Bourguignon et al. 2017). Accession numbers of mitogenomes and individual sequences can be found in Table S1.

Alignment was performed with the MUSCLE (Edgar 2004) plugin in Geneious Prime 2021.1.1 (Kearse et al. 2012) as follows: (i) CDSs 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 were retained. The final concatenated supermatrix alignment included 62 sequences with a total length of 11,823 bp (Table 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 version 2.6.6 (Bouckaert et al. 2019). For further details on phylogenetic inferences and divergence dating, see Supporting Information (S2).

**GEOREFERENCED RECORDS AND PREDICTOR VARIABLES**

For mOTUs clearly attributable to described species (Fig. 1 and Table 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 (Supporting Information, Table 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. The biotic variables included the species richness of three major termite predator groups, including ants, lizards, and mammals (Supporting Information S3 and Table S4), and Australia’s Pre-1750 (pre-European, preclearing) native vegetation was reclassified into 10 major vegetation groups from...
Figure 1. Concordance of molecular species delimitation using three different methods (ASAP, ABGD, and bPTP), 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 gray vertical bars mark mOTU limits as delineated by ASAP, except mOTU17 *D. perniger*-NE and mOTU48 (turquoise and green, respectively).

the Natural Vegetation Information System (NVIS) version 6.0 (see Supporting Information 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 2022). One variable from each >75% correlated pair was randomly discarded, resulting in a final set of 16 uncorrelated predictor variables (Supporting Information, Table 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; Table 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 that 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 Table 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 assess 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 a high phylogenetic signal (Fig. 3), suggesting that climatic niches are phylogenetically conserved over evolutionary time, so we also used them in ecological niche modeling (see below) to compare our reconstructions of past climatic niches with predictions of present and future habitat suitability.

**PRESENT AND FUTURE HABITAT SUITABILITY**

The 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 (Pearson et al. 2007, Galante et al. 2018), (ii) different geographic distributions (southwestern, central, northeastern) and (iii) different nesting habits (‘subterranean’, ‘subterranean + mound’, ‘mound’). For the number of georeferenced records (i.e., GBIF records and field records) per taxon; see Table S7.

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 subselected 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 (Table S8) 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 (Table S8). We used complementary log-log (cloglog) as the model output (Phillips et al. 2017). For each model, we retained only variables with high permutation importance, i.e., permutation value higher than 15% (Table 1).

| 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             |

To project the 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 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 approximately 4°C of warming above preindustrial 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 bPTP returned 65 and 62, respectively (Fig. 1). Unlike ASAP, which uses sequence data directly to calculate pairwise genetic distances (Puillandre et al. 2021), bPTP 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 Table 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). Consensus could not be reached for three sequences (ANIC_112, ANIC_121, and ANIC_0472) associated with *D. perniger*-NE: ANIC_0121 and ANIC_0472 were excluded by ABGD, and
ANIC_0112 was excluded by bPTP (Fig. 1). For D. perniger-SW, ABGD recovered ANIC_0054 as an independent evolutionary lineage (mOTU) rather than as part of D. perniger-SW as in the other two methods (Fig. 1).

MOLECULAR PHYLOGENY
Fifty of 54 mOTUs in the supermatrix alignment were represented by two or all three of the target genes (Table S1). Phylogenetic analyses based on Bayesian and ML inferences recovered mostly congruent topologies and comparable support values (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. 2022).

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. 2022). The split between A. dentatus and (Australian Amitermes + Drepanotermes) was dated at 9.27 million years ago (95% HDP: 6.66-13.67 million years ago) (Fig. S1). Drepanotermes was found to have diverged from Australian Amitermes approximately 6.2 million years ago (95% HDP: 5.33-8.93 million years ago). The majority of lineages in this study originated within the Pleistocene (2.58 million years ago to the present), many with divergence times of approximately 1 million years ago or less (Fig. S1).

ANCESTRAL NESTING HABIT AND PHYLOGENETIC SIGNAL
The best-fitting ER model indicates that subterranean nesting was the ancestral nesting habit (Akaike weight 0.41; fit of alternative rate models SYM = 0.39 and ARD = 0.2). 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).

Seventeen out of 19 bioclimatic variables showed evidence for phylogenetic signals (p values <0.05) as measured by Blomberg’s K and Pagel’s λ (Fig. 3). We found a high phylogenetic signal (λ ≤ 1 and K > 1) in bioclimatic variables that capture information about seasonal mean conditions and intrayear 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 the aridity index and, only for K, elevation (Fig. 3).

PRESENT HABITAT SUITABILITY
The 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 (Table S8). In five out of seven species, the abiotic variable set showed the lowest AICc score (often coupled with a low regularization multiplier), and the biotic variable set never performed best (Table 1 and S8). 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 Table 1). Precipitation in the warmest quarter (BIO18) was the most frequent predictor variable, with a permutation importance above 15%.

In most cases, sampling sites were located within the largest contiguous portion of the 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).

FUTURE HABITAT SUITABILITY
Present-day ENMs analogous to future habitat models based on the uncorrelated bioclimatic variables (BIO01: mean annual temperature; BIO02: mean diurnal range; BIO03: isothermality; BIO09: mean temperature of driest quarter; and BIO18: precipitation of warmest quarter; for further details see Table S3) 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 RCP8.5 scenario than under RCP2.6 (Fig. 5). D. perniger-NE is the only species that shows suitable habitat loss, suggesting range compression toward the coastline of Queensland and New South Wales.

Discussion
DREPANOTERMES DIVERSITY
Compared to other termite radiations within the last 5 million years ago (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 the described *Drepanotermes* species represents species clusters or intergradations (Watson and Perry 1981), and indeed, our data demonstrated sufficient genetic divergence within several described species to make taxonomic reconciliation with historical morphology-based records impracticable. Our data set lacks sequences from at least 12 described species, mainly from regions that were dramatically undersampled in this study, including the center of *Drepanotermes* diversity in the Northwest Cape region (Watson and Perry 1981, Watson and Abbey 1993). Extrapolating from the 54 recovered mOTUs, of which eight could be unequivocally attributed to described species, we suggest that there may be at least 75 to 100 independently evolving lineages 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 onward (Heimburger et al. 2022). This study, covering the most *Drepanotermes* taxa to date, shows considerable species divergence in the past 1 million years ago. 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 the 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.
Figure 4. MaxEnt predictions of present-day habitat suitability for eight *Drepanotermes* species with nesting habitats given in parentheses (subt. = subterranean). Red dots indicate georeferenced records for each taxon (see also Table S7). Darker colors represent higher habitat suitability, and brighter colors represent lower habitat suitability. The bar chart shows the permutation importance (>15%) of predictor variables for each species based on the best model (see also Table 1).
NESTING HABITS AND CLIMATE-RELATED CONSTRAINTS

Our results indicate that the last common ancestor of *Drepanotermes* most likely lived in subterranean nests (Fig. 2). This is consistent with the position of *Drepanotermes* as a crown group within Australian *Amitermes* (Heimburger et al. 2022), which are primarily soil dwellers (Gay 1968, Gay and Calaby 1970). Many early-branching lineages are subterranean and occur near the northwest cap in western Australia, the likely origin of the genus (Watson and Perry 1981, Heimburger et al. 2022), 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 habits (D. columnellaris, 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.

A strong phylogenetic signal, especially in bioclimatic factors, indicates that niches are phylogenetically constrained in Drepanoterms. 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 support Wijas et al. (2022), who demonstrated that nesting habits of Australian termites in general are distributed along a temperature and rainfall gradient and thus subject to climatic controls. It therefore appears likely that the acquisition of mound-building in Drepanoterms played a crucial role in the expansion into tropical and mesic regions of Australia.

Drepanoterms 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 Drepanoterms. 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). However, 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 signals can be distorted due to incomplete sampling of species and/or taxonomic oversplitting (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 in nesting habits reflects the strong selection pressure that climate places on them.

**Habitat Suitability in Relation to Predation Pressure and Vegetation Cover**

The 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, Sholtz et al. 2021). However, we were unable to find clear connections between distributions and biotic variables in our ENMs for Drepanoterms. Overall, biotic variables were found to be more important predictors of habitat suitability than the biotic variables we included, which may suggest that other biotic factors are more relevant. 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.

The species richness of predators was a dominant factor in only one out of eight species we tested, D. clarki. We 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 termites. Forging the protection of foraging tunnels (as in *Amitermes*), *Drepanotermes* rely on large numbers of large, heavily scleritized soldiers and fierce large workers, suggesting an evolutionary arms race between *Drepanotermes* and their predators, especially ants (Holldobler 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.

**DRESPANOTERMES 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 becomes 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 a 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 were found for *D. barretti* and *D. columellaris*. Under both emission scenarios, their projected ranges are largely congruent with predicted increases in arid conditions on the continent by 2070 (Larkin et al. 2020, Fig. S3). Other southwestern 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 the dispersal of the termites themselves but also the 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 that 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. 2022), 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 occurring. 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. The 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. A 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, and mounds are more common in hot and moist environments. Present habitat suitability is mainly shaped by abiotic factors, especially bioclimatic variables such as the mean annual temperature and precipitation of the warmest quarter, but the 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.

**AUTHOR CONTRIBUTIONS**

Bastian Heimburger was associated with conception and design, acquisition of data, analysis and interpretation of data, and drafting the manuscript. S.S.M. was associated with acquisition of data, analysis and interpretation of data, and drafting the manuscript. L.S. was associated with conception and design, interpretation of data, and drafting the manuscript. T.R.H. was associated with conception and design, interpretation of data, and drafting the manuscript. T.R.H. was associated with conception and design, interpretation of data, and drafting the manuscript.

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**CONFLICT OF INTEREST**

The authors declare no conflicts of interest.

**DATA ARCHIVING**

Data are stored at the Dryad Data Repository (https://doi.org/10.5061/dryad.n2z34tn02).

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Supporting Information

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

**Supporting Table S1.** 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. Source publication of mitochondrial genome sequences is given in the ‘References’ column.

**Supporting 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 modeled are indicated in bold. Nesting habits were assigned based on field notes or, if possible, literature data (see ‘References’ column).

**Supporting Table S3.** Predictor variables and sources. Gray-shaded variables were used for ecological niche modeling. The remaining variables were involved in pairwise Pearson’s correlations above 75% (Tab. S6) and thus discarded prior to ecological niche modeling.

**Supporting Table S4.** Taxa included in predator groups.

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

**Supporting 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.

**Supporting Table S7.** Number of georeferenced records used for ecological niche modeling.

**Supporting Table S8.** 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.

**Supporting 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.

**Supporting 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 sequences belonging to each mOTU.